

BEHAVIOUR OF PINNIPEDS



EDITED BY

Deane Renouf



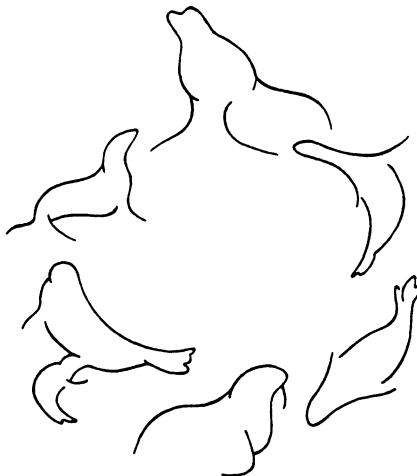
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The Behaviour of Pinnipeds

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Edited by
Deane Renouf

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*To Bora, Justin, Luke, Colin and Laura who encourage
the intrusion of projects like this into the otherwise
smooth running of a family.*

To Meem, facilitator and peace-maker.

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Preface

We teach our students of behavioural science that one first defines a research problem, and then the most appropriate animal is selected to investigate hypotheses. The reverse order of events is improper: a particular class of animals should not be studied for its own sake. In the case of the Pinnipeds (seals, sea lions, fur seals and walruses) the organism and the problem are essentially the same. The research questions presented in this volume in one way or another relate to survival in two worlds, the ocean for foraging, and the terrain at its edge or frozen above it for breeding.

The evolution of Pinniped behaviour and the mechanisms which underlie it are a consequence of having to cope with two seemingly incompatible sets of environmental constraints. The physiological adaptations for concomitant functioning in two media with very different physical characteristics have produced correlated behavioural modifications. The energetic demands of reproduction and foraging are idiosyncratic because each activity occurs on opposite sides of the air/water interface. As a result, the mating system must reconcile aquatic design for such functions as locomotion and thermoregulation, with the terrestrial requirements for successful pupping. Similarly, the ecology of this dual habitat prescribes the rules governing the behaviour of the neonate and its interactions with its mother. Sensation, perception and cognition* and consequently the vehicle for communication must operate properly in air and underwater either by using different mechanisms in each medium, or by modifying systems which are designed for use in one medium to operate effectively in the other.

Throughout the chapters which follow, whenever possible the

* This volume was to have a chapter entitled 'Learning and cognition in pinnipeds: a quarter century of research' by Ronald J. Schusterman, but at the eleventh hour he was unfortunately unable to provide it.

lines of distinction between Otariidae (sea lions and fur seals) and Phocidae (true seals) are clearly drawn. Too often, either inadvertently or as a result of a paucity of information, the behavioural literature has treated the two families collectively as if they were a single group. In fact the differences between phocids and otariids reflect variation in the extent of each family's re-adaptation to the marine habitat. Therefore, contrasts between the two groups illuminate aspects of adaptation. Behavioural investigations of the third pinniped family, the Odobenidae (walrus) are unfortunately few, but they are described when available.

The intention of this collection is to examine the behaviour of Pinnipeds from the point of view of evolution and mechanism. The history of these two schools of thought is riddled with controversy, and in the 1960s could have been described as the American versus the European positions in what was a rather lively warfare. (Consider the battles in the scientific journals between the late Daniel Lehrman and Konrad Lorenz and their respective proponents.) Fortunately rapprochement has occurred since then, though occasionally one hears behavioural ecologists and physiologists/psychologists arguing from the floor of conferences, when in fact they are agreeing. This volume is a demonstration of this rapprochement, wherein the present and historical functions as well as the operating machinery of Pinniped behaviour are presented as mutually important components of its explanation.

Unless stated otherwise, the nomenclature used in this book is that of Harrison and Ridgeways' 1981 *Handbook of Marine Mammals*, volumes 1 and 2. Where possible, all units have been changed to conform with the SI metric system.

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I am indebted to many people who assisted in various ways throughout the production of this volume, not the least of whom are the authors who agreed to participate, and thereafter put up with incessant nagging about their contributions. Bob Carling was remarkably patient while I nagged. Elizabeth Noseworthy ensured that my other duties were taken care of when the book took over my time. She moved into the library when required, and when necessary became illustrator and photographer. I am grateful for her steadfast competence. Mary Scott's assistance was similarly invaluable. I am thankful to Daryl Boness, Don Bowen, John Lawson, Elizabeth Perry, David Piggins, David Rosen, Mike Sherrick, and Jack Terhune for their insightful reviews and editorial assistance. Brenda Crewe and Bernice St Croix were exceedingly tolerant when I monopolized the services of the general office. I would like to give special thanks to Cherelyn Williams whose cheerfulness, skill and speed in the preparation of the manuscripts and accoutrements was always much appreciated.

Foreword

People come to study pinnipeds from a diversity of scientific backgrounds. However, it is difficult to maintain a narrow disciplinary focus on these fascinating animals. Many active researchers on pinnipeds become generalists, ranging widely in their studies. Collectively, the authors in this book have done research at the molecular, individual (anatomical, physiological and behavioural), population and ecosystem levels of biological organization. This book is, of course, focused on behaviour, and the authors have been assigned particular tasks denoted by their chapter titles. But there is much creative lateral thinking in their analyses and syntheses of the enormous literature on seals.

Not so many years ago a book on behaviour of a group of animals would have been grounded in experimental animal psychology, leavened somewhat by stirrings of ethology. In this book, behaviour is seen as part of the whole complex of anatomical, physiological, and life-history properties that determine the animal's fitness in challenging environments. It is worth noting that one of the first quantitative life-history analyses of a group of related animals was the study of seals by Laws (1960). It is also worth noting that one of the classics of behavioural ecology and sociobiology is the work of Bartholomew (1970) on pinniped polygyny. This book has strong roots in such approaches.

Arguments about adaptiveness or optimality of behaviours are sometimes viewed with suspicion or even derision by those who prefer more readily testable hypotheses. There are two valid reasons for such suspicion. First, in the enthusiasm for 'explanation', the phenomena to be explained can be poorly or even wrongly delineated. The chapters by Miller and Renouf bring the rigours of ethology and experimental psychology to bear on the description, measurement, naming and categorization of behaviours. Secondly, the 'naive pan selectionist' view that all phenotypic attributes of animals, including

their behaviours, are closely adapted to the environment, fails to recognize such constraints as phylogeny, co-adaptations, and unpredictable environments. The authors in this book, with their diverse backgrounds, are fully alert to the complexity and contexts of behaviours. Of course biologists seek generalizations and patterns, but sometimes deviations and exceptions are equally informative. For example, in the last few years much has been written on the divergent patterns of maternal care by otariid and phocid seals: the former with prolonged lactation interrupted by feeding bouts at sea, and the latter with intense, uninterrupted lactation cycles. The chapters by Costa and Bowen, among others, enlarge upon this generalization and show that some animals are not all they should be. Boness, Wartzok and Le Boeuf deal extensively with mating systems of pinnipeds, about which there have been shaky generalizations and premature conclusions.

The authors in this book have been privileged to carry out large, long-term programs of collaborative research. Yet much research on pinnipeds, especially on their behaviour, has been done independently and opportunistically by students and others, often motivated by the emotional appeal of these beautiful animals. Perhaps one of the greatest values of this book will be as an inspiration for future research on any scale. There remain explicit hypotheses to be tested, and there are guidelines to shape enquiries, even on seemingly trivial scales. In a charming little aside on methodology, Miller shows how observations on the position, horizontal or vertical, of a seal's head in water could be elevated into a more penetrating analysis of social behaviour. He also concludes with an eloquent appeal for the importance of such studies in a world where our companion species are increasingly threatened by those who seem not to see them. We must be grateful to Deane Renouf for organizing this broad focus on such fascinating creatures.

Ian A. McLaren
Halifax, Canada
March 1990

1

Determinants of mating systems in the Otariidae (Pinnipedia)

Daryl J. Boness

1.1 INTRODUCTION

Substantial advances have been made in the past two decades toward a theory of mating systems (Orians, 1969; Selander, 1972; Trivers, 1972; Jarman, 1974; Emlen and Oring, 1977; Bradbury and Vehrenamp, 1977; Kleiman, 1977; Wittenberger, 1979; Thornhill and Alcock, 1983; Rubenstein and Wrangham, 1986). These recent efforts have focused on the interplay between sexual selection and environmental factors that determine temporal and spatial dispersion of males and females (e.g. resource distribution, predation pressure). Increased information on behavioural reproductive strategies has led to examination of theory both within and between taxa to assess the breadth of its applicability (see Bradbury and Vehrenamp, 1977; Ostfeld, 1985; Rubenstein and Wrangham, 1986 for reviews of different taxa). A comparison between antelope and emballonurid bats has shown that the form of mating systems in both groups is set within the bounds of female dispersion, which is strongly related to food distribution (Bradbury and Vehrenamp, 1977). On the other hand, factors such as habitat type and body size are good predictors of social dispersion and mating strategies in antelopes but not bats. Thus Bradbury and Vehrenamp suggested that application of a general model requires measurement of critical variables that determine social dispersion.

Species of the order Pinnipedia have evolved from a terrestrial ancestry to a mainly aquatic life style. In the course of this evolution, they have retained certain terrestrial traits while having undergone many changes to adapt to pelagic foraging. Critical factors important

2 Determinants of mating systems in the Otariidae

in shaping mating systems in pinnipeds may be different from those of land mammals. Previous reviews suggest that otariid mating systems are limited in diversity (Nutting, 1891; Peterson, 1968; Bartholomew, 1970; Stirling, 1975, 1983), but these reviews lacked evidence from a variety of species. In this chapter, I will examine factors most likely to be important determinants in the evolution of otariid mating systems, the diversity in existing mating systems, and compare empirical data on reproductive behaviour of otariids to current theory.

The family Otariidae appears to have originated in the warming waters of the north Pacific Ocean about 22 million years ago (Repennig *et al.*, 1979). The distribution of otariids remained northern temperate and subpolar until about 5 million years ago, when species dispersed to and diversified in the tropics and southern hemisphere (Repennig, 1976). Today, the Otariidae is comprised of 14 species divided into two subfamilies, the Arctocephalinae (fur seals) and the Otariinae (sea lions) (King, 1983). The geographical distribution of these species ranges from near one pole to the other, although most are temperate with only two species being tropical and three being polar or subpolar (Table 1.1). Unlike phocid species, the polar otariids do not breed on ice, but instead breed, during spring and summer, on islands or coastal beaches inaccessible to humans (Table 1.1).

1.2 OVERVIEW OF CURRENT THEORY

Emlen and Oring (1977) proposed a model which explains variation in mating systems in relation to sexual selection ecological and phylogenetic constraints. Accordingly, when conditions are such that the fitness of members of one sex can be increased by controlling access to the other sex, competition among the controlling sex increases and potential for polygamy is high. Polygamy is defined here as any mating system in which some members of one sex mate with more than one member of the other within a single breeding season. A high polygamy potential occurs when resources or other environmental factors bring potential mates into close temporal and spatial proximity such that accrual of multiple mates is feasible either through simultaneous defence of several mates or sequential defence of single mates. Monogamy, defined here as exclusive mating between one male and one female within a season, results when multiple mates are not monopolized (Emlen and Oring, 1977; Wittenberger, 1981).

Polygamy is known as polygyny when males acquire multiple females and polyandry when the reverse is true. Polyandry, while uncommon, occurs primarily in birds (Jenni, 1974; Wittenberger,

Table 1.1 Breeding distribution, season, and habitat of otariids

Species	Distribution (° latitude)	Season										Habitat
		Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
		Spring					Autumn				Winter	
Northern Hemisphere												
<i>Arctocephalus townsendi</i>	28											
Guadalupe fur seal												
<i>Callorhinus ursinus</i>	38-57											
Northern fur seal												
<i>Eumetopias jubatus</i>	35-60											
Steller's sea lion												
<i>Zalophus californianus</i>	28-33N											
California sea lion												
Southern Hemisphere												
<i>A. Australis</i>	8-48											
South American fur seal												
<i>A. forsteri</i>	35-47											
New Zealand fur seal												
<i>A. galapagoensis</i>	2											
Galapagos fur seal												
<i>A. gazella</i>	55-64											
Antarctic fur seal												
<i>A. philippii</i>	25-33											
Juan Fernandez fur seal												
<i>A. pusillus</i>	18-44											
S. African/Australian fur seal												
<i>A. tropicalis</i>	38-48											
Subantarctic fur seal												
<i>Neophoca cinerea</i>	28-34											
Australian sea lion												
Southern sea lion	5-45											
<i>Phocartes hookeri</i>	48-55											
Hooker's sea lion												

N = northern hemisphere
S = southern hemisphere

4 *Determinants of mating systems in the Otariidae*

1981) presumably because it is likely to occur only when males assume the bulk of parental care. According to Emlen and Oring, this might occur when the female's future physical condition is of importance to the male or when the lack of dependability of breeding conditions places a premium on a female's ability to produce a replacement clutch. As polyandry does not occur in pinnipeds, I shall refer only to polygyny hereafter.

A high potential for polygyny does not necessarily result in a polygynous mating system; both phylogenetic and ecological factors constrain the ability to capitalize on the polygamy potential (Trivers, 1972; Emlen and Oring, 1977). If substantial male parental care is required to rear offspring successfully, then polygyny is not likely to occur or it will occur at a low level. Examples of this are abundant among colonially breeding birds, such as the Laridae, in which clusters of thousands of nesting females can occur, yet each female has a separate mate that contributes to incubation of eggs and feeding of hatchlings. Individual birds may re-pair for several years in succession or form new pair bonds annually, depending on the species (Johnston and Ryder, 1987). The trait of lactation in mammals often relieves mammalian males of any responsibility in caring for the young. Commensurate with this, males can invest greater energy in activities associated with controlling access to mates. Studies of mammals have shown that fewer than 5% have monogamous mating systems (Kleiman, 1977). In contrast, among birds, where male parental care is often critical for successful rearing of the young, 90% of species studied are monogamous (Lack, 1968; Wittenberger, 1981; Oring, 1982).

Based on the extent to which resources critical to females or females themselves are monopolizable, four major forms of polygyny have been suggested: resource defence, female defence, male dominance (lek and mating swarm) and scramble competition (Emlen and Oring, 1977; Bradbury and Vehrencamp, 1977; Alcock, 1980; Thornhill and Alcock, 1983; Schwagmeyer and Woontner, 1986). In resource defence polygyny, males monopolize females indirectly by controlling access to critical resources. Most often these resources are food (Jarman, 1974; Cronin and Sherman, 1976; Alcock and Houston, 1987), nesting sites (Wittenberger, 1976) or places to avoid predation (Howard, 1978; Gosling, 1986). Resource defence has been equated with territoriality since most examples of resource defence involve non-moveable resources or defence of an area within which the resource occurs. In principle, defence of mobile resources critical to females could be accomplished by non-site-specific dominance strategies although examples of this are not apparent. In female defence polygyny, females are defended directly. This system is likely to occur when the clustering of females is not associated with a

critical resource (Emlen and Oring, 1977) or the stability of female clusters is high and clusters are relatively mobile (Bradbury and Vehrenamp, 1977). In male dominance and scramble competition polygyny, neither defence of females nor resources are energetically feasible (Bradbury, 1981; Schwagmeyer and Woontner, 1986). Hereafter I shall refer only to lek forms of male dominance systems since mating swarms are most common among invertebrates and reported in only one mammalian genus, *Antechinus* (Cockburn and Lee, 1988). In a lek system, males aggregate and females mate with one or more males from the aggregation. There is still much controversy over whether this system evolved through female behaviour influencing male behaviour and mating success (e.g. female choice or hot-spots models; Bradbury, 1981; Bradbury and Gibson, 1983; Bradbury *et al.*, 1986; Clutton-Brock *et al.*, 1989) or through male behaviour influencing that of females (e.g. hotshots model; Beehler and Foster, 1988). Regardless, leks are likely to arise when: resources are superabundant but widely dispersed, female dispersion is patchy and critical resources are unpredictable in space and time, or females are clustered in a defendable pattern but the cost of defending them is too high. In scramble competition, males search for receptive females. Two ecological conditions appear to lead to this system: when females are spatially scattered and oestrus is not highly synchronous and when females are concentrated in space and time but are relatively mobile and male competition is high (Thornhill and Alcock, 1983; Schwagmeyer and Woontner, 1986). While these systems are treated as discrete, there are examples which do not fit clearly into one or the other of them (see Bradbury, 1981; Oring, 1982). This seems especially true in distinguishing leks from resource defence systems.

1.3 TYPES OF MATING SYSTEM AMONG OTARIIDS

Figure 1.1 shows what are thought to be the major determinants of mating systems in otariids, following the general scheme of Emlen and Oring (1977). I will first discuss factors that account for the uniform occurrence and variation in degree of polygyny in this pinniped family and then discuss variation in the form of polygyny.

1.3.1 Potential for polygyny

The potential for polygyny is high in the Otariidae. In all species, females gather in high densities on island beaches or rocky shelves, where they can find suitable birthing sites (Tables 1.1 and 1.2). Individual females come into oestrus within a few days postpartum.

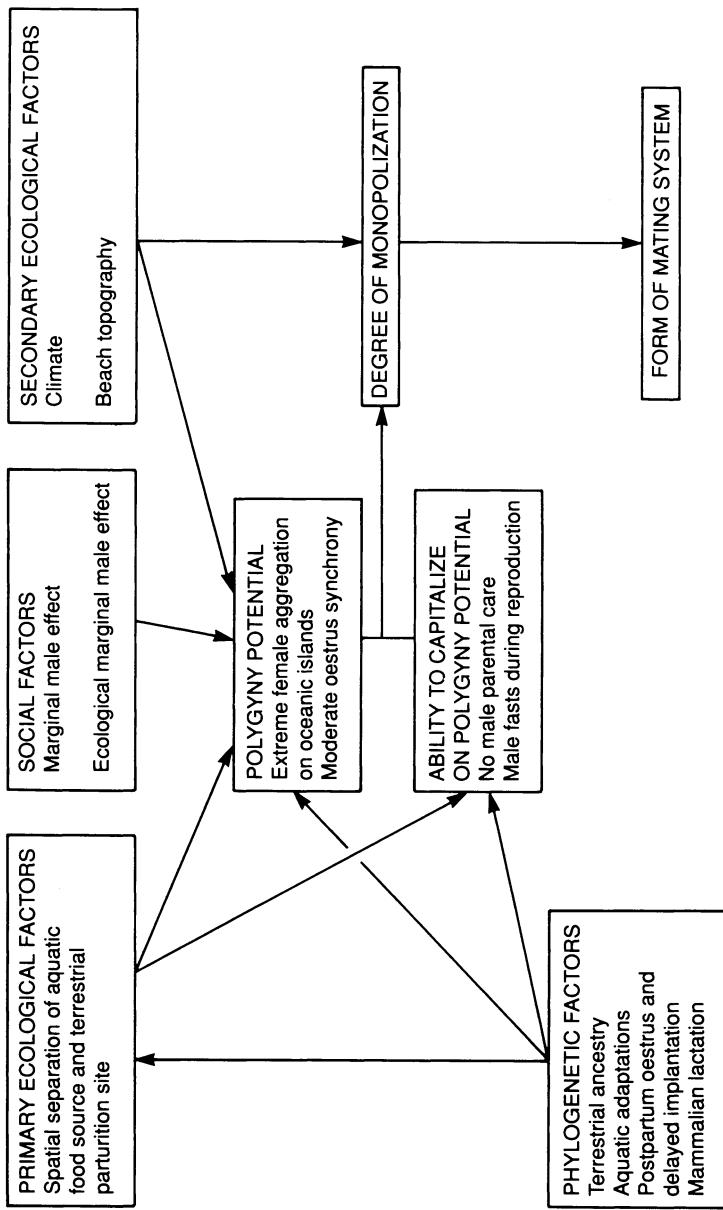


Figure 1.1 A schema of the important ecological and phylogenetic factors underlying variability in otariid mating systems.

Table 1.2 Spatial and temporal dispersion of otariid females

<i>Species</i>	<i>Density</i> (f/m ²)	<i>Distance</i> (km) to foraging site/transit time (h)	<i>Oestrus</i> synchrony (d)	<i>Source^a</i>
<i>Arctocephalus australis</i>	0.5-1.0	200/9	40	35, 36, 37
<i>Arctocephalus forsteri</i>	0.1	Pelagic/ coastal	28 ^c	13, 22, 31, 32
<i>Arctocephalus galapagoensis</i>	0.04	19/3	70	19, 34
<i>Arctocephalus gazella</i>	0.4-1.1 ^b	200/16	21	3, 6, 20, 23, 25
<i>A. pusillus pusillus</i>	1.4-1.9	100/9	26-34	4, 5, 28
<i>A. p. doriferus</i>	0.2	-	26	30
<i>Arctocephalus townsendi</i>	-	Coastal	42	10, 27
<i>Arctocephalus tropicalis</i>	0.1	-	29-35	1, 18, 29
<i>Callorhinus ursinus</i>	0.2-0.6	250/15	24-29	14, 26
<i>Eumetopias jubatus</i>	0.1-0.7	Pelagic/ coastal	20	7, 9, 12, 16
<i>Neophoca cinerea</i>	-	Coastal	75	17, 21
<i>Phocartos hookeri</i>	-	-	18	15
<i>Zalophus californianus</i> <i>californianus</i>	0.1-0.2	100/4	32	2, 8, 11, 24
<i>Z. c. wollebaeki</i>	-	< 10 / < 1	112	33

^a1. Bester, 1977; 2. Boness, unpubl. data; 3. Croxall *et al.*, 1985; 4. David, 1987; 5. David and Rand, 1986; 6. Doidge *et al.*, 1984; 7. Edie, 1977; 8. Feldkamp, 1985; 9. Fiscus and Baines, 1966; 10. Fleischer, 1987; 11. Francis, 1987; 12. Gentry, 1970; 13. Gentry, 1975; 14. Gentry and Kooyman, 1986; 15. Gentry and Roberts, in prep.; 16. Gisner, 1985; 17. L. Higgins, pers. comm.; 18. Kerley, 1987; 19. Kooyman and Trillmich, 1986; 20. Kooyman *et al.*, 1986; 21. Ling and Walker, 1976; 22. Mattlin, 1978; 23. McCann and Doidge, 1987; 24. Odell, 1972; 25. Payne, 1977; 26. Peterson, 1965; 27. Pierson, 1978; 28. Rand, 1967; 29. Roux, 1987; 30. Shaughnessy and Warneke, 1987; 31. Stirling, 1971; 32. Stirling, 1983; 33. Trillmich, 1986; 34. Trillmich, 1987; 35. Trillmich *et al.*, 1986; 36. Trillmich and Majluf, 1981; 37. Majluf, 1987; 38. York, 1987.

^b The value is based on pups/m² plus an adjustment for the fact that in other species in which the data are presented as females/m² a percentage of the females will always be gone on foraging trips. The adjustment is based on the mean percentage of time females are at sea foraging.

^c These values are based on about 80% of the period over which births occur. Values for 90% of the birth period are not available.

Oestrus is moderately synchronized with most females in a given species becoming receptive within about 20-35 days, although in a few species this period may be more than double this length (Table 1.2).

8 Determinants of mating systems in the Otariidae

(a) Spatial dispersion

The aquatic specialization of pinnipeds, coupled with terrestrial whelping and care of the young (see Bonner, 1984; Gentry and Kooyman, 1986; Oftedal *et al.*, 1987 for reviews of pinniped lactation strategies) appear to have played a primary role in the evolution of a clustered dispersion pattern among otariid females during the breeding period. The early otariids and their immediate ancestors probably fed close to shore (Mitchell and Tedford, 1973), but at some point during the radiation of otariid species began to exploit more pelagic resources. Among living species, there is considerable variation in feeding patterns. Some species are known to feed within 10 km of the coast whereas others may feed more than 250 km out to sea (Table 1.2; Stirling, 1983). While increased aquatic adaptations permitted exploitation of pelagic resources, they reduced terrestrial mobility, making animals more vulnerable to terrestrial predation (cf. Howell, 1930; Tarasoff *et al.*, 1972; Tarasoff and Kooyman, 1973; English, 1977). These combined effects of aquatic adaptations are presumably what led to the use of oceanic islands for breeding. Oceanic islands would have been the closest land to food available for pupping and would have had fewer land-based predators than mainland beaches.

The high density of females then is in part due to the fact that oceanic islands are relatively rare and unevenly dispersed. Furthermore, on many islands heterogeneity of microhabitat and microclimate may limit suitable pupping sites, leading to even greater female clustering and hence greater polygyny potential. In species inhabiting low temperate to tropical islands, daytime ambient air temperature may require access to shade or water because the subcutaneous blubber layer common to all pinnipeds, and necessary for heat conservation in an aquatic medium, severely hampers heat dissipation on land (Bryden and Molyneux, 1978; Whittow, 1978). Thus females preferentially choose pupping locations that have large boulders to provide shaded resting sites (Vaz Ferreira and Palerm, 1961; Miller, 1971; Gentry, 1973; Bester, 1977; Trillmich, 1984), tide pools, or easy access to the tide wash (Paulian, 1964; Eibel-Eibesfeldt, 1984; Campagna, 1987).

Although patchiness of oceanic islands and limited pupping sites on given islands appear to be primary determinants of clustering in otariids, these factors alone cannot account for the extreme clustering observed in some species (Bartholomew, 1970; Stirling, 1983; Francis, 1987). At many colonies there seems to be plenty of space available for females to disperse, but they do not. The marked gregariousness reported in otariids may relate to other selective pressures operating to maximize the fitness of individual females. Two hypotheses proposed specifically in relation to pinnipeds are the

'marginal-male' and 'ecological-marginal-male' hypotheses. These hypotheses are not mutually exclusive. The marginal-male hypothesis suggests that sexual selection should favour female gregariousness because any female that moves to the periphery of female clusters is likely to be fertilized by a male that has been unsuccessful in establishing himself among the herd (McLaren, 1967; Bartholomew, 1970). While there are ample data indicating that single-season reproductive success of males centrally located in a breeding colony may be higher than that of peripheral males (e.g. Buechner and Schloeth, 1965; Kruijt *et al.*, 1972; Emlen, 1976; Le Boeuf, 1974; Gisner, 1985), evidence linking a female's fitness to proximity to a fit male is lacking.

The ecological-marginal-male hypothesis argues that injury and death of females, and pups caused by harassment from peripheral males should lead to increased gregariousness through natural selection (Trillmich and Trillmich, 1984; Campagna *et al.*, 1989). According to Francis (1987) dominant males in some species might also cause injury and death to females that locate peripherally to a cluster of females. Territorial northern fur seal (*Callorhinus ursinus*) males will grab and toss females during herding, which can lead to female mortality (Peterson, 1965; Francis, 1987). Females at higher densities are not approached and herded as often as females in lower densities. Similar intensive herding and tossing of females occurs in other otariids and may contribute to extreme clustering in them as well (Table 1.3).

A third hypothesis, the selfish-herd hypothesis, explains gregariousness of animals in relation to predation pressure (Hamilton, 1971). According to this hypothesis, natural selection should favour an individual that moves close to other conspecifics if doing so increases the likelihood that its neighbour rather than itself will be taken by a predator. It is difficult to evaluate the importance of predation pressure on clustering of otariid females since most living otariids breed on oceanic islands, where there are no predators, although some species use both oceanic islands and coastal beaches (Table 1.1) (Stirling, 1983; Bonner, 1984; Croxall and Gentry, 1987; Oftedal *et al.*, 1987). One species which inhabits both offshore islands and mainland beaches, where this hypothesis can be examined, is the South African fur seal (*Arctocephalus pusillus pusillus*). There are no predators on the island rookeries, but pups on the mainland are preyed on by black-backed jackals (*Canis mesomelas*) and brown hyenas (*Hyaena brunnea*) (Shaughnessy, 1979; David, 1987).

(b) Temporal dispersion

In addition to close spatial proximity of females, a high polygyny potential also requires a moderate amount of synchrony in oestrus.

Table 1.3 Characteristics of reproductive behaviour in various otariid species

Species	Timing of arrival of males and females	Female movements between parturition and oestrus	Male herding behaviour	Rate of male threat display	Size of male's area of influence (m ²)	Male tenure as % birth synchrony	Mating system	Sources ^a
<i>A. fosteri</i>	Males before females; initial large areas of influence become rigid territories	Very little movement before oestrus; oestrus occurs at parturition site	Moderate	0.6/h	23	81 ^b	Resource defence	11, 20, 21, 22, 32
<i>A. galapagoensis</i>	Males and females present year round; males start aggressiveness before new births	Short daily shifts to tide line; may make one foraging trip before oestrus; oestrus usually at parturition site	-	Low	200	60	Resource defence?	33, 34, 35
<i>A. gazella</i>	Males before females; initial large areas of influence become rigid territories	No female movement; oestrus at parturition site	Moderate	1.5/h	22	162	Resource defence	3, 8, 18
<i>A. p. pusillus</i>	Males before females	About 60% begin foraging before oestrus	-	-	20	161	Resource defence?	7, 28, 38
<i>A. p. doriferus</i>	Males before females	Little movement before oestrus; do not begin foraging before oestrus	-	-	62	-	Resource defence?	30, 31
<i>A. tropicalis</i>	Males before females; largest males arrive after some females	Small predictable movements to tide line; oestrus probably near parturition site	Intense	-	23	74	Resource defence?	2, 29
<i>C. ursinus</i>	Males before females; initial areas of males are large and poorly defined	No movement before oestrus; oestrus occurs at parturition site	Intense	-	30	132	Resource defence	1, 6, 25, 26, 39

<i>E. jubatus</i>	Most males before females but some territories develop after; territorial activity became obvious when females arrived	Small thermoregulatory movements up and down the beach, females may begin foraging before oestrus but 65-75% of estrus within 20m of parturition site	Mild 0.9h 1.8/h	225	-	Resource defence	10, 13, 15
<i>O. byronia</i>	Male arrival and establishment does not precede female arrival; initial boundaries disappear as number of animals increases	Small thermoregulatory movements up and down beach; oestrus occurs before foraging begins near parturition site	Intense 9.0/h	11 ^c	~100 ^b	Female defence/ Resource defence	4, 36, 37
<i>P. hookeri</i>	Some males present before females but do not organize before females arrive	Individual and group movement occurs laterally along beach; oestrus does not occur near parturition site	None 11.0/h	7	66	Modified lek	12, 17
<i>Z. californianus</i>	Males and females arrive simultaneously; movements of males decreased as the number of males and females increased	Large thermoregulatory movements of individuals and group; oestrus occurs after foraging begins and usually occurs other than at parturition site	Mild	-	130	84	Modified lek 27, 40

^a1. Bartholomew and Hoel, 1953; 2. Bester, 1977; 3. Bonner, 1968; 4. Campagna, 1985; 5. Campagna and Le Boeuf, 1988; 6. Campagna and Le Boeuf, 1987; 7. David, 1987; 8. Dodge et al., 1984; 9. Francis, 1987; 10. Gentry, 1970; 11. Gentry and Roberts, in prep.; 12. Gentry and Francis, 1985; 14. Heath and Francis, 1983; 15. Higgins et al., 1988; 16. Kenyon, 1960; 17. Marlow, 1975; 18. McCann, 1980; 19. McCann and Dodge, 1987; 20. Miller, 1974b; 21. Miller, 1975a; 22. Miller, 1975b; 23. Odell, 1972; 24. Payne, 1977; 25. Peterson, 1965; 26. Peterson, 1958; 27. Peterson and Bartholomew, 1967; 28. Rand, 1967; 29. Roux, 1987; 30. Shaughnessy, 1979; 31. Shaughnessy and Warneke, 1987; 32. Stirling, 1971; 33. Trillmich, 1984; 34. Trillmich, 1986; 35. Trillmich, 1987; 36. Vaz Ferreira, 1975; 37. Vaz Ferreira and Ponce de Leon, 1987; 38. Warneke and Shaughnessy, 1985; 39. York, 1987; 40. Heath, 1989.

^bThese estimates are based on about 80% of the pupping period. Values for 90% are not available.

^{c,d}Values for Punta Norie and Punta Piramide respectively.

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If oestrus were completely synchronous a male would not be able to mate with many females, regardless of how closely females were spaced. Conversely, if receptivity among females in close proximity was distributed over a long interval, the energetic costs of maintaining control over females might be too high to continue defending them or critical resources (cf. Ims, 1987). This is likely to be especially important in otariids because the spatial separation of food resources from breeding colonies requires males to fast in order to assure access to females when they become receptive.

The timing of 90% of births is used as an indicator of oestrus synchrony, as suggested by McCann (1987), because oestrus is closely linked to parturition in all species and the temporal spread of births has been measured in more studies than that of copulations. One potential problem with this measure is that it will not account for the timing of oestrus in nulliparous females if they become receptive outside the period for females with pups. The impact of this problem cannot be evaluated for most species because of a lack of information. Estimates of oestrus synchrony for the northern fur seal and southern sea lion (*Otaria byronia*), using timing of births, might be low because virgin fur seal females are reported to be mated at the end of the breeding season (Bartholomew, 1953) and nulliparous sea lion females may not even be mated at the rookery (Hamilton, 1934), although Campagna (1987) implies some nulliparous females are present. In several species, such as Hooker's sea lions (*Phocarctos hookeri*) (R. Gentry pers. comm.) and California sea lions (*Zalophus californianus*) (Peterson and Bartholomew, 1967; D. Boness, unpubl. observations), substantial numbers of non-parous females are observed at rookeries and mate during the same period as do females with pups.

Otariid oestrus synchrony is remarkably similar among species, with 90% of females giving birth and becoming receptive within a 3-4-week interval (Table 1.2). There are three species that exhibit 2-3 times this spread of oestrus, however, and the Galapagos fur seal (*Arctocephalus galapagoensis*) may be even more asynchronous (Table 1.2).

The degree of oestrus synchrony probably evolved secondarily to pupping synchrony as a result of the relatively fixed temporal relationship between birth and oestrus. In some mammalian groups, birth synchrony appears to be associated with both seasonality of food resources and predation pressures (see Ims, 1987; Rutberg, 1987). This is likely to be true for otariids as well although predation pressure can only be suggested as plausible since there is little historical evidence available to assess its impact on the evolution of birth synchrony. The probable importance of seasonality of food resources and climatic conditions at pupping sites appears to be

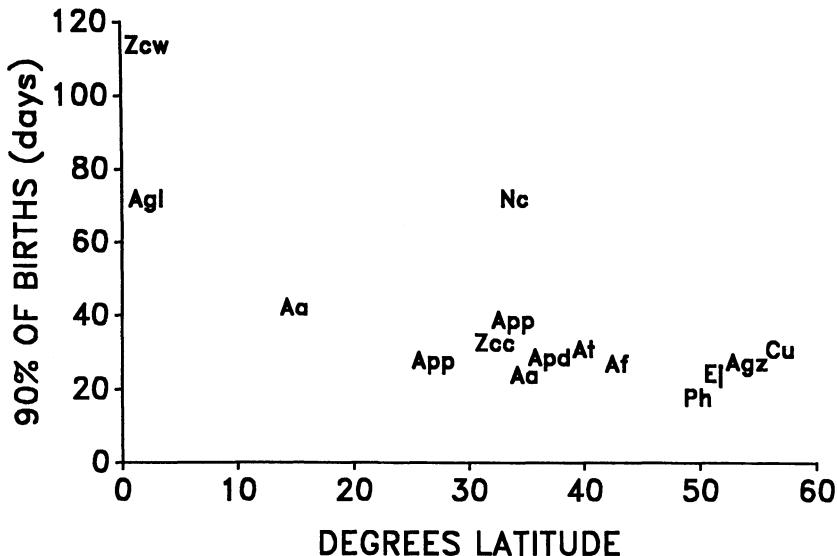


Figure 1.2 The relationship between oestrus synchrony (as measured by the period over which 90% of births occur) and latitude of otariid breeding colonies. The label near each point represents the species: Aa = *Arctocephalus australis*, Af = *A. forsteri*, Agl = *A. galapagoensis*, Agz = *A. gazella*, Apd = *A. pusillus doriferus*, App = *A. p. pusillus*, At = *A. tropicalis*, Cu = *Callorhinus ursinus*, Ej = *Eumetopias jubatus*, Nc = *Neophoca cinerea*, Ph = *Phocartos hookeri*, Zcc = *Zalophus californianus californianus*, Zcw = *Z. californianus wollabaeki*. (Note - duplicate points for the same species represent different populations.)

reflected in the different timing of pupping and mating in species inhabiting the northern and southern hemispheres. Breeding periods in both hemispheres occur in the same seasons respectively (late spring or early summer). Using latitude as a measure of climatic seasonality, a correlational analysis of birth synchrony and latitude shows a strong negative relationship (Figure 1.2).

Sexual selection might have operated to further synchronize oestrus, particularly in light of the fact that males must fast in order to maintain control over females. Presumably those males that are most successful at competing for females will maximize reproductive success by ensuring tenure on the rookery during the peak period of receptive females. If these males are unable to maintain tenure over the entire period during which females become receptive, females that give birth late in the season are more likely to mate with a less fit male (i.e. a temporal-marginal-male effect). Among some living species, we know that dominant breeding males for a given reproductive season tend to depart before the last females become receptive (see Table 1.3). When these males depart, their positions on the rookery are taken over by males that had been located peripherally

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to the female herd (Gisner, 1985; Roberts, 1987). These peripheral males are more likely to come and go from the rookery than central males, and may even feed during absences (Gisner, 1985; Roberts, 1987). As with the marginal-male hypothesis, this temporal hypothesis seems plausible, but there are no data available to evaluate whether female fitness is affected by the timing of oestrus.

1.3.2 Ability to capitalize on polygyny potential for males

In most species the major factor governing capitalization on the potential for polygyny is the degree to which males are free of responsibility in caring for young (Trivers, 1972; Emlen and Oring, 1977). Otariid males should be able to take advantage of the high polygyny potential because females provide the nutritional requirements of dependent offspring through maternal milk. There is also no substantive evidence of any other paternal role. Barlow (1972, 1974) provides limited evidence of paternal protection against shark predation among Galapagos sea lions (*Zalophus californianus wollebaeki*) (but see Miller, 1974a).

A second factor which most likely contributed to otariid males capitalizing on the polygyny potential and, achieving extreme levels of polygyny, is fasting. The importance of the male fast to the evolution of polygyny in pinnipeds was first suggested by Bartholomew (1970). According to Bartholomew, and others since (e.g. Bonner, 1982; Pierotti and Pierotti, 1980), large size and a high proportion of body fat were critical adaptations to extreme thermal conditions resulting from low water and air temperatures and the relatively high thermal conductivity of water. Clutton-Brock and Harvey (1983), in reviewing variation in body size among mammals, concluded that large size per se is less important in heat conservation than is the insulatory properties of the body since absolute heat loss increases with body weight. The extensive subcutaneous blubber stores of pinnipeds were thus presumably more important in thermoregulation than size although larger size may have permitted larger absolute stores. A 48-ton fin whale, *Balaenoptera physalus*, can last on its body stores for about one third as long as a 37-ton whale (Brodie, 1975). Blubber stores for heat conservation might then have served as a preadaptation for a male fast during the mating season.

1.3.3 Degree of monopolization of females

As one would expect from the preceding discussion, otariids are uniformly polygynous. Three measures of reproductive performance of males are presented in Table 1.4: the operational sex ratio (OSR), an index of the intensity of sexual selection (I_s) and the maximum

Table 1.4 Several measures of level of polygyny in various otariid species

<i>Species</i>	<i>Operational sex ratio</i>	<i>Intensity of sexual selection</i>	<i>Maximum number of females mated by a single male</i>	<i>Sources^a</i>
<i>A. forsteri</i>	7.9	6.5	30	13
<i>A. galapagoensis</i>	6.0	3.3	14	17
<i>A. gazella</i>	10.0	-	8	11, 12
<i>A. p. pusillus</i>	7.5	-	-	15
	53.0	-	-	5
<i>A. p. doriferus</i>	10.0	-	-	16
<i>A. tropicalis</i>	6.6	-	-	2
<i>C. ursinus</i>	39.0	45.9	161	1
	16.0	-	-	14
<i>E. jubatus</i>	10.0	9.7	32	7
	-	5.3	24	9
<i>O. byronia</i>				
Punta Norte	3.3	2.3	18	4
Puerto Piramide	5.3	-	20	4
<i>P. hookeri</i>	-	3.3	19	8
<i>Z. californianus</i>	25.0	5.9	27	10
	23.0	-	-	6
	19.0	-	-	3

^a 1. Bartholomew and Hoel, 1953; 2. Bester, 1987; 3. D. Boness, unpubl. data; 4. Campagna, 1987; 5. David, 1987; 6. Francis, 1987; 7. Gentry, 1970; 8. Gentry and Roberts, in prep.; 9. Gisner, 1985; 10. C. Heath, unpubl. data; 11. McCann, 1980; 12. McCann and Dodge, 1987; 13. Miller, 1975b; 14. Peterson, 1965; 15. Rand, 1967; 16. Shaughnessy and Warneke, 1987; 17. Trillmich, 1987.

number of females mated by a single male. The OSR is defined as the average ratio of fertilizable females to sexually active males at any given time (Emlen and Oring, 1977). I_s is the variance in mean copulatory success of a population of males scaled in relation to average fitness (Wade and Arnold, 1980; see also discussions by Clutton-Brock, 1988 and Grafen, 1988).

A precise OSR is not available for most otariid species, but one can obtain an approximation of it by taking the number of males which become resident among females and the maximum number of females at the rookery (or pups, whichever is largest). Unfortunately this introduces extraneous variation since not all males in residence copulate and presumably not all females become receptive.

Calculation of I_s is less prone to extraneous variation because it requires more detailed information on mating success of individuals. However, because it requires knowing such information for individuals there are fewer species for which this measure can be calculated. Furthermore, one must know or be able to estimate the

proportion of the sexually mature male population which does not succeed in mating. For otariids, where many sexually mature and even some socially mature males may be excluded from the central part of rookeries, it is difficult to obtain a representative sample of the variation in mating success among the mature male population. Failure to obtain a representative sample can produce extremely misleading I_s values. For example, if one simply uses copulatory success data reported for territorial males (e.g. in I_s calculations given by Miller, this volume) the data of Bartholomew and Hoel (1953) on northern fur seals would yield an I_s value of 0.80, suggesting a very low level of sexual selection. This seems contrary to what one would expect given the extreme level to which some males control access to many females (over 100) while other males acquire no females. The surprisingly low value occurs because only 3 of 19 territorial males did not copulate, implying that only 16% of the mature male population is excluded from mating. Bartholomew and Hoel do not provide any estimate of the proportion of the mature male population that is not holding territories or hold territories in peripheral areas not sampled, and do not obtain any matings. As there are life tables available for male and female northern fur seals (Lander, 1981), it is possible to calculate for a given sample of females the expected number of mature males; in this case the life tables indicate one should expect half as many mature males as females. Using this information and Bartholomew and Hoel's data then, we see that actually 97% of the mature male population is excluded from mating. When the calculation of I_s is made with this estimate of the number of males having zero matings the value is 45.9. This is much more consistent with what we expect intuitively, from the other measures which estimate levels of polygyny (see Table 1.4), and from values for I_s for elephant seals (*Mirounga angustirostris*) calculated from lifetime reproductive success of several cohorts tagged as pups (Le Boeuf and Reiter, 1988). Unfortunately life tables are not available for other otariids so in calculating I_s for other species in which mating success data exist, I will assume the number of mature males is half that of females, as it is for northern fur seals.

The third measure of male reproductive performance, the maximum number of observed copulations (Table 1.4), can be biased both by differential observation effort across species and by uneven distribution of copulations with respect to observation times. Despite the potential imprecision of the three measures, they provide a first approximation of variation in levels of polygyny both within and across species and there is a high correlation among them (OSR vs. $I_s - r = 0.857, n = 6, p = 0.029$; OSR vs. Max. - $r = 0.860, n = 6, p = 0.028$; I_s vs. Max. - $r = 0.998, n = 8, p = 0.0001$).

Regardless of the measure chosen, considerable variation in the

level of polygyny is apparent among otariids. Not enough information is available to evaluate the level of intraspecific versus interspecific variation. A 6-fold difference in OSR reported for the South African fur seal is the largest intraspecific variation. Variation across species is as large as 10-fold (Table 1.4).

The most extreme level of polygyny appears to occur in the northern fur seal. At one colony, the average number of females controlled by males was more than triple that reported for most other species. A single male mated with 161 females (16% of all observed matings). It is possible that South African fur seals might also achieve a similarly high level of polygyny at some colonies given the OSR reported by David (1987). The South American sea lion, Galapagos fur seal and Hooker's sea lion have the lowest levels of polygyny. The ratio of sexually active males to females in these species ranges from 3:1 to 5:1 in a single season.

Polygyny in other mammals and birds does not reach such extremes. Among other mammals copulatory success within a given year is common in the range of 2-15 females (e.g. Barash, 1974; Clutton-Brock *et al.*, 1977; Owen-Smith, 1977; Gibson and Guinness, 1980). In birds, males often mate with only two females (e.g. McLaren, 1972; Martin, 1974; Carey and Nolan, 1975). Moderate polygyny is seen in red-winged blackbirds (*Agelaius phoeniceus*; Payne, 1979) and ring-necked pheasants (*Phasianus colchicus*; Ridley and Hill, 1987), where a successful male copulates with up to 5-7 females (Payne, 1979). A high degree of polygyny among birds is seen in the orange-rumped honeyguide (*Indicator xanthonotus*; Cronin and Sherman, 1977) and sage grouse (see Wiley, 1973; Gibson and Bradbury, 1986), where one male mates with approximately 15-20 females.

To examine the relationship between level of polygyny and the extent to which females cluster, comparable measures of female dispersion are required from several species or populations of a given species. A dispersion index, which takes both spatial pattern and average distance between individuals into account, would be ideal, but such measures are rarely available (see Brown, 1964; Boness and James, 1979; Boness, 1990 for examples). In contrast, female density has been measured at some otariid rookeries, and can serve as a crude estimate of degree of clustering. Explanations of density calculations are not always given so some interspecific or interpopulation variation may be due to sampling method.

There is a significant positive correlation between OSR and female density ($r = 0.825$), suggesting that female clustering is an important determinant of the level of polygyny in otariids (Figure 1.3a). I used OSR rather than either of the other two measures of polygyny level because it provided the largest sample for this analysis. There are

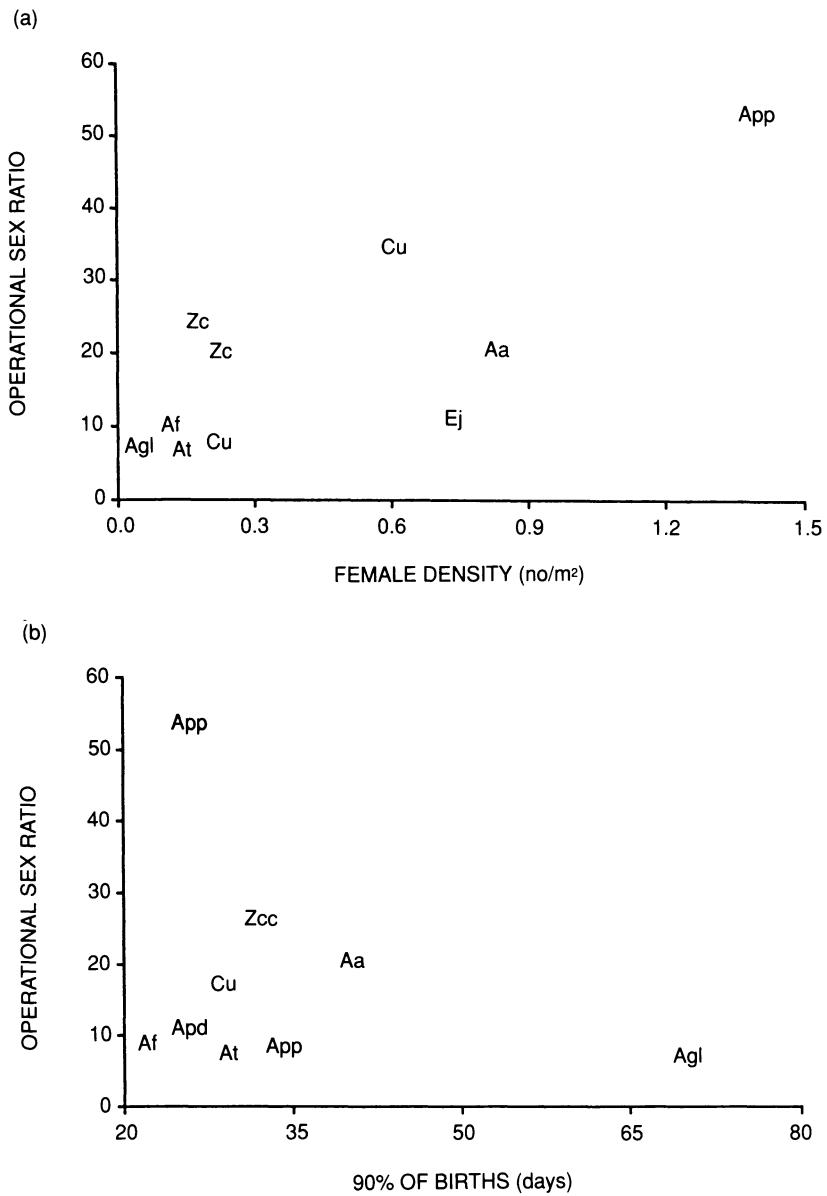


Figure 1.3 The relationship between level of polygyny as measured by operational sex ratio (OSR) and density (a) and oestrus synchrony (b) for several otariid species. Data are only used when measures are taken from the same colony. Labels near points are the same as in Figure 1.2. (Note - duplicate points for the same species represent different populations.)

species not shown in Figure 1.3a for which density measures and OSR are available, but in these species both measurements were not taken from the same population. In Figure 1.3a, the OSR might be slightly higher than expected for California sea lions and slightly lower than expected for Steller's sea lions (*Eumetopias jubatus*). This may be because there is considerable movement by females of these species. I will discuss this in greater detail later.

In contrast to the positive correlation between female dispersion and level of polygyny, there is no clear relationship between oestrus synchrony, as measured by the spread in timing of births, and OSR (Figure 1.3b; $r = -0.283$). Lack of a correlation probably results from a brief mating period in most species. The most successful males appear to have sufficient energy stores to remain in control of females until the majority of females have departed (Table 1.3). In one species where the availability of receptive females is substantially longer, the Galapagos fur seal, mean male tenure covers about 60% (the maximum is 72%) of the period and the level of polygyny is among the lowest for any species shown in Figure 1.3(b). A similar situation may exist for Australian sea lions (*Neophoca cinerea*) (L. Higgins, pers. comm.). At the other end of the continuum for oestrus synchrony, there is little evidence to suggest that males in control of females lose mating rights or fail to mate with receptive females because the period over which females become receptive is too compressed. It would appear that in extant otariids the degree of oestrus synchrony is not a limiting factor on the level of polygyny.

1.3.4 Intensity of polygyny and sexual dimorphism

On theoretical grounds, sexual dimorphism in body size (i.e. males larger than females) has been used as an indicator of polygyny in a variety of species (e.g. Jehl, 1970; Shine, 1979; Stamps, 1983; Vitt and Cooper, 1985). Although there are only a few mammalian groups (e.g. primates and ungulates) in which the relationship between sexual dimorphism and degree of polygyny has been evaluated, they do show a positive correlation between sexual dimorphism and the level of polygyny (Clutton-Brock *et al.*, 1977; Alexander *et al.*, 1979; Leutenegger and Cheverud, 1982). Sexual dimorphism in both body mass and length is high in otariids; males are on average three times heavier (weight ratio range 1.7-4.3 and a third longer (mean length ratio 1.35) than females. In contrast, the average ratio of male to female mass in 44 primate species in which males are larger than females is 1.37 (calculated from Gaulin and Sailer, 1984). Comparable male to female ratios for body length in primates and ungulates are 1.13 and 1.05, respectively (calculated from Alexander *et al.*, 1979).

As polygyny and sexual dimorphism are both extreme in the

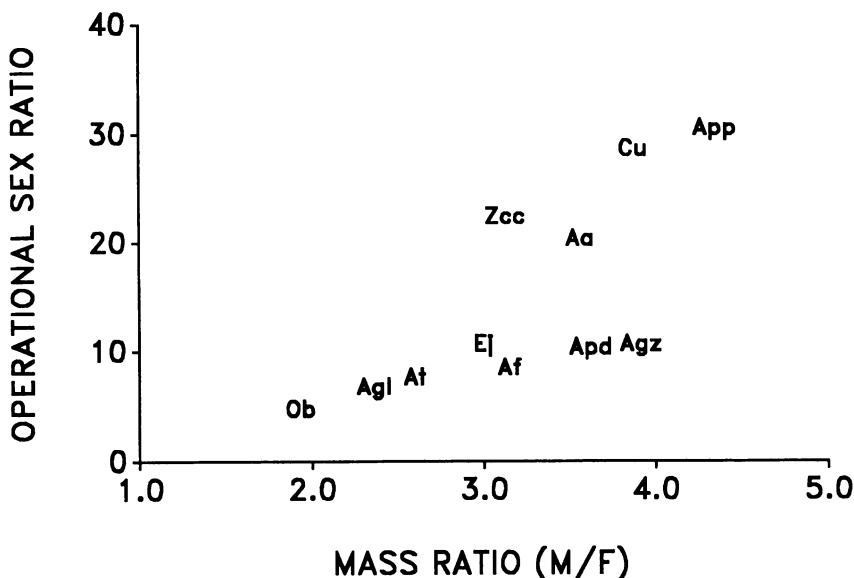


Figure 1.4 The relationship between level of polygyny as measured by operational sex ratio (OSR) and degree of sexual dimorphism in adult body mass for several otariid species. Labels near points are the same as in Figure 1.2 with the exception of Ob (*Otaria byronia*) which is not shown in Figure 1.2.

otariids, a strong correlation might be expected between the extent of polygyny and sexual dimorphism. Adult mass and estimates of polygyny are not available from the same study for any species, so to examine the relationship between these variables mean values from different studies must be used. Figure 1.4 shows a positive relationship between OSR and male/female mass ratio ($r = 0.583, p = 0.03, n = 13$). The correlation coefficient is low, however, because, for large mass ratios especially, there is a considerable range in OSR for a given ratio. Until more data are available on intraspecific variation in OSR, using sexual dimorphism as an indicator of degree of polygyny in the otariids should be done with caution.

As Ralls (1976) has pointed out, there are selective forces which might compete with intrasexual selection to reduce, or even reverse, the expectation of larger males in polygynous animals. Possible examples of this may be found in some phocid species. Behavioural observations strongly suggest that Weddell seals (*Leptonychotes weddelli*) are polygynous, yet adult females are slightly larger than males (Kaufman *et al.*, 1975; Bryden *et al.*, 1984). Similar observations are available for crabeater seals (*Lobodon carcinophagus*) (Siniff *et al.*, 1979), although crabeater seals are probably less polygynous than Weddell seals. One potential explanation for reversed sexual dimorphism in these Antarctic phocids, based on in-air thermoregulatory

stress from extreme cold (Pierotti and Pierotti, 1980), has been discounted (Lavigne, 1982).

1.4 VARIATION IN THE FORM OF OTARIID MATING SYSTEMS

1.4.1 Difficulty of distinguishing resource and female defence

Extreme care must be taken in drawing conclusions about the form of mating systems in pinnipeds. Behaviour occurs on a spatial scale markedly reduced from that of most mammals because of the difficulties of terrestrial locomotion in these species. A move of 5-10 m in most mammals the size of pinnipeds would have little or no impact on the outcome of mating, but in most otariids a move of this distance means the difference between a female being in one male's sphere of influence or in another's. It is therefore important to be able to identify individual animals and to examine the behaviour of males in relation to both their location in space and the movement of individual females.

An example of the importance of this was made clear in studies of a phocid, the grey seal, *Halichoerus grypus*. Early research on the grey seal concluded that individual males were defending fixed territories, that is, a resource defence mating system (Davies, 1949; Hewer, 1957; Boyd *et al.*, 1962; Cameron, 1967). The researchers, however, did not record daily behaviour of individually known males in relation to behaviour and movements of females. Conclusions about territoriality were drawn from observations of relatively even spacing among males and the tendency for certain areas to be continually occupied by males. Such information alone cannot distinguish between males defending females that happen to be in a given location and males defending the location because it is a resource critical to females - a place to give birth and rear their pups. Subsequent daily observations of identifiable males and females showed that males changed locations in relation to movements of sexually receptive females and that these movements led to substantial overlap in the use of rookery areas by individual males (Boness and James, 1979). These facts are much more consistent with a female defence system than with a resource defence system.

Territoriality and resource defence become synonymous when the resource defended by males is a plot of land that is suitable for females to give birth and rear their young. Three conditions seem essential in distinguishing a resource defence system from one of female defence: (1) the areas of the rookery should be defended independently of females; (2) aggressive encounters should be concentrated along the

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perimeter of defended areas, not distributed throughout an animal's sphere of movement; and (3) the male defending the area should either occupy it exclusively or have exclusive mating rights within it (cf. Floody and Arnold, 1975). Aggression between resident males and neighbouring animals or intruders should not just be associated with the presence of or movements of females. For example, during temporary absences of females, males should maintain their locations and not follow females. If males tend to follow females when the females move away from them, it is more parsimonious to describe the system as female defence than as resource defence or territoriality.

1.4.2 Resource defence polygyny

Early assessments of otariid reproductive strategies concluded that males acquire mates by defending a discrete section of the rookery (see Peterson, 1968; Evans and Bastian, 1969; Bartholomew, 1970 for reviews). As more otariid species are studied, this form of mating system predominates (Table 1.3) although information is still not available for about half the species.

Resource defence has been demonstrated clearly in five species: the New Zealand fur seal (*Arctocephalus forsteri*), Antarctic fur seal (*A. gazella*), northern fur seal, Steller's sea lion and the South American sea lion. The South American sea lion also exhibits a female defence strategy at a separate colony (Campagna and Le Boeuf, 1988b). Males hold and defend exclusive parts of the beach, some in areas where females will locate and others in regions that will have no females. Threat displays are given in discrete locations which divide the areas of neighbouring males, and the displays need not be associated with the movements of females.

Several characteristics are common to those species or populations which exhibit resource defence polygyny: (1) territorial males arrive before females; (2) females become receptive in close proximity to where they give birth; (3) the rookery substrate is discontinuous; and (4) there may be a relatively low level of aggressive interactions among males (Table 1.3).

Territories are established during the period of male activity on the rookery before females arrive. Territory size is large early in the season and decreases as more males arrive (Kenyon, 1960; Miller, 1975b). For example, territory size may decrease from 400 m² at the beginning of the season to just under 100 m² at the peak as it does in Steller's sea lions (Gentry, 1970), or from 60 m² to 22 m² as in Antarctic fur seals (McCann, 1980). Individuals apparently are unable to defend the larger areas against the increasing number of competitors.

Females haul out onto the beach and take up positions where they will give birth to their young within a day or two of arrival. Females' locations appear to be more related to beach topography and temperature than to the proximity of males. There are no data for any species on female site tenacity over subsequent years. The high mid-day temperatures to which many species are exposed require animals to maintain access to water or wet sand since pinnipeds generally are limited in their physiological means for dissipating heat (White and Odell, 1971; Matsura and Whittow, 1974). In a species like the Galapagos fur seal, which breeds near the equator and must cope with consistently high ambient temperatures, most females locate along the tide wash although a few females seek refuge in the shade of large boulders inland from the tide wash (Trillmich, 1986). In other species, such as, Steller's sea lion, there are only certain days that temperatures are high enough to require moving near the water's edge (Gentry, 1970; Gisner, 1985). In these species many females may reside close to the tide line, but many will also disperse further inland and move to the tide wash during the hottest parts of extremely warm days (see Chapter 5).

The predictability of the location of females at oestrus and the extent to which females move are thought to be important factors in resource defence polygyny (Emlen and Oring, 1977; Bradbury and Vehrencamp, 1977). In four of the five species of otariids that clearly exhibit resource defence polygyny, females do not move extensively; the limited movements they undertake are predictable (Table 1.3). Female Steller's sea lions are an exception. In addition to non-regular thermoregulatory movements, many Steller's sea lion females begin foraging trips to sea before they become receptive (see Gentry and Kooyman, 1986; Oftedal *et al.*, 1987 for reviews of maternal attendance patterns). Although females apparently return to the island when they are receptive, their foraging trips and thermoregulatory movements seem to diminish the advantages of territorial defence. Forty-six per cent of identified females in one study copulated with a male other than the one they had been with an hour before the copulation (Gisner, 1985) and in two other studies 25–35% of known females copulated more than 20m from their birthing sites (Gentry, 1970; Edie, 1977). Nevertheless, in all three studies most females mated near their place of parturition. The net effect of females' movements seems to be that those males defending territories along paths of departure acquire a disproportionately large number of females, especially relative to the number of females that reside there with their pups (Gentry, 1970).

Some Steller's sea lion females may become receptive away from the rookery, potentially making it worthwhile for males that are not successful in territorial defence to follow these females on their

foraging trips (Gentry, 1970). The difficulty of observing animals at sea has precluded determining whether some males use such a strategy.

The relatively low level of aggressive activity in species exhibiting resource defence polygyny (Table 1.3) may reflect the 'dear enemy' phenomenon and the exclusion of non-territorial animals from the rookery area (see Wilson, 1975; Jaeger, 1981; Yasakawa *et al.*, 1982; Picman, 1987). In territorial species an animal's neighbour should change less often than in systems in which the movements of males are more flexible. While these comparisons are not available for otariids with a non-resource defence system, one can compare the territorial displacement rate for northern fur seals with that of grey seals, a phocid exhibiting female defence polygyny; the turnover rate of northern fur seal males is 10% for the entire season (Peterson, 1965), while that for grey seals is 10% per day (Boness, 1979). Territorial intruders among otariids are primarily males attempting to take over the territory. Those males that are clearly sexually mature, but not large enough to have a chance of capturing a territory, are seen infrequently on the rookery or maintain locations peripheral to the main area of breeding activity (e.g. Hamilton, 1934; Bartholomew, 1953; Stirling, 1971; Vaz Ferreira, 1975).

Several otariid species for which less detailed information is available may also exhibit resource defence polygyny (South African fur seal, Australian fur seal (*Arctocephalus pusillus doriferus*), Galapagos fur seal, and Subantarctic fur seal (*A. tropicalis*), but further study is required for confirmation. For example, Trillmich (1986) called Galapagos fur seal males territorial and indicated that they defend areas 200m² in size. He also reported that these males do not have the ability to exclude other males from their areas because of the rugged terrain. This apparent contradiction cannot be clarified until further information is available, as Trillmich's account is primarily qualitative.

Male South African, Australian and Subantarctic fur seals also have been described in qualitative accounts as defending territories (Rand, 1967; Stirling and Warneke, 1971; Bester, 1977; Warneke and Shaughnessy, 1985; Shaughnessy and Warneke, 1987). They inhabit discontinuous rocky terrain which would facilitate territorial defence. The males are wide-ranging in their movements before females arrive and the number of males increases, at which time the males restrict their movements to smaller areas (Table 1.3). These characteristics are comparable to those of the other species exhibiting resource defence polygyny, but critical information is lacking to ascertain whether the location of females at oestrus is predictable or whether males defend territories rather than females directly. In the South African fur seal, for example, 60% of observed females begin

their foraging trips before becoming receptive (David and Rand, 1986) so it is possible that oestrous females are dispersed and cannot be monopolized by defending an area on the rookery. However, they could be like female Steller's sea lions and return to their parturition site when they are receptive.

1.4.3 Female defence polygyny

To date, the only unambiguous evidence of female defence polygyny in an otariid comes from one Argentine population (Punta Norte) of the South American sea lion (Campagna and Le Boeuf, 1988b). The only other South American sea lion population for which detailed observations have been reported, Puerto Piramide, exhibits resource defence polygyny. There are several interesting contrasts between the behaviour of this species at Punta Norte and that of species which have resource defence systems. Although males are present at the rookery before the first females arrive, the number is a small proportion of the number of males that eventually become established among the females (Campagna and Le Boeuf, 1988b). Early arriving males behave in a manner similar to that of territorial males in other species, but as the number of animals increases, males follow females when the females move rather than remaining in the areas they had been defending.

Campagna presents several lines of evidence in concluding that males defend females directly: (1) some males leave their positions among females to follow stray females; (2) males preferentially defend females near oestrus over non-receptive females; (3) males follow females when group movements occur in response to temperature or other disturbances; (4) the aggressive activities of males seem to take a form that minimizes the time males must spend away from nearby females; (5) some males abandon the breeding area when they lose all their females; (6) the rate of aggressive interactions correlates positively with defending at least one female; and (7) intruding males do not attempt to capture positions but instead try to capture females directly. Not all these characteristics by themselves would permit one to distinguish between resource and female defence; however, in combination the information is clearly more consistent with a female defence system than one of resource defence.

The movements of South American sea lion females do not appear to be different enough from those of species exhibiting resource defence to account for the difference in male strategy. Females move predictably over short distances up and down the beach each day as temperatures rise and fall. The breeding beach topography is nearly homogeneous, which would make boundary locations less precise; although it should not preclude defence of a territory encompassing resources. Territoriality occurs in other mammalian species where

topography is fairly uniform (Estes, 1969; David, 1973; Kitchen and Bromley, 1974). For some of these species, olfactory markings may assist in maintaining boundaries (Owen-Smith, 1977; Walther, 1984). If some mechanism such as olfactory marking is not available to otariids, we might expect that a habitat which has few features for delineating boundaries would increase the cost of defence of an area.

The female defence system of the South American sea lion may relate to the nearly uniform distribution of females and the extremely high level of aggressive interactions among males. Density measurements of females were not reported at Punta Norte by Campagna, but females there form one large cluster with individuals in close proximity rather than being dispersed in smaller clusters such as occurs at Puerto Piramide, where resource defence occurs (Campagna and Le Boeuf, 1988b).

The rate of aggressive interactions between males at Punta Norte is almost an order of magnitude higher than that of any species exhibiting resource defence polygyny (Table 1.3). This appears to be related to a large influx of males competing for females. The number of males that remain amongst the females increased from 15 to 100 from the beginning of the season to the peak (Campagna and Le Boeuf, 1988b). There was also a marked increase in the number of transient males that remained on the periphery of the central breeding area (from 10 to 40).

Numerous studies have shown or postulated that both increased density of a resource or mates and increased intrusion rates on territorial males can lead to reduction in territory size and even the breakdown of territoriality (Brown, 1964; Wilson, 1975; Carpenter and MacMillan, 1976; Wittenberger, 1981; Davies and Houston, 1981; Brown, 1982; Stamps, 1983; Hixon *et al.*, 1983). In a recent review of intraspecific variation in territoriality, Stamps and Buechner (1985) noted that for many animals resource or female density and increased costs of territorial defence often occur simultaneously. They suggested that although many of the effects of these two factors on behaviour are similar, one can distinguish the relative importance of each by examining changes in the payoff (e.g. copulatory success). If territory size reduction or breakdown is the result of increased resource density, then there should be either an increase or no change in payoff, whereas if increased aggressive competition is responsible, then the payoff should decrease. I apply this same reasoning to examine the possible importance of high competitive costs versus female superabundance in distinguishing resource defence from non-resource defence systems among otariids. South American sea lion males, especially at Punta Norte, show a lower mean reproductive success than do the species exhibiting resource defence polygyny (Table 1.4). This suggests that higher costs of

competition for females may be more of a factor than female density in distinguishing the female defence system of South American sea lions from those of resource defence in other otariid species.

In contrast, differences in female dispersion reported for the two South American sea lion colonies may contribute more to the observed differences in mating systems than the cost of male competition. The mean payoff to males at Punta Norte, the colony exhibiting female defence polygyny, is not significantly different from that at Puerto Piramide, the colony showing resource defence polygyny (4.5 copulations per male vs. 7.1, respectively, $t = 1.33$, d.f. = 32). Associated with this, females at Punta Norte formed one continuous patch covering most of the beach area, whereas at Puerto Piramide female dispersion was patchy because a few inland ponds provided opportunities to dissipate heat. Unfortunately, Campagna did not report rates of aggression amongst males at both locations. It may be that interspecific and intraspecific variation in mating systems are likely to be driven by somewhat different factors.

1.4.4 Male dominance (lek) polygyny

Bradbury (1981) suggests that there are four major features of classical lek systems: (1) there is no male parental care; (2) males aggregate at an arena to which females come to mate; (3) the display sites of males contain no critical resources required by females; and (4) females have an opportunity to select mates at the arena although the extent to which females have an opportunity to select mates is controversial (see Beehler and Foster, 1988). Bradbury has suggested that few species exhibit classical lek mating systems, but there are many that have leks which are intermediate between a resource defence system and classical leks.

The California sea lion and Hooker's sea lion exhibit behaviour and dispersion patterns characteristic of intermediate leks. Heath and Francis (1983, 1987 and Heath, 1989) were the first to provide evidence of lek behaviour in any pinniped. There are two aspects of males' behaviour in particular that set these species apart from other otariids: males do not settle in their locations before the arrival of at least some females, and the locations of males that account for most copulations do not coincide with where most females give birth and care for their pups (Table 1.3).

Females in both species engage in behaviour suggestive of female choice (Heath and Francis, 1983, 1987; R. Gentry, pers. comm.). As in most animals in which female choice has been described, there are no data that relate the apparent female choice to increased female fitness (see Lightbody and Weatherhead, 1987). Just prior to becoming receptive, Hooker's sea lion females leave their pups and wander among the

males, which make little effort to control females as they move past. The lack of effort to control females is a marked contrast to the often intense herding efforts of male otariids defending fixed areas or females directly (see Table 1.3).

Unlike Hooker's sea lions, receptive California sea lion females do not appear to 'wander' among the males, but temporarily move to 'group milling sites' in shallow water (Heath and Francis, 1983). At these sites females wallow in small groups, 'attracting the attention' of the nearby males. These males copulate with oestrous females in the groups. Females then return to their pups. Most observed copulations occur at milling sites, but some occur on other parts of the rookery, where females and pups normally reside. Recent evidence suggests that both site and individual male characteristics may play a role in female choice (Heath and Francis, 1987), but the data on choice of male characteristics must be viewed as preliminary at this point.

There are several differences between the lek system of these two otariids and a classical lek system as defined by Bradbury (1981). The arena fills most of the habitat used during the whelping period so there is not a complete separation between the arena location and the habitat normally used by females and pups. Unlike in classical leks, the display sites of California sea lion males are relatively large. Those of Hooker's sea lions, however are small. Lastly, male Hooker's sea lions have an extremely high rate of threat displays when one should expect a shift away from aggressive defence and toward sexual display. Rates of aggression are not available for California sea lions. It is possible that the high rate of threat displays, reflects the use of these encounters as sexual displays as well as for maintaining a location in the arena. Evidence of male-male competition as a mechanism of sexual selection to promote female choice has been reported in northern elephant seals and grey seals (Cox and Le Boeuf, 1977; Boness *et al.*, 1982). Such a mechanism may occur in other mammals and birds as well (see Cox and Le Boeuf for a review).

What factor(s) might have led to a shift from resource defence to 'attracting' females? Three hypotheses which need not be mutually exclusive have been proposed to explain the evolution of leks: group-size, density, and home-range size hypotheses (Bradbury, 1981). The group size hypothesis suggests that leks are a product of the evolution of large groups in response to predation pressure or enhanced foraging efficiency. The exact mechanism of how large group size might have resulted in lek behaviour was not specified by Bradbury. He discounted the hypothesis because except for grouse there is not a correlation between large group size and lek systems in other taxonomic groups. This lack of correlation applies to otariids as well; there is no evidence to suggest that the occurrence of leks is related to colony size.

According to the density hypothesis, in a territorial species where male density can increase independent of defendable resources, territory size will decrease as male density increases because of the increasing cost to defend an area. At some point, the cost of defence outweighs the benefits of enhanced access to females and alternative strategies are adopted. A lek should evolve under these conditions when female defence is not advantageous. Assuming defence of sea lion females is not advantageous, this hypothesis is plausible for Hooker's sea lions. Aggressive competition between males is high and males' 'display areas' are relatively small; since areas are contiguous, male density is relatively high (see Table 1.3). In contrast, and contradictory to the density hypothesis, the areas of California sea lion males are large, although we do not know the rate of aggression among males in this species.

The home-range hypothesis, however, could explain the evolution of leks in both otariid species. In essence this hypothesis suggests that it is the expanded movements of females, for whatever reason, that led to abandonment of resource defence by males in favour of 'advertisement of traits' to females. With wider ranging movements by females, it may no longer be economical for males to defend areas encompassing the females. Furthermore, the movements expose females to more males, yielding a net effect of each male having increased indirect competition for each female. These conditions would therefore set up selection for males to behave in a manner to attract females by conveying their fitness to them and for the females to enhance their fitness by selecting good-quality males. Both female California and Hooker's sea lion move considerable distances from where they give birth to where they copulate (Heath and Francis, 1983; Gentry and Roberts, in prep.). California sea lion females depart from the rookery on their feeding trips before they become receptive, and while on the rookery their movements may take them distances of 30-50 m. Female Hooker's sea lions do not leave the rookery before becoming receptive, but the female herd shifts more than 90 m across the beach throughout the course of the mating period. Furthermore, the exact location on the beach where colonization of females begins varies from year to year.

1.4.5 Plasticity of otariid mating systems

Environmental conditions in given habitats vary from time to time, and many species have populations that inhabit different environments. It has been argued that it would be adaptive for animals to have evolved some level of behavioural plasticity to accommodate environmental variation (Trivers and Willard, 1973; Wilson, 1975; Emlen and Oring, 1977). Among otariids clear

evidence of a fundamental shift in the form of mating systems has been presented for only one species, the South American sea lion (Campagna, 1987). As described earlier, in the discussion of female defence polygyny, temperature and topography differences at the two rookeries appear to result in differences in the dispersion and movements of females, which in turn affected male behaviour and dispersion.

Intraspecific variation in reproductive behaviour in response to habitat variation, without a fundamental shift in form of mating system, has been reported in studies of the California sea lion. The primary habitat differences for the various colonies are air and water temperatures and foraging conditions (Heath, 1985). At one colony temperatures are less extreme and the routine foraging trips made by females are relatively long. Under these conditions females gather at shallow-water milling sites and mate with the nearby male. In another colony, temperatures are more extreme and female foraging trips are shorter. In this situation females still apparently choose males but do not form milling groups. As this work is preliminary, the reasons for the observed differences in reproductive behaviour are unclear, although Heath (1985) has suggested that the lack of milling groups might be related to a protracted breeding season brought about by the high temperatures and the apparently high cost of foraging to sustain lactation.

Many otariid species inhabit a wide range of beach topographies and environmental conditions. Our understanding of intraspecific malleability of reproductive behaviour and mating systems, both in the short term and through isolation of populations, is very limited and requires much attention.

1.4.6 Secondary male strategies

While there is often one reproductive strategy that yields the highest reproductive success for a given sex, some less successful individuals might use alternative strategies to maximize their chances of mating. For example, small male anolids (*Anolis garmani*) behave more like females than like territorial males and are tolerated within the territories of large males. This behaviour sometimes leads to smaller males achieving copulations, whereas if they tried to compete for a territory they would fail (Trivers, 1976). Similarly, small Banksia bee (*Hylaeus alcyoneus*) males patrol from flower to flower rather than compete with larger males for control over flower spikes, which are a critical food resource for females (Alcock and Houston, 1987). Patrolling males take over flower spikes that become free of an occupant, but it is unknown whether patrolling results in matings directly.

Secondary mating strategies have been reported in otariid species and, as with other animals, individuals exhibiting them are smaller than those that acquire the greatest number of mates. In some species there are numerous males that loosely 'defend' positions on the periphery of the main breeding area, where larger males hold territories. In contrast to the larger males, these males often temporarily leave the rookery, possibly to forage. Among northern fur seal males, during a single season 36% of these males copulated at least once and 48% of them eventually gained a territory (Roberts, 1987).

Small (and probably young) Hooker's sea lion males roam the periphery of the rookery, waiting for females to depart on a foraging trip, and then chase the females in an effort to mate with them. This activity sometimes leads to copulations, although the female usually has mated already (Gentry and Roberts, in prep.). It is unknown what percentage of these copulations result in insemination.

Possibly, a more coordinated effort to capture mates is made by South American sea lion males that roam the periphery of the central breeding area (Campagna *et al.*, 1988). Males form raiding parties and attack females in the main breeding area; 63% of males joining raiding parties copulate at least once during a season. Subadult males in these raiding parties abduct the pups of attacked females and treat them sexually as if they were females. The experience gained from this activity may lead to enhanced success as the males get older (Campagna *et al.*, 1988). A similar pattern of non-resident males 'banding' together and raiding females appears to occur among Australian sea lions (Marlow, 1975).

'Post-season' territoriality, observed in Steller's sea lions (Gisner, 1985) and northern fur seals (Roberts, 1987), may not result in copulations directly, but indirect benefits to future reproductive success have been suggested. Some males take up territories at the end of a season when resident males abandon them. Post-seasonal territorial males rarely copulate because most remaining females mated with resident males before the resident males leave. However, new territorial males in the following season appear to come from the pool of males that held post-seasonal territories.

1.5 CONCLUSIONS

1.5.1 Determinants of polygyny level and mating system form

The Otariidae are uniformly polygynous with some species obtaining extreme levels of polygyny. The primary ecological and phylogenetic

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determinants of polygyny appear to be: (1) aquatic adaptations which led to a marine food source and large size; (2) retention of terrestrial maternal care, which in conjunction with the marine food source led to the use of oceanic islands and some level of spatial aggregation; (3) further spatial aggregation induced by enhanced fitness through natural selection (e.g. ecological-marginal-male effect) and intersexual selection (e.g. marginal-male effect); (4) postpartum oestrus and delayed implantation, which led to a moderate level of oestrus synchronization; and (5) mammalian lactation, where females have sole responsibility for providing young with milk nutrients.

Secondarily climate and beach topography dictate the level and form of polygyny via effects on female movements and dispersion and degree of male competition. Neither factor alone can account for all variation in the form of otariid mating systems. The effects of a given environmental condition on the behaviour of animals can be dependent on topography. For example, high temperatures may result in: (1) increased clustering and patchiness of females because there is limited shoreline or tide pools; (2) decreased clustering because shaded resting sites are scattered and large enough for only one or two females; or (3) increased movements because animals not near the shoreline move there during the peak temperatures.

Stirling (1975, 1983) emphasized the importance of aquatic mating in diminishing the level of polygyny among pinnipeds. While this trait may have played a major role in shaping phocid mating systems, it is unlikely that it was similarly important for otariids, as there is limited evidence of aquatic copulations in living otariids. Yet, the principle behind the reduced polygyny associated with phocid aquatic mating is similar to that which accounts for the instances of diminished polygyny in terrestrial mating otariids, or for that matter other terrestrial mammals. Both movements and widespread dispersion of females make the locations of receptive females less predictable and their defence more costly.

An interesting contrast between otariid species which show substantial female movements and phocids that have aquatic copulations and/or widespread dispersion is that the otariids have lek-type mating systems whereas the phocids appear to have female defence systems (Boness and James, 1979; Siniff *et al.*, 1979; Stirling, 1983; Boness *et al.*, 1988). One possible reason for this difference may be that female density among these otariids is higher than among these phocids, making a female defence system too costly for male otariids.

1.5.2 Effects of specialization on diversity in mating systems

The impression that otariid mating systems are restricted to territoriality or resource defence is not correct. Aquatic specialization

in otariids, resulting from divergence to a marine food source, has not severely constrained variation in the form of mating system exhibited by this family. Most forms of polygyny that have been described for other mammals are found among otariids. The high degree to which they aggregate, their relative immobility on land, and their use of traditional rookeries, however, appear to predispose them to resource defence polygyny.

Of those forms of polygyny described for other mammals, scramble competition is the only one not reported among otariids. The two ecological conditions that apparently underlie this system are: (1) mobile females concentrated spatially and temporally, with a high competitor density; and (2) females or resources important to females that are spatially scattered (Schwagmeyer and Woontner, 1986). Based on spatially scattered females and patrolling behaviour by males, a scramble competition system has been suggested for one phocid, the Hawaiian monk seal (*Monachus schauinslandi*) (Deutsch, 1985). As there may be a couple of otariids (e.g. Australian and Galapagos sea lions) where female dispersion is similar to that of Hawaiian monk seals, it would not be surprising with further study to find this form of polygyny among otariids as well.

1.5.3 Plasticity in reproductive behaviour and mating systems

Campagna (1987) and Heath (1985, 1989) have shown that different environmental conditions may lead to intraspecific variation in reproductive behaviour and form of mating system. The adaptiveness of such plasticity has been argued in theoretical discussions and has been described in empirical studies of terrestrial mammals. The breadth of plasticity, especially within given populations, is still poorly understood. With more careful quantitative observations of several colonies of given species and long-term studies of given populations, such as Le Boeuf and his colleagues have done with northern elephant seals (Le Boeuf and Peterson, 1969; Le Boeuf, 1972; Le Boeuf, 1974; Reiter *et al.*, 1981; Le Boeuf and Reiter, 1988), it is likely that otariids will be shown to be extremely malleable in their reproductive strategies. The breeding distributions of many otariid species span a wide range in latitude, for which there should be considerable differences in climatic conditions that will in turn affect female dispersion and movement patterns (see Chapter 6).

1.5.4 Directions for future research

The relationships between environmental variables, level of polygyny and form of mating system proposed in this paper must be viewed as

preliminary. For some species, conclusions may not have been rigorously tested by repeated study. Quantitative data are often sparse, coming from different colonies and different years for a given species such that the pieces cannot be put together easily. Much information is not collected or reported thoroughly enough to permit comparison to other studies.

It is important to choose the best measures possible for relevant variables. Although I used density to characterize female dispersion, density is not the best measure for this purpose. I used it because I could obtain values for a relatively large number of otariid species, recognizing that sometimes the measures were calculated differently. A dispersion index, such as that used by Boness and James (1979), would be better because it takes into account both within- and between-cluster distances. There will always be difficulties in assessing level of polygyny in studies of free-ranging animals no matter what measure is used. However, regardless of the measure chosen, extraneous variation in interspecific comparisons can be reduced by using methodology that is consistent with previous studies.

Lastly, dispensing with the notion that big males threatening one another is sufficient to infer territoriality will help to free pinniped researchers from an *a priori* bias toward describing otariid mating systems as territorial. The actual behaviour of individual males with respect to space and females should be given critical examination before conclusions are drawn. Likewise, we must give quantitative treatment to the costs and benefits of different patterns of female behaviour. Historically, research on pinniped mating systems has focused on the male role. This needs to be changed.

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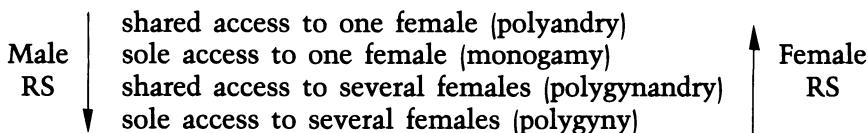
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2

Pinniped mating systems on land, ice and in the water: Emphasis on the Phocidae

Burney J. Le Boeuf

Dunnocks, *Prunella modularis*, are small brown passernines that exhibit an extremely variable mating system. The mating system of a population of 90 breeders, studied by Nicolas Davies and collaborators in the Cambridge University Botanic Garden, consists of several mating combinations (Davies, 1983, 1985; Davies and Lundberg, 1984, 1985). These can be viewed as different degrees of female monopolization by males varying in increasing order of male reproductive success (RS), from:



Male RS increases to a high with polygyny; female RS increases to a high with polyandry. Clearly, there is sexual conflict. Males are selected to be polygynous (access to several mates); females polyantrous (shared male parental care). Davies and Lundberg (1984) show that the main factor influencing the ability of male dunnocks to monopolize females is female range size which, in turn, is determined by food distribution. Where food is sparse, female range is large and it is difficult for one male to monopolize a female (hence polyandry). When food is densely distributed, female ranges are smaller and it is easier for a male to defend a female alone (monogamy) or even to defend several females at once, either alone (polygyny) or with another male (polygynandry).

What does this bird tell us about mating systems in seals, sea lions, fur seals and walruses or in terrestrial mammals? Despite large

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discrepancies in size, habitat, life styles and genetic relatedness, the following generalizations from this study of a hedge sparrow apply to pinnipeds.

1. Mating systems are not fixed attributes of populations or species (see also Lott, 1984). Mating systems are not inherited and they are not the same because of a common ancestor. Mating systems in birds and seals may be similar despite their distant relationship.

2. The two sexes are in conflict, being under selection pressure to seek different mating arrangements. Males maximize their RS by seeking more mates and females maximize their RS by successfully rearing young that have been produced and, when possible, obtaining as much assistance as possible from mates.

3. Female distribution determines to a great extent the degree to which males can obtain multiple mates, i.e. the degree of polygyny that develops.

4. The distribution of females results from the self-interest of individual females and is associated closely with resources necessary for producing and rearing the young (e.g. food distribution, nest or parturition sites). Female fecundity is limited by energetics.

5. The observed mating system reflects the outcome of sexual conflict and the arrangement that is advantageous to the sex with the momentary advantage. Which sex predominates and the mating system that results is determined by several interacting variables that set the stage for mating. These include phylogenetic inertia in reproductive physiology, physical factors such as weather, temperature and substrate, ecological factors such as predators and resources (food, nesting or parturition sites), and social factors such as the operational sex ratio, density and behaviour of the other sex.

In the cursory analysis and speculations that follow, I stress on the costs and benefits involved for each sex and the element of sexual conflict inherent in sexual reproduction between two genotypes. This approach provides a framework for understanding what we observe and enables us to make predictions for what we have not yet observed.

My aim is to compare pinniped mating systems, especially those of phocids, with those of terrestrial mammals without producing an exhaustive review. The literature on pinnipeds is of two kinds. We know a great deal about some species and virtually nothing about others. I summarize mating systems in well-studied terrestrial mammals and compare these systems to those observed in social pinnipeds. I speculate about possible mating systems in those pinnipeds about which we know little. In comparing pinnipeds with terrestrial mammals, I ask the questions: What do we expect to find? What do we observe? What are the principal determinants of what we observe? Do pinnipeds have unique features that influence the form

of their mating systems? What are the consequences of mating in water or on land?

Mating systems have been defined and categorized in a number of ways (e.g. Crook, 1965; Selander, 1965, 1972). Agreement is not universal and this has led to confusion. All treatments emphasize the number of mates that one sex can accumulate. I follow Emlen and Oring (1977) in emphasizing ecological and behavioural potential to monopolize mates and the manner in which this is done. As they point out, the mating system of a population refers to the general behavioural strategy employed in obtaining mates. It encompasses features such as: (1) number of mates acquired; (2) manner of mate acquisition; (3) presence and characteristics of any pair bonds; and (4) patterns of parental care provided by each sex. Generally, three basic types are distinguished: polygyny, monogamy and polyandry. The forms that each takes varies considerably as well as the particular set of forces that shape the mating system. I exclude promiscuity (copulation with more than one member of the opposite sex) as a category because the RS of pinniped females does not vary with the number of sexual liaisons. Females are inseminated by only one male regardless of how often they copulate.

It is useful to distinguish degrees of polygyny, especially in comparing pinniped species. This can be done with measures of mating success such as the number of females with whom a male mates during a breeding season (variance in male mating success) or with a cruder estimate, the number of females with whom a male is associated during the breeding season (harem size; see, for example, Alexander *et al.*, 1979). In this chapter, I define slight polygyny as the case when a male mates with 2–5 females, moderate polygyny refers to the case when a male mates with 6–15 females, and extreme polygyny obtains when a male mates with 16–100 or more females during a breeding season.

2.1 WHAT DO WE EXPECT IN PINNIPEDS AND OTHER MAMMALS?

The phylogenetic history of each animal group introduces bias and sets limits on the mating strategy of each sex. Mammals are predisposed to polygyny because of internal fertilization, gestation and lactation in the female. The unique mother-young relationship is critical for the survival and development of the young; the physiology of reproduction dictates a minor role for males in the care of offspring because males cannot nurse. Gestation and lactation saddle females with all or most of the parenting, commit her to a particular reproductive strategy and free the male to philander. Female mammals cannot produce and rear offspring at the rate that males can father

them. Consequently, females and males maximize their RS in quite different ways; females are limited by the number of young produced and raised, males are constrained by the number of females fertilized. Females are the limiting sex and males the limited sex (Trivers, 1972; Maynard Smith, 1977).

In contrast to mammals, the differences between the sexes among birds is small. After egg laying, males are equally adept at investing in the offspring as females. Consequently, the route to monogamy and polyandry is far easier in birds. Monogamy is found in over 90% of bird species, followed in frequency by polygyny and polyandry (Lack, 1968; Selander, 1972). However, recent studies on extra-pair copulation show that birds are not as monogamous as they appear (e.g. Burke *et al.*, 1989; Westneat, 1987).

2.2 WHAT DO WE FIND IN MAMMALS?

Polygyny is the most commonly observed mating system in mammals (Trivers, 1972; Alcock, 1984). This includes most ungulates, rodents, primates and carnivores. Harem or female defence, where female groups are defended by a single male, is common. This is characteristic of patas monkeys, *Erythrocebus patas* (Hall, 1968), North American elk, *Cervus canadensis* (Altmann, 1956; Franklin *et al.*, 1975), peccaries, *Pecari angulatus* (Sowls, 1974), horses, Equidae (Tyler, 1972), and some bats, Chiroptera (Bradbury and Vehrencamp, 1977). Equally prevalent is resource defence, where males defend habitat configurations in which females find better foraging or safety from predators, e.g. male pronghorn antelope defend areas containing water holes and high-quality grazing sites (Kitchen, 1974) and male marmots defend overwintering sites important for females (Downhower and Armitage, 1971). Male dominance polygyny (lekking), in which males display in traditional areas and females come to them to mate, is a rare form of polygyny in mammals that has been recorded in several African ungulates such as the Uganda kob (Leuthold, 1977). Lekking is much more common in birds (Payne, 1984). In many solitary species of rodents and felids, males leave their territories to find females in oestrus and the dominant males achieve the most copulations (Eisenberg, 1966).

Monogamy is rare, comprising only about 3% of all mammals (Kleiman, 1977). The exceptions include a number of terrestrial carnivores where males help feed pups and female RS is reduced without male parental investment, e.g. wolves, coyotes, foxes, African wild dogs, badgers, dwarf mongooses and several viverrids (MacDonald, 1983). Females in these groups prevent subordinate females from breeding, thus preserving monogamy. About 14% of

primate species, mostly nocturnal species that live in forests, are monogamous (Rutberg, 1983). Tamirins and marmosets, Callithrichidae, form social groups to defend territories but only the dominant male and dominant female breed; subordinates are prevented from breeding as in social carnivores (Rothe, 1975; Dawson, 1976). Males of these groups carry young (Clutton-Brock and Harvey, 1976). Monogamy occurs in a few ungulates that live in the open and rely on each other to detect predators (e.g. klipspringer (*Oreotragus oreotragus*), Kirk's dik dik (*Madoqua kirkii*), oribi (*Ourebia ourebia*), southern reedbuck (*Redunca*) and among ungulates that live in dense cover or rely on concealment to escape predators (e.g. dik dik (*M. phillipsi*)). Monogamy is expected when both sexes must invest in offspring to ensure their survival and when environmental or social conditions discourage mate dissension (Wittenberger, 1981).

2.2.1 Land-breeding pinnipeds

Extreme polygyny is characteristic of nearly all land-breeding pinnipeds (Nutting, 1891; Bertram, 1940; McLaren, 1967; Bartholomew, 1970; Stirling, 1975; Le Boeuf, 1986b). This includes all of the sea lions and fur seals, the two species of elephant seals, *Mirounga*, and the grey seal, *Halichoerus grypus*. This conclusion is inferred from behavioural observations (mating success) and the ratio of males to females on rookeries (e.g. Alexander *et al.*, 1979). There are fewer sexually active males than fertilizable females at any given time during the breeding season, i.e. relatively few males monopolize mating. In northern elephant seals, *M. angustirostris*, the variance in lifetime reproductive success is estimated to be four times greater among males than females (Le Boeuf and Reiter, 1988), a measure reflecting the intensity of sexual selection acting on males (Wade and Arnold, 1980). Comparable figures are expected of northern fur seals, *Callorhinus ursinus* (Bartholomew and Hoel, 1953), and several other otariids because of their similar mating systems. The red deer (*Cervus elephas*) on Rhum, studied by Clutton-Brock *et al.*, (1982) exhibit a similar degree of polygyny.

Female pinnipeds aggregate on beaches, rocky shelves, caves or flat areas on islands in groups numbering from a few individuals to over 1000 individuals. Mating occurs principally on land as opposed to in the water in most of these species. Polygyny takes two principal forms when viewed from the male perspective: (1) female or harem defence as in elephant seals (males fight for social status in a dominance hierarchy that confers priority of access to grouped females); and (2) resource defence - males compete for territories that include parturition sites and in some species, nursery sites, needed by females, e.g. Steller's sea lion, *Eumetopias jubatus*, and northern fur

seals (Gentry, 1970; Bartholomew and Hoel, 1953). Resource defence polygyny takes on aspects of male dominance polygyny if one emphasizes the female's point of view, i.e. the female may be choosing among territories and male territorial holders determined by dominance relationships among males, e.g., California sea lions, *Zalophus californianus* (Heath, 1985; Heath and Francis, 1983). In either case, polygyny among most pinnipeds that breed on land is extreme.

Circumstantial evidence and behavioural observations suggest that two species, the walrus, *Odobenus rosmarus*, and Weddell seal, *Leptonychotes weddelli*, are moderately polygynous. Both mate in the water, which makes them difficult to observe and the hypothesis difficult to confirm. Female walruses in the Bearing Sea congregate in groups on ice floes. Males display in the water on the perimeter of these floes competing with each other to attract receptive females (Fay *et al.*, 1984). This resembles the strategy of lekking birds, that of a male gaining multiple mates by attracting females to him (Payne, 1984). Leks are observed in birds and mammals when males cannot hold females directly or defend a resource needed by them (Bradbury, 1981). Atlantic walruses in the central Canadian High Arctic exhibit a mating system which more closely resembles female defence polygyny (Sjare, 1989). Male Weddell seals are thought to hold underwater territories (literally, maritories) near breathing holes used by females (Ray, 1967; Cline *et al.*, 1971; Kaufman *et al.*, 1975; Siniff *et al.*, 1977; Wartzok *et al.*, 1989). It is not clear whether males intercept and detain females moving through these areas or whether females shop for the most 'attractive' male on her way to forage, i.e. which sex is in control. A similar arrangement may occur in harp seals, *Phoca groenlandica*, near leads in the ice where females haul out.

2.2.2 Ice-breeding and water-breeding seals

Little is known about the remaining phocids that mate in the water or on ice. This category includes all of the pagophilic phocids: harp, ringed (*Phoca hispida*), ribbon (*P. fasciata*), bearded (*Erignathus barbatus*), hooded (*Cystophora cristata*), Baikal (*P. sibirica*), Caspian (*P. caspica*), and larga seal (*P. largha*) in the northern hemisphere and Ross (*Ommatophoca rossi*), leopard (*Hydrurga leptonyx*) and crabeater seal (*Lobodon carcinophagus*) in the southern hemisphere, plus the monk seals (*Monachus monachus* and *M. schauinslandi*) that mate in temperate waters and the harbour seal (*P. vitulina*), that mates in the water near land or ice. The spatial organization of most of these animals suggests slight polygyny or facultative monogamy, e.g. hooded seals (Kovacs, 1989). Females of species that breed on

pack ice are widely distributed from each other and appear in solitary pairs of a female and her pup, or in triads consisting of male, female and her pup, e.g. crabeaters, leopards, Ross, bearded and hooded seals. In some species (e.g. crabeaters, hooded seals), a male appears to attend a female and her pup on an ice floe until she becomes receptive and then departs after copulation, perhaps to attend another female (Siniff *et al.*, 1979; Kovacs, 1989). It is not clear how males or females acquire mates or the extent to which some males obtain multiple mates. The monk seals and harbour seals copulate in the water and are more gregarious but little is known about their mating arrangements. The solitary distribution of females leads to the suspicion that slight polygyny occurs in all of these species. Defence of one female, monogamy, is expected to develop when resources required by females are not economically defensible and the sex ratio is skewed to excess males as in some shrimp, wood roaches, frogs in which males hold onto the female's back, some migratory ducks and some songbirds (see Wittenberger, 1981 for review). But as is typical of mammals, the sex ratio in solitary seals is probably skewed the other way and females outnumber males (Rasmussen, 1952; Oritsland and Benjaminsen, 1975; Siniff *et al.*, 1977; Helle, 1980) or it is equal (Smith, 1973a; Oritsland and Benjaminsen, 1975). In all likelihood, male seals of solitary species desert females after copulation then try to pair with another pre-oestrous female (see Kovacs, 1989). In this way, a male might copulate with 2–5 females and the mating system would be characterized as slightly polygynous. In seals, even when a male pairs with only one female or a few of them during a breeding season, there is no evidence that males invest in the offspring in any way as is the case in some primates and terrestrial carnivores.

2.3 WHAT DETERMINES THE DISTRIBUTION OF FEMALES AND THE DEGREE OF POLYGYNY?

In some birds and mammals the distribution of females (clumped or not clumped) is largely determined by food (or predators) and male distribution is determined by the distribution of females (Orians, 1969). For example, in long-billed marsh wrens, *Telmatodytes palustris*, females choose territories according to the richness of the food even if this means sharing a male with other females (Verner, 1964; Verner and Willson, 1966; Verner and Engelsen, 1970). Females choose to join other females on a rich territory defended by a male rather than mate alone with a male on an inferior territory. Here, clumping and the mating system (monogamy, bigamy, trigamy) is a function of food resources for the female; reproductive success

correlates with richness of the territory. Polygynous females on productive areas enjoy greater reproductive success than monogamous ones.

Macdonald (1983) argues that resource (particularly food) distribution is fundamental to the spacing and structure of social carnivores in that it sets limits to the group and territory size within which other combinations of selective pressures operate. Grouping in some terrestrial carnivores is associated with: (1) need for assistance in hunting and killing large prey (e.g. wolves that eat large dangerous quarry as opposed to red foxes that hunt singly and eat small food items); (2) need for defence against attacks by other predators. Mongooses live in packs for the increased vigilance provided against marauding predators and the potential for intimidating predators (Rasa, 1977). Opportunities to learn from the experiences of other group members, division of labour, care of the sick and several advantages associated with alloparental care also play a role. Among less social carnivores, the spatial organization of females is determined by food distribution and that of males by the distribution of females, e.g., where several female territories are encompassed in one male territory (bobcat (*Lynx rufus*), wolverine (*Gulo gulo*), stoat (*Mustela*)).

Resources and avoidance of predators also make grouping advantageous in many well-studied ungulates and primates. Ungulates like wildebeest, *Connachaeetes taurinus*, and gazelles, *Gazella*, that feed in the open, form groups for defence against large carnivores (Estes, 1967; Walther, 1965); hamadryas baboons (*Papio hamadryas*) form small groups for foraging and larger groups on hillsides at night for increased vigilance against predators (Kummer, 1968, 1971).

Among some pinnipeds, females appear to determine the general mating system in that polygyny varies with the degree of female clumping and oestrus synchrony (see Boness, this volume). Stirling (1975) summarized the relationship between size of female groups and substrate and ecological factors. Female clumping is associated with breeding on islands but not with breeding on ice, except where there is a need to maintain breathing holes (Weddell) or possibly to exploit a patchy resource (walrus). The hypothesis is that females clump on islands because of several advantages offered by terrain or substrate: (1) parturition sites and nurseries for rearing pups; (2) no terrestrial carnivore predators (a necessity when animals are adapted for swimming and not for running); and (3) proximity to food. The latter is necessary to cut commuting costs in lactating sea lions and fur seals that make feeding excursions from the rookery (Costa, this volume). Proximity to food may also help ease the transition of phocid young from reliance on mother's milk to feeding on their own. But islands are limited, especially in some parts of the Pacific, as are suitable beaches on islands, and females must group to get

these benefits. There must also be additional factors causing clumping because females do not spread out from each other as much as they might even when space is abundant. Rather, they cluster tightly. This was evident when northern elephant seals began recolonizing San Miguel, San Nicolas and Año Nuevo Islands during the 1960s (Le Boeuf, 1972) and similar observations have been recorded for otariids (see Boness, this volume). Another factor in some species is that males intensify the clumping of females. In competing for females that gather loosely in one place, males of some species harass females by their repeated mating attempts and force them to clump closer together for self-protection. In northern elephant seals, a female that remains apart from a female group is accosted repeatedly by males and runs a higher risk of injury. Every breeding season, at least one out of every thousand females on the Año Nuevo rookery is killed by a male during a mating attempt (Le Boeuf, 1981; Le Boeuf & Mesnick, in press). In South American sea lions, *Otaria flavescens*, most females that give birth early in the season before a female group has formed become separated from their pups. One male claims the female and another the pup. They cannot approach each other and eventually, the pup dies from starvation (Campagna *et al.*, 1988).

Female resources, such as food and parturition sites, coupled with lack of predation may determine initial distribution in island breeding pinnipeds as primary factors before other factors become important. However, we know little about where pinnipeds get food, its availability and the cost of getting it. Work in progress using time-depth recorders, doubly labelled water techniques to estimate energetic costs at sea, transmitters and satellite tracking to determine location of feeding in relation to bathymetry and other variables, is promising (Davis *et al.*, 1983; Gentry and Kooyman, 1986; Le Boeuf *et al.*, 1986, 1988, 1989; Kooyman *et al.*, 1982; Croxall *et al.*, 1985; and see Chapter 6).

Pinnipeds are not found in large groups on expansive ice habitats (Smirnov, 1927; Burns, 1970; Fay, 1974; Burns *et al.*, 1981; Stirling, 1975). The environmental potential for polygamy is low because females are not forced to clump and there is no need for them to clump together (Emlen and Oring, 1977). *A priori*, a female gets little from joining other females. Clutton-Brock and Harvey (1976), writing about mammals in general, state: 'The advantages to a female of maintaining mating access to several males will in almost all circumstances, be less than the advantages to a male of maintaining mating access to several females'. Perhaps the most important impetus for not clumping on ice is that females find their food resources directly under it. Seals evolved on the ice edge; the waters under pack ice are evidently rich and continue to be exploited by several species. Females disperse widely to feed along the ice edge. There appears to

be no reason to avoid giving birth and copulating close to where feeding occurs. The female is supporting a fetus and it seems safe to assume that it is good to feed up to the point of giving birth. Under these circumstances, the onus is on the male to find females, which they do quite well. The fecundity rate is as high in females that breed in isolation on ice as it is in gregarious island-breeding pinnipeds: 85-94% in harp seals (Bowen *et al.*, 1981), 85% in bearded seals (Burns, 1967, 1981; Burns and Eley, 1978), 80% in Weddell seals (Stirling, 1971), 80-95% in ringed seals (McLaren, 1958; Smith, 1973a) versus 85-94% in grey seals (Mansfield and Beck, 1977; Harwood and Prime, 1978), 82.5-88% in southern elephant seals (*Mirounga leonina*) (Laws, 1956, 1960), 95% in northern elephant seals (Le Boeuf, 1979) and 90% in northern fur seals (Lander, 1981; Smith and Polacheck, 1981). The leopard seal may have an exceptionally low pregnancy rate (Siniff, 1981), but this observation is based on little data. Evidently, male distribution follows that of females.

2.4 DO THE UNIQUE FEATURES OF PINNIPEDS GIVE AN ADVANTAGE TO ONE SEX AND AFFECT THE FORM THAT MATING SYSTEMS TAKE?

Pinnipeds differ from land mammals in having a body type adapted to swimming and diving and, for at least some, in being able to copulate in the water. The marine-adapted body makes them vulnerable to attack by fleet-footed terrestrial predators which may explain why most of them stay close to the safety of the water. In addition, their insulation against the cold marine environment makes them prone to overheating on land, making it prudent to remain close to haul-out points. These morphological features make grouping more likely on islands than on ice because there are few terrestrial predators on ice (polar bears in the Arctic are one exception) and overheating is no problem because temperatures are low (Bartholomew, 1970).

In what way does the water medium shape the social fabric of reproduction in pinnipeds? The pagophilic phocids that are widely distributed on ice are thought to copulate in the water (Ortsland, 1964; Stirling, 1975, 1983; Merdsoy *et al.*, 1976). This conclusion is typically the result of not seeing copulation on ice, or from seeing it only rarely, e.g. harp seals (Kovacs, 1985). Indeed, many investigators that have studied these seals on ice for years have never seen a copulation above or below the water, (e.g. Don Bowen, John Burns, Kathy Frost, David Lavigne, Lloyd Lowry, and Ian Stirling, pers. comms). The only direct observation of copulation was in the under-water study of Merdsoy *et al.* (1976). For all the hours spent observing Weddell seals in the Antarctic, only one copulation, in the water,

has been recorded and reported (Cline *et al.*, 1971). Because of the aggressive courtship of males on ice floes, Siniff *et al.* (1979) concluded that the crabeater seal copulates on ice, but they never witnessed it. The capacity, if not the inclination, is there, for some seals will copulate on ice when conditions dictate, e.g. harp and hooded seals copulate above water when the ice freezes over (Ortland, 1964; Sergeant, 1965; Popov, 1966). When copulation has not been observed and it is not known whether mating occurs on the surface or under water, one can only speculate about mating systems. The circumstances on ice may bear little relationship to what is going on below in the water. Phrases that crop up in the literature such as 'mating takes place on ice', 'a monogamously breeding species', 'pairs last until mating', and 'appears polygynous', must be interpreted with caution.

Copulation usually occurs on land in pinnipeds that give birth on islands (Bartholomew, 1970; Stirling, 1975) however: (1) harbour seals and monk seals are an exception (Venables and Venables, 1957; Kenyon and Rice, 1959; Johnson and Johnson, 1978; Allen, 1984); (2) California sea lions mate in the water in the high temperatures of the Gulf of California and predominantly on land at major rookeries in southern California (Peterson and Bartholomew, 1967; Heath and Francis, 1983; Heath, 1985); (3) in all species, copulation in the water is possible and in many, occurs at low frequencies, e.g. less than 5% of copulations observed in northern elephant seals and northern fur seals (Le Boeuf, 1972; Bartholomew and Hoel, 1953).

Which sex determines where mating takes place and which benefits from mating on land or in the water? We lack data for mating on ice and in the water but a logical analysis by sex is instructive. A logical hypothesis derived from observations of terrestrial mammals is that females determine the location of copulation. Mating on land is advantageous to males seeking multiple mates but only occurs if females also benefit. When mating on land is not beneficial to females, mating will occur in the water because females can more readily determine whether copulation occurs and with whom.

Males increase their RS by obtaining multiple mates and, consequently, they are expected to take them where they find them. The more females aggregate, the easier the males' task. If females are grouped on land, a male will attempt to prevent other males from gaining access to them and he will copulate with as many as possible. This may involve fasting and never leaving his post, not being so aggressive as to cause females to run away or cross to another territory (cf. ungulates and birds on leks), defending his boundaries against other males, conserving energy and attracting the female to him, stealing females from adjacent males' territories or, more

infrequently, forcing copulation with an uncooperative female. Land is the male's element for this strategy. As far as we know, females do not group in the water (with exceptions like rafts of sea lions) and the three-dimensional environment makes it easier for females to escape.

Females require energy to produce and raise pups. Males do not help in this regard; they contribute only a small quantity of sperm to get the process started. Since a female's pup gets half of its genetic complement from the male, it is advantageous for the female to choose the 'best' sire. She should mate with a male of 'demonstrated fitness', a male with 'superior genes' wherever she finds him or he finds her (Selander, 1972; Trivers, 1972). The selection pressure is on getting the best genes, and the location of mating should serve this end for the female unless the decision is forced on her. I do not agree with Stirling (1983) that the location of mating is a legacy of ancestral forms and hence selectively neutral. Phylogenetic inertia may explain parental investment patterns in mammals, and other conservative deep-seated physiological designs, but location of mating strikes me as a most malleable behaviour, one that each sex might use to its advantage. For similar reasons, I part from Bartholomew (1970) who has reasoned that terrestrial copulations are explained by the fact that females stay on land until they come into oestrus. Females of some species do and others do not (e.g. *Zalophus*, *Arctocephalus pusillus*). His conclusion implies that the female is a passive vessel for endocrines that dictate her behaviour and that she is not under selective pressure to mate where it is most advantageous for her to do so.

On islands, female sea lions and fur seals select parturition sites where males are defending territories. In a sense, males provide a relatively undisturbed place for females to give birth and nurse. These males are adults that have bested their rivals, which is an indication of fitness. Females should mate with these males and do. Similar logic holds for mating with high-ranking elephant seal males. Male-male competition gives females information about which males are most fit. Copulation on land versus water is incidental to the main issue, which is that females should maximize their reproductive success. On land, the interests of females and successful males coincide. The 'victorious' males are eager to mate (being selected to pass on their genes) and these are the best partners for females who may be more apt to spread their genes if their male progeny have similar traits as their fathers.

If males are not competing amongst themselves on land or ice, a female does not benefit by mating out of the water. There is no *a priori* reason for a female that gives birth alone on the ice to mate with the first male that simply attends her. He may have a deleterious

gene that will strike him dead before he reaches his prime and that might be passed on to her offspring. At minimum, she should mate with an adult who has passed this test. It would be better still to let all males in the vicinity know that she is ready, cause them to compete on some arbitrary basis and mate with the winner. Inciting male-male competition is a common female strategy for identifying fit mates in many terrestrial mammals, birds and reptiles (Cox and Le Boeuf, 1977). The solitary female does not have much latitude for choice on ice. She may have more control in the water where she can get away from an unwanted suitor more easily, solicit specific males, incite several males to compete and mate with the winner, visit displaying males or males defending food-rich territories. Logic predicts that the attending male will try to keep the female on ice or copulate with her before she goes into the water where there are other competing males. If mating occurs in the water, the behaviour of females is expected to influence the mating strategies of males.

2.5 WHAT ARE THE CONSEQUENCES OF MATING ON LAND VERSUS IN THE WATER?

Sexual size dimorphism with males being larger is a consequence of harem defence, resource defence and male dominance polygyny in terrestrial mammals and all pinnipeds breeding on land. This is because of sexual selection; great size gives males an edge in fighting, which leads to access to females. Phocids that live in close association with ice or breed aquatically lack sexual size dimorphism. This is not necessarily because polygyny does not exist in these species. Sexual selection may be intense among pinnipeds mating under water but, because of the different medium, the consequences are different and may not be reflected in size. We do not know the male mating strategies under water but size is probably not as important in winning fights as it is on land. For example, to defend an under-water territory, swimming speed, agility, or the ability to dive for long periods may be more crucial.

If attracting a female separates successful from unsuccessful males, loudness or persistence of calls may be selectively advantageous. Bearded seals, harp seals, Ross seals, Weddell seals, walruses and California sea lions are extremely vocal under water (Schevill and Watkins, 1965; Ray and Schevill, 1967; Schusterman, 1967; Poulter, 1968; Schusterman and Balliet, 1969; Ray *et al.*, 1969; Ray, 1967; Møhl *et al.*, 1975; Thomas, 1979; Ray, 1981). Sex differences in calls are evident in several species. For example, only the male bearded seals sing during the breeding season (Ray *et al.*, 1969). Among Weddell seals, both sexes share a number of calls but trills, knocks,

cricket calls, 'eeyoo and guttural glugs' are unique to males (Thomas, 1979). The vocal component of male walruses' soliciting females to approach them in the water has been noted (Schevill *et al.*, 1966; Ray and Watkins, 1975; Sjare, 1989). One explanation for the extremely vocal behaviour of male California sea lions in air (Peterson and Bartholomew, 1969) and under water (Schusterman, 1967) comes from recent observations of oestrous females moving across territories to solicit a particular male (Heath, 1985). Incessant vocalizing in air and under water would be a way of getting the female's attention as well as letting other males know that the territory is being patrolled. Auditory and visual displays may signal more than adulthood and readiness to mate: the behaviour may serve as an indicator of health and vigour. It takes energy to emit complex, high intensity calls or evolve elaborate colourful visual displays. Parasites may limit the extent of such signalling thereby providing females with a cue to male fitness. According to Hamilton and Zuk (1982), females would be favoured who could discriminate among males according to parasite load and damage. They present supportive evidence on some birds but no one has tested this hypothesis with seals. This may be one purpose of the elaborate, stereotyped bladder nose and blood-red septum displays of male hooded seals, (Berland, 1965) that are given in air and under water or the ribbon markings on ribbon seals that are darker in males than females (Burns, 1981).

Are females choosing among these singing and displaying seals under water? How do mating arrangements differ in seals that are migrating or borne passively on floating ice from those that are more stationary or that feed on the bottom like bearded seals? What are the optimal mating strategies for males under water? They might set up territories near places where females gather. They might intercept the females, hold them, attract them with sound, visual displays, or resources, or they could get to a female first and stay with her.

2.6 CONCLUSIONS

Mating systems in pinnipeds, like those of terrestrial mammals and birds, are determined by two classes of phenomena: phylogenetic inertia in parental investment pattern that sets limits on the reproductive strategies of each sex, and environmental variables that affect the optimal way for each sex to behave in order to maximize their reproductive success. The latter include physical variables like the substrate and temperature, ecological variables like food, predators and birthing sites, and social variables like density, the sex ratio and what the other sex is doing.

Pinnipeds follow the mammalian rule of polygyny more closely

than terrestrial mammals. Monogamy of the type seen in terrestrial carnivores, and primates, where males help females feed, protect or carry offspring, is absent. The mating system of pinnipeds is least like those of social canids - , animals with whom they share a recent common ancestor. Perhaps this is because food is distributed differently in the sea and may be less limiting, the prey are smaller than the predators, the female can rear her precocial young alone, and this frees males to pursue multiple matings. All pinniped species appear to be polygynous but the degree varies considerably from extreme to moderate to perhaps slight. Slight polygyny is suspected in pagophilic seals from their distribution patterns but mating is almost exclusively under water and, consequently, we are ignorant of the frequency and nature of mating arrangements. Most island breeding pinnipeds show a higher degree of polygyny than terrestrial mammals and birds, and in those pinnipeds that are sexually dimorphic the size discrepancy between the sexes exceeds that seen in terrestrial mammals.

The distribution of female pinnipeds, like that of terrestrial mammals, may be determined in a general way by resources and predators. The circumstances that lead to females aggregating are more varied among terrestrial mammals than among pinnipeds. Male mating strategies intensify female clumping in some pinnipeds. Male distribution follows female distribution.

Mating in the water may give an element of control to females that is lacking in their terrestrial counterparts. Aquatic mating selects for different male mating strategies and secondary sexual characteristics than those associated with terrestrial mating. Speculations about the underwater mating strategies and behaviour of pinnipeds need to be studied.

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3

Behavioural ecology of pinniped neonates

W. D. Bowen

3.1 INTRODUCTION

Although the social organization and behaviour of pinnipeds has received considerable attention, the focus of much of this work has been on adults (e.g. Bartholomew, 1970; Stirling, 1975a, 1983; Le Boeuf, 1978; Jouventin and Cornet, 1980; Gentry and Kooyman, 1986). Generally, the problems faced by the pup and the behavioural adaptations which have evolved to cope with them are given cursory treatment if mentioned at all. In this chapter, I review what is known about the early development of seals with the objective of gaining an insight into the factors which have shaped their life history patterns and to point out the current deficiencies in our understanding of pinniped neonatal behaviour. Because of gaps in information on many critical points, many of the conclusions drawn in this chapter must be considered tentative. Wherever possible, I have tried to identify unanswered questions in the hope of stimulating research in these areas.

It will be obvious to those who have studied pinnipeds even in a casual way, that in addition to differences between species, there are striking differences in the life history patterns of the two major families of pinnipeds, namely the Phocidae and the Otariidae (Bonner, 1984). In most species, phocid mothers fast during the lactation period, relying on energy stored prior to parturition to support the rapid fattening and growth of their pup over a nursing period which is generally less than two months in duration. On the other hand, otariid mothers are able to store adequate energy to support only the first week of a lactation period which may last one to two years. Thereafter, mothers alternate between foraging trips of 1-6 days at sea and several days at the rookery when pups are able to suckle.

Stirling (1975a, 1983) has argued that ecological factors are primarily responsible for the evolution of mating and social systems in pinnipeds, but notes that phylogeny has also been influential. He considered availability and access to suitable habitat for parturition as the most important factor leading to the divergence in mating systems of phocids and otariids. Considered as a group, most phocid species are ice-breeding whereas otariids are land-breeding. This coupled with predation pressure or the lack of it (Stirling, 1977) has had a dominant influence on the behaviour of pinnipeds.

The thesis of this review is that the nature of the breeding habitat, which largely determines the attendance pattern of mothers during lactation and the nature and duration of the mother-pup interaction, has exerted a strong influence on the major features of the ecology and behaviour of the neonate. Differences in the nature of preweaning mortality, postparturient behaviour, changes in neonatal behaviour (including suckling) over the period of lactation, mother-pup recognition, weaning and post-weaning behaviour of pups can all be traced back to the constraints imposed by differences in breeding habitat and the need for pinnipeds to give birth on land or ice and secure food from the sea (Bartholomew, 1970).

3.2 LIFE HISTORY CHARACTERISTICS

3.2.1 Time and place of birth

In this section I review the seasonal distribution of births and the characteristics of the nursing habitat of pinnipeds, as these are thought to exert a strong influence on the evolution of behaviour. In most species, pups are born over a period of two or three months in the late winter, spring or early summer (King, 1983). In general, this means that pups will begin independent feeding at a time of the year of increasing marine production (Cushing, 1975). Within this period, the distribution of births tends to be skewed to the right and in some species the majority of pups are born over only a few days. For example, in the harp seal (*Phoca groenlandica*) most of the several hundred thousand pups off southeastern Labrador are born over 2 or 3 days in early March and yet newborn pups can still be found on 24 March (Myers and Bowen, 1989). In several species, such as the harbour seal (*Phoca vitulina richardsi*) and to a lesser extent the larga seal (*P. largha*), the protracted temporal distribution of births appears to be related to their widespread latitudinal distribution. The very long period of pupping in the Galapagos sea lion (*Zalophus californianus wollebaeki*) and the Galapagos fur seal (*Arctocephalus galapagoensis*) and in monk seals (*Monachus monachus* and *M.*

schauinslandi) is correlated with their distribution at low latitudes, a more favourable climate throughout the year, and less pronounced seasonal variation in marine productivity than found in temperate and arctic waters (Cushing, 1959).

The seasonal distribution of births in grey seals (*Halichoerus grypus*) is particularly unusual among phocids. There are differences of almost six months in the pupping dates in individual grey seal colonies (autumn in Britain and early to mid-winter in Canada and the Baltic), although, as in most other species, there is normally little variation between years in the same colony. Based on the analysis of variation in mean birth dates of grey seals on the Farne Islands, Northumberland and also geographic differences in the date of pupping in the Baltic, on Sable Island, Canada and other colonies around England, Coulson (1981) found a relationship between sea surface temperatures just prior to the period of delayed implantation and pupping date. On the assumption that the period of gestation is fixed, Coulson suggested that the timing of pupping is most likely affected by factors which end the period of delayed blastocyst development. However, Coulson provided no evidence that in fact the period of delayed implantation differs between colonies in a way consistent with the hypothesis or a mechanism whereby this variation could be achieved. It is also possible that autumn pupping of grey seals in the UK is a response to the strong autumn peak in primary productivity in the North Sea (Cushing, 1975).

Pups are born on landfast ice ($n=3$) or floe ice ($n=10$), in 13 of the 18 (72%) extant phocid species. In the other five species, pups are born primarily on mainland or island rookeries. Several species give birth on ice in part of their range (i.e. grey seals in the Gulf of St Lawrence, Canada (Mansfield and Beck, 1977) and in the Baltic (Curry-Lindahl, 1970); harbour seals in the Gulf of Alaska (Calambokidis et al., 1987); and southern elephant seals (*Mirounga leonina*) on Signy Island (Laws, 1953)). In contrast, all 14 species of otariids give birth on land. The only surviving member of the Odobenidae, the walrus (*Odobenus rosmarus*), is also an ice-breeding species. Thus the selection of pup-rearing habitat is a fundamental difference in the ecology of these two families of pinnipeds, a difference which has had a major influence on the mating system (Bartholomew, 1970; Stirling, 1975a, 1983) and as we shall see on the behavioural ecology of the neonate.

Whether on land or ice, most seals are born into an environment which affords little protection against unfavourable weather or potential predators. The ringed seal (*Phoca hispida*) and Baikal seal (*P. sibirica*) are exceptional in this regard. In these species, females construct birth lairs from wind-compacted snow drifts around ice hummocks and along pressure ridges (Pastukhov, 1969; Smith and

Stirling, 1975, 1978). Ringed seal birth lairs have a main chamber measuring approximately 2.5 × 3.5 m and smaller tunnels off the central cavity dug by the pup. Lairs serve both as thermal shelter and concealment from predators such as arctic foxes, *Alopex lagopus* and polar bears, *Ursus maritimus* (McLaren, 1958; Smith and Stirling, 1975; Smith and Hammill, 1981).

3.2.2 Duration of the lactation period

There have been several reviews of the length of the lactation period in pinnipeds in recent years (King, 1983; Bonner, 1984; Bowen *et al.*, 1985; Kovacs and Lavigne, 1986a; Anderson and Fedak, 1987; Oftedal *et al.*, 1987). However, as the duration of the mother-pup association is likely to exert an important influence on the development of the neonate, it is valuable to include the most recent data on the duration of the lactation period in this chapter. As Oftedal *et al.* (1987) have noted, the quality of data on lactation length is variable and often poorly documented. Thus, in constructing Table 3.1, I have tried to indicate the type and quality of data used by the author to arrive at an estimate. Where available, I have only included estimates supported by quantitative data. Estimates of lactation duration based on the dates of births and sightings of independent pups tend to be too long. For example, early estimates of the length of lactation in harp and hooded (*Cystophora cristata*) seals were about 20 days (Chapskii, 1964) and 7–12 days (Shepeleva, 1971; Sergeant, 1976), respectively – significantly longer than present values. Similarly, recent data presented by Shaughnessy and Kerry (1989) for the crab-eater seal (*Lobodon carcinophagus*), although based on few samples, suggest that lactation may be as short as 17 days rather than 28 days as previously reported (Table 3.1). For the same reason, we might expect to find that species such as the larga, Caspian (*Phoca caspica*), and ribbon (*P. fasciata*) seals have shorter lactation periods than current information would suggest.

Quantitative estimates of lactation length, based on following known-age individuals to the end of nursing, are available for only 8 of 18 species of extant phocid species and 2 of 15 otariids (Table 3.1). In the remaining species estimates are often derived from survey-data estimates of peak pupping dates and observations of what are assumed to be independent pups, but frequently only unsupported qualitative statements are provided. The difficulty in obtaining quantitative estimates of lactation length is clearly greater in otariids than in phocids because of the need to follow individual mother-pup pairs over periods of a year or more. The remote location of the whelping areas has hampered efforts to determine the duration of lactation in many ice-breeding phocids in both the northern and southern hemispheres.

Table 3.1 Duration of lactation period in pinnipeds

				Lactation Duration (days)	Quality	Data ^a	Weaning	Source
PHOCIDAE	Floe-ice	Hooded seal		4		n = 16	abrupt	Bowen <i>et al.</i> (1985)
		Harp seal		12		n = 21	abrupt	Kovacs (1986)
		Bearded seal		12-18		BW Int	unknown	Burns (1967)
		Grey seal		17	Sable Is. Isle of May	n = 38	abrupt	Boness (1979)
		Caspian seal		20-25		n = 30	abrupt	Kovacs (1986)
		Ribbon seal		21-28		n.d.	unknown	Krylov <i>et al.</i> (1980)
		Largha seal		14-21		n.d.	abrupt	Burns (1981)
		Crabeater seal		≈ 28		BW Int	unknown	Naito and Nishiwaki (1972)
				≈ 17 ^b		n.d.	abrupt	Siniff <i>et al.</i> (1979)
		Ross seal		≈ 30		n.d.	unknown	Shaughnessy and Kerry (1989)
Phocidae	Fast-ice	Leopard seal		≈ 30		n.d.	King (1983)	
		Weddell seal		50	Bay of Whales	n = 18	unknown	King (1983)
				53	McMurdo Sound	n = 19	gradual	Lindsey (1937)
				33-44	McMurdo Sound	n = 10		Thomas and DeMaster (1983a)
Otariidae	Ringed seal			≈ 60		BW Int	unknown	Kaufman <i>et al.</i> (1975)
		Baikal seal		41-48		BW Int	unknown	McLaren (1958), Smith (1973), Hammill (1987)
		Southern elephant seal		60-75		n.d.	abrupt	Pastukhov (1975)
				23	Macquarie Is.	n = 60		Carrick <i>et al.</i> (1962)
				23	Marion Is.	n = 28		Condy (1980)
				24	South Georgia	n = 12		McCann (1982)

Northern elephant seal	27	Ano Nuevo	n = 44	abrupt	Reiter <i>et al.</i> (1978)	
	28	Ano Nuevo	n = 41		Le Boeuf <i>et al.</i> (1972)	
Harbour seal (<i>vitulina</i>) (concolor)	26	Ano Nuevo	n = 6		Costa <i>et al.</i> (1986)	
	26	Schleswig-Holstein	BW Int		Drescher (1979)	
	23	Sable Island	n = 7		Godsell (1988)	
	24	Sable Island	n = 52	abrupt	Muelbert and Bowen (unpubl.)	
		Miquelon			Renouf and Diemand (1984)	
(<i>richardsi</i>)	35-42		BW Int		Bigg (1969)	
(<i>stejnegeri</i>)	28-42		BW Int		Newby (1973)	
	28 ^c				Naito and Nishiwaki (1972)	
Hawaiian monk seal	39				Alcorn (1984)	
	41				Boness (in press)	
Mediterranean monk seal	42-49				Boulva (1979)	
Antarctic fur seal	117	South Georgia	n = 8	abrupt	Dodge <i>et al.</i> (1986)	
	112	Marion Is.	n.d.		Kerley (1983)	
Northern fur seal	118		n = 65	abrupt	Gentry and Holt (1986)	
Steller's seal lion	180-365		n.d.	unknown	Pitcher and Calkins (1981)	
	240-365		n.d.		Mate and Gentry (1979)	

[contd over]

Table 3.1 contd

	<i>Whelping Habitat</i>	<i>Species</i>	<i>Lactation Duration (days)</i>	<i>Data^a</i>	<i>Weaning</i>	<i>Source</i>
	Sub antarctic fur seal New Zealand fur seal	300-330 300-365		BW Int BW Int	unknown unknown	Kerley (1983) Stirling (1971), Miller (1975), Mattlin (1981)
Cape fur seal		300-330	n.d.	gradual?	Rand (1955); Stirling (1970)	
California sea lion		=365	n.d.	gradual	Peterson and Bartholomew (1967), Boness <i>et al.</i> (in press)	
Australian sea lion		=365	n.d.	unknown	Marlow (1975)	
Southern sea lion		=365	n.d.	unknown	Hamilton (1934)	
Hooker's sea lion		=365	n.d.	unknown	Marlow (1975)	
Galapagos sea lion		180-365 ^d	gradual	gradual	Trillmich (1981, 1986b)	
South American fur seal		365-730	n.d.	unknown	Vaz-Ferreira (1975)	
Galapagos fur seal		=730 ^e	gradual	gradual	Trillmich (1986a)	
ODOBENIDAE	Walrus	=730	n.d.	gradual?	Mansfield (1958b), Fay (1982)	

^a *n*, number of individuals followed to weaning [i.e. quantitative estimate]; BW Int, interval between most births and observations of apparently independent young; n.d., no data given to support estimate.

^b Based on estimate birth weight, weaning weight (*n* = 4) and rate of mass gain during lactation (*n* = 2).

^c Based on tagged pups but *n* not given.

^d 32 of 40 females had weaned their pups before giving birth again 1 year later.

^e 18 of 46 2-year-olds weaned.

Despite the need for improved information, it is clear that the length of lactation is highly variable both within and between pinniped families (Table 3.1). In phocids, this variation likely reflects differences in the stability, predictability and harshness of the whelping habitat (Stirling, 1975a; Bonner, 1984; Bowen *et al.*, 1985; Oftedal *et al.*, 1987). Species which give birth on floe-ice have the shortest lactation periods ($x = 18.3 \pm 7.6$ days, * $n = 9$). One floe-ice species, the hooded seal, nurses its young for only 4 days - the shortest lactation period of any mammal (Bowen *et al.*, 1985). Destruction of ice suitable for nursing pups by rising temperatures and spring storms and predation by polar bears may have been important selection pressures contributing to the evolution of such an abbreviated lactation in this species (Bowen *et al.*, 1985).

Available data indicate that fast-ice-breeding species nurse their young longer ($x = 57.1 \pm 9.0$ days, $n = 3$) than those which give birth on land ($x = 31.9 \pm 10.2$ days, $n = 5$) (Table 3.1). The two northern hemisphere species, the ringed seal and Baikal seal which are among the smallest pinnipeds, construct birth lairs which serve as protection against the harsh climate and predators (McLaren, 1958; Pastukhov, 1975; Smith and Stirling, 1975; Smith, 1976; Lydersen and Gjertz, 1984). Thus, the relatively long lactation period in these species may reflect the advantage of remaining in the lair for as long as possible to reduce both the risk of predation and the pup's energy requirements. This may be particularly important for these small, slow-growing species. The other fast-ice species is the Weddell seal (*Leptonychotes weddelli*), a relatively large phocid that does not construct birth lairs. Oftedal *et al.* (1987) suggest that protection from aquatic predation by the leopard seal (*Hydrurga leptonyx*) may have contributed to the evolution of the relatively long 50-day lactation period in this species.

With the exception of the Antarctic (*Arctocephalus gazella*), Galapagos and northern (*Callorhinus ursinus*) fur seals, most otariids suckle their young for 9–12 months and two species suckle for up to 24 months (Table 3.1). The relative consistency of the duration of lactation among these species perhaps can in part be attributed to the fact that they all give birth on land. However, some of the variation we see may be associated with differences in environmental predictability and climate. Gentry *et al.* (1986) argue that high latitudes with harsh weather and strong but predictable seasonality seem to favour short lactation, whereas low latitudes with less seasonality but unpredictable environmental oscillations such as El Niño, seem to favour longer lactation. Trillmich and Limberger (1985) suggest

* Throughout the text, means are given with the standard deviation unless otherwise stated.

that the unusually long lactation period of about 2 years in the Galapagos fur seal may buffer young from the effects of minor El Niño events. However, as Oftedal *et al.* (1987) have pointed out, having considered the two subpolar species, there is no evident relationship between lactation length and latitude in the remaining nine species. Perhaps when more precise data on lactation length are available the effect of environmental variation on the duration of nursing will be more apparent.

3.2.3 Some physical characteristics of the newborn

(a) Pelage

Pelage colour of pinniped neonates appears to reflect the evolutionary histories of the Phocidae and Otariidae (Scheffer, 1958; Ling, 1978). Otariids are thought to have originated in the North Pacific Basin and dispersed to colonize mainly the tropical and subtropical oceans, whereas phocids arose in the North Atlantic in arctic and subarctic waters, although the monachines group had a more southern distribution than did the phocene group (Reprenning, 1980).

The dark brown to black pelage of otariid pups (Ling, 1978) is generally shed 2–4 months postpartum (Table 3.2). Thus the neonatal moult takes place about the time or shortly after pups begin to enter the water (see Section 3.3.3). This corresponds to the first third of the lactation period in most otariids, but to the middle and the end of the nursing period in the Antarctic fur seal and the northern fur seal, respectively.

The situation is considerably more complex among phocids. The natal pelage of northern hemisphere ice-breeding phocids is white with the exception of the bearded seal (*Erignathus barbatus*), the hooded seal, and harbour seals (*Phoca vitulina*) (Table 3.2). The bearded seal has a brownish-grey coat with up to four indistinct whitish spots on its back (Chapskii, 1938). Burns (1967) has suggested that the dark colour of the bearded seal may be an adaptation reflecting the large amount of time spent in the water by the pup from an early age, perhaps to avoid aquatic predation, although it seems more likely to reflect an evolutionary link to the tropical monachines (McLaren, 1975). The hooded seal sheds its light grey pelage before birth (Beloborodov and Potelov, 1966; W. D. Bowen, unpubl.). The harbour seal also sheds its whitish fetal pelage before birth, but there appears to be geographic variation in the proportion of the population undergoing this prenatal moult. On Sable Island, Boulva (1975) reported that between 70% and 85% of harbour seal pups had moulted in utero, whereas, in the eastern Pacific, Shaughnessy and Fay (1977) indicate that >95% of harbour seal pups have moulted at

Table 3.2 Initial pelage colouration and the timing of the first moult in pinnipeds

Family	Species	Colour of first pelage	First Moulting			Source
			Onset [d]	Duration [d]	Location	
PHOCIDAE	Hooded seal <i>Cystophora cristata</i>	grey	before birth			Bowen (unpubl.)
	Harp seal <i>Phoca groenlandica</i>	white	10	10-15	White sea	Chapskii (1964)
	Bearded seal <i>Erignathus barbatus</i>	brownish-grey	12-18			Chapskii (1938), Davies (1949), Bowen and Stobo (unpubl.)
	Grey seal <i>Halichoerus grypus</i>	white	9-15	10		Frost and Lowry (1981)
	Caspian seal <i>Phoca caspica</i>	white	14-28	=30		Burns (1981), Tikhomirov (1964), Naito and Nishiwaki (1972)
	Ribbon seal <i>Phoca fasciata</i>	white	completed by	35		
	Largha seal <i>Phoca largha</i>	white	14-28			
	Crabeater seal <i>Lobodon carcinophagus</i>	greyish-brown	14-21			Ling (1978)
	Leopard seal <i>Hydrurga leptonyx</i>	greyish-white	7			Ling (1978), Lindsey (1937), Mansfield (1958a)
	Weddell seal <i>Leptonychotes weddelli</i>	brown	14	30	South Orkneys	Thomas and DeMaster (1983a)
		18	17		McMurdo Sound	Smith and Hammill (1980), Frost and Lowry (1981)
	Ringed seal <i>Phoca hispida</i>	white	14-28	=30		
	Baikal seal <i>Phoca sibirica</i>	white	14-28			
	Ross seal <i>Ommatophora rossi</i>	grey	14-21			
						Ling (1978)

(contd over)

Table 3.2 contd

Family	Species	Colour of first pelage	First Molt			Source
			Onset [d]	Duration [d]	Location	
Southern elephant seal <i>Mirounga leonina</i>	black	10 14 3% before birth	24 10	South Georgia Marion Is. Signy Is.	Laws (1953) Carrick et al. (1962)	
Northern elephant seal <i>Mirounga angustirostris</i>	black	=28			Laws (1953) Le Boeuf et al. (1972), Reiter et al. (1978)	
Harbour seal <i>Phoca vitulina vitulina</i>	grey	70-85% before birth		Sable Is.	Boulva (1975)	
<i>Phoca vitulina concolor</i>	grey	>95% before birth			Burns (1970), Naito (1973)	
<i>Phoca vitulina stejnegeri</i>	grey	>95% before birth			Bishop (1967), Fisher (1952)	
<i>Phoca vitulina richardsoni</i>						
Hawaiian monk seal <i>Monachus schauinslandi</i>	black	28	≈ 14		Kenyon and Rice (1959)	
Mediterranean monk seal <i>Monachus monachus</i>	black	completed by 28-42			Kenyon (1981)	
Antarctic fur seal <i>Arctocephalus gazella</i>	brownish-black	50-60	30-40		Bonner (1968), Kerley (1983)	
Northern fur seal <i>Callorhinus ursinus</i>	black	60-90			Gentry (1981)	
Steller's sea lion <i>Eumetopias jubatus</i>	brown	180			Ling (1978)	
California sea lion <i>Zalophus californianus</i>	brown	90-120 120-150			Ling (1978) Trillmich (1981)	
<i>Z. c. wollebaeki</i>						
OTARIIDAE						

Southern sea lion	black	30	Vaz-Ferreira (1981)
<i>Otaria byronia</i>			
Australian sea lion	brown	60	Marlow (1968)
<i>Neophoca cinerea</i>			
Hooker's sea lion	brown	30-90	Ling (1978), Walker and Ling (1981)
<i>Phocarcos hookeri</i>			
Subantarctic fur seal			
<i>Arctocephalus tropicalis</i>	black	90-120	Bester (1977), Kerley (1983)
New Zealand fur seal	black	60-90	Ling (1978)
<i>Arctocephalus forsteri</i>			
South African fur seal	black	60-65	Rand (1956)
<i>Arctocephalus pusillus</i>			
South American fur seal	black	28-35	Bonner (1981)
<i>Arctocephalus australis</i>			
Jaun Fernandez fur seal	black		Bonner (1981)
<i>Arctocephalus philippi</i>			
Galapagos fur seal	black	= 120	Trillmich (1981)
<i>Arctocephalus galapagoensis</i>			
Guadalupe fur seal			
<i>Arctocephalus townsendi</i>	black		Bonner (1981)
ODOBENTIDAE			
Walrus	white	60-90 before birth	Ling (1978)
<i>Odobenus rosmarus</i>			

birth. Although grey seals now generally give birth on land over much of their range, pups are also white at birth, likely reflecting an evolutionary history as an ice-breeding species (Davies, 1957; Scheffer, 1958; McLaren, 1960). Ice-breeding grey seals are found in the Baltic Sea (Curry-Lindahl, 1970) and in the southern Gulf of St. Lawrence where production accounts for about half of the pups born in eastern Canada (Zwanenburg and Bowen, 1990).

The newborn pups of ice-breeding phocids in the southern hemisphere are brown to greyish-brown in the Weddell seal, and the crab-eater seal (Lindsey, 1937; Mansfield, 1958a; Thomas and DeMaster, 1983a; Ling, 1978) are reportedly light grey to greyish-white in the leopard seal, and the Ross seal, *Ommatophoca rossi* (Ling, 1978).

The land-breeding monachines, the monk seals and elephant seals (*Mirounga*), give birth to pups with black pelage (Scheffer, 1958; Ling, 1978), suggesting no evolutionary experience with predators on ice (Stirling, 1983). Thus, species that evolved in cold waters are covered with a white natal coat, an adaptation to reduce detection by predators on ice or to increase the efficiency of solar heating (Øritsland, 1971). Those species that evolved in warm oceans, namely the otariids and the monachine group of phocids, are covered with a dark pelage at birth.

(b) Size and growth

The body mass of pinniped newborns ranges from about 3 kg in the Caspian seal and the New Zealand fur seal (*Arctocephalus forsteri*) to 60 kg in the Pacific walrus (*Odobenus rosmarus divergens*) (King, 1983). Based on data in Table 3.3, at birth phocids ($x = 20.7 \pm 12.2$ kg, $n = 12$) are about three times heavier than otariids ($x = 7.1 \pm 5.76$ kg, $n = 7$, including Steller's sea lion (*Eumatopias jubata*) data from King (1983) not shown in Table 3.3). However, when expressed relative to maternal mass, there is no significant difference between phocid ($x = 9.0 \pm 2.7\%$) and otariid ($x = 10.9 \pm 2.8\%$) birth weights (see Costa, this volume).

There is considerable variation in daily mass gain within and between phocid species (Table 3.3) during a brief lactation period of generally less than 2 months (Table 3.1). A number of proximate factors undoubtedly contribute to this variation: maternal milk production and energy content of the milk, the pattern of maternal attendance, energy intake by the pup, and the rate of energy expenditure by the pup. This will depend on body size, ambient air and/or sea temperature, the proportion of time spent in these different environments, and the overall level of activity. Risk of predation and premature separation from the mother may also have influenced growth rate (Bowen *et al.*, 1985). Unfortunately, this kind of information is available for relatively few species or populations within

species. Hence, it is difficult to examine the observed variation in mass gain in relation to ecological hypotheses (but see Figure 6.4). However, studies of the behavioural ecology of pups during lactation may provide insight into differences between populations such as the greater rate of mass gain by grey seal pups on Sable Island, Canada compared with those in the UK, and the differences in the rate of mass gain among several populations of the southern elephant seal (Table 3.3).

The rapid fattening of phocid pups results in a weaning mass two to five times ($x = 3.2$ times, $n = 11$) that at birth (Table 3.3). However, despite this variation, relative body mass at weaning is remarkably consistent across species, with pups weighing about one-quarter to one-third of maternal mass in the 11 species for which data are available. The value of 16% in the ribbon seal and 43% in the crabeater seal may be an artefact of our current uncertainty in estimates of weaning and maternal mass in these species.

Mass gain by phocid pups is inversely related to the length of the lactation period (Figure 3.1), when expressed relative to maternal metabolic mass (Oftedal, 1984; Bowen *et al.*, 1985). This relationship likely reflects a reduction in the mother's overhead costs (i.e. her non-milk production costs during the lactation period), such that a higher proportion of the female's stored energy can be transferred to her pup (Fedak and Anderson, 1982; Bowen *et al.*, 1987). However, it may be significant that the lowest relative mass gains are found in species such as the harbour, Hawaiian monk (*Monachus schauinslandi*) and Weddell seal in which the pups are relatively active and begin to swim early in lactation thereby increasing energy expenditure.

Information on otariids is less extensive, with reasonable data being available for only 6 of the 15 species (Gentry *et al.*, 1986). Nevertheless, it is clear that the rate of mass gain is considerably lower in otariids than it is in phocids (Oftedal *et al.*, 1987), and there is much less variation among species (Table 3.3). Reported mass gains by otariid neonates range from 0.0450 kg/day to 0.135 kg/day during lactation. Although otariid pups gain mass at an overall lower rate than phocid neonates, they are significantly (*t*-test, $P = 0.037$) heavier at weaning, relative to maternal mass ($x = 37.8 \pm 10.3\%$ for 6 otariid species versus $x = 28.3 \pm 6.4\%$ for 10 phocids, excluding the doubtful low value for the ribbon seal).

(c) Preweaning mortality

In this section I review the causes and magnitude of preweaning pup mortality in pinnipeds. Given species differ in the attendance of pups by mothers, the nature of the nursing habitat, and the overall

Table 3.3 Mass gain of pinniped neonates during lactation (sample size in parentheses)

Family	Species	Maternal ^a wt (MW) (kg)	Birth wt (BW) (kg)	% BW/MW	Daily wt Gain (WG) kg d ⁻¹	Relative wt Gain (WG MW ^{-0.75}) g kg ^{-0.75} d ⁻¹	Weaning wt (%) (WW)/MW	Source
PHOCIDAE	Hooded seal	179.0 [13]	22.0 [21]	12.3	7.1 [37]	145	23	1.9 Bowen <i>et al.</i> (1985)
	Harp seal	134.0 [28]	9.6 [40]	7.2	2.3	58	26	3.6 Bowen (unpubl.)
	Bearded seal	130.0 [A] 250.3 [5]	10.8 [40] 33.6 [13]	8.3 13.4	2.2 [21] 3.4	57 54	27 34	3.2 Stewart and Lavigne (1980) 2.5 Burns (1967, 1981), Burns and Frost (1979)
Grey seal								
Sable Is. UK	190.4 [6] 174.5 [45]	16.3 [28] 14.6 [95]	8.6 8.4	2.7 [40] 1.8 [42]	53 37	33 26	3.8 Bowen and Stobo (unpubl.) 3.1 Coulson (1960), Coulson and Hickling (1964), Fedak and Anderson (1982), Anderson and Fedak (1987)	
Crabeater seal	220 [5]	20	11.0	4.2 [2]	74	43	4.7 Schaugnessy and Kerry (1989)	
Ribbon seal	141.0	10.5	7.4			16	2.1	
Weddell seal	447.0 [9] 62.0 [est]	24.0 [13] 4.5	5.4 7.3	2.0 [13] 0.76	21 35	21	3.9 Tedman and Green (1987)	
Ringed seal								
S. elephant seal								
Macquarie Is.	≈400.0	36.9 [46]	9.4	2.3	26	22	2.4 Carrick <i>et al.</i> (1962)	
Marion Is.	38.5 [15]	42.5 [14]	3.6				2.8 Breyden (1968)	
South Georgia		2.6					2.5 Condy (1980)	
Signey Is.	≈608.0	44.0 [6]	4.7				2.8 McCann (1980)	
N. elephant seal	504.0 [6]	47.4 [15]	7.0	5.2 [15]	39	26	3.7 Laws (1953)	
Harbour seal	84.5 [95]	40.0 [5] 10.8 [175]	7.9 12.8	3.2 [5] 0.6 [93]	30 22	26 30	3.3 Costa <i>et al.</i> (1986) 2.3 Bowen, Oftedal and Boness, (unpubl.)	
Hawaiian monk seal	272.0 [est]	15.6 [17]	5.7	1.4	21	26	4.6 Wirtz (1968), Kenyon (1981)	

OTARIIDAE	Antarctic fur seal	47.3 (79)	5.9 (27)	12.5	0.079 (27)	4	31	2.6
	Northern fur seal	37.0	5.6	15.1	0.065	4	35	2.3
	S. African fur seal	57.0	5.7	10.0	0.080	4	44	4.4
	Galapagos fur seal	27.0	3.6	13.3	0.051	4	56	4.2
	New Zealand fur seal	≈45.0	3.6	8.0	0.045	3	≈30	3.7
	California sea lion	88.0 (9)	8.4 (39)	9.6	0.132	5		
	Galapagos sea lion	80.0	≈6.0	7.5	0.135	5	≈31	≈4.2

^a Initial maternal mass.

A = estimate from asymptotic growth curve.
est = estimate.

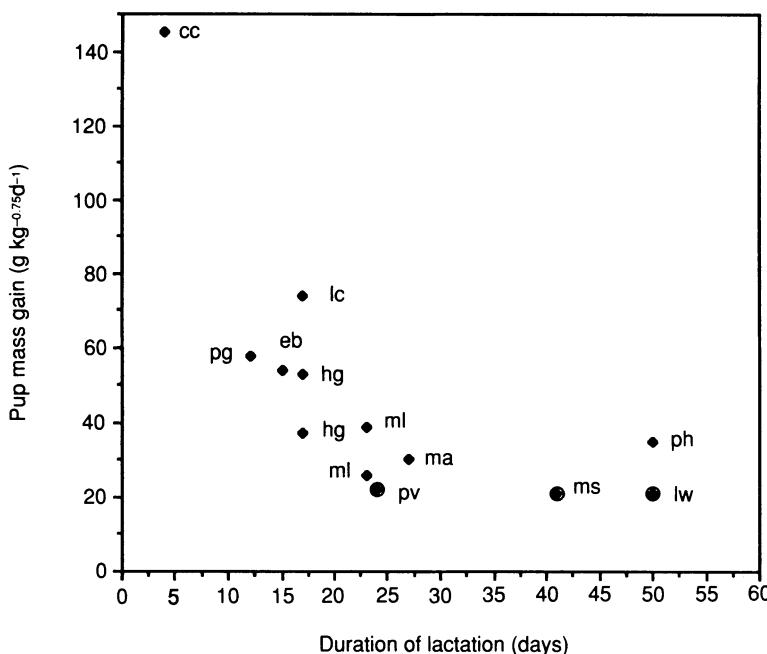


Figure 3.1 Mass gain of phocid pups during lactation relative to maternal metabolic mass ($\text{g kg} \text{maternal mass}^{-0.75} \text{d}^{-1}$) in species which do not normally enter the sea until after weaning (solid symbols) and those that spend considerable time in the sea before weaning (circled symbols). cc: *Cystophora cristata*, eb: *Erignathus barbatus*, hg: *Halichoerus grypus*, lc: *Lobodon carcinophagus*, lw: *Leptonychotes weddelli*, ma: *Mirounga angustirostris*, ml: *Mirounga leonina*, ms: *Monachus schauinslandi*, ph: *Phoca hispida*, pg: *Phoca groenlandica*, pv: *Phoca vitulina*.

density of individuals in breeding colonies, we might expect differences in the magnitude and causes of pup mortality during the lactation period. Unfortunately, information on preweaning pup mortality is available for less than half of pinniped species. As expected, our knowledge of preweaning mortality is better in phocids which have a relatively short lactation period.

Based on available information, it is clear that preweaning mortality within and between species can be highly variable (Table 3.4). Four factors appear to influence the level of pup mortality:

1. the nature and topography of nursing habitat;
2. weather or more generally, environmental variation;
3. population density; and
4. disturbance caused by adults on the rookery. These are schematically depicted in Figure 3.2.

We might expect that the pups of floe-ice breeding species, such as the harp seal, would experience high mortality as a result of being reared on an inherently unstable habitat. However, this is not generally the case. In fact, preweaning mortality in harp seals is among the lowest recorded for any pinniped (Table 3.4). However, ice break-up caused by storms can result in increased levels of mortality in harp seals (Popov, 1971) and other ice-breeding species. Preweaning pup mortality in Weddell seals is generally in the range of 3–16% (Thomas and DeMaster, 1983a). However, early break-up of ice resulted in 30–50% mortality at the South Orkneys (Mansfield, 1958a) and an estimated 45% mortality at Pionte Geologie (Cornet and Joventin, 1980). Laws (1953) reported that in 1948 and 1949 from 60 to 99% of southern elephant seal pups were born on the fast ice at Signy Island. When this ice broke up, more than 80% of the pups were drowned or crushed in tide-cracks.

There is good evidence that the density at land rookeries varies directly with the level of preweaning mortality in several species of colonially breeding phocids and otariids. Coulson and Hickling (1964) found a positive correlation between the mortality rates of grey seal pups and the mean number of pups/100 m of shore in the Farne Islands during the period 1956 to 1962. This relationship was confirmed and updated for the period 1963 to 1970 on the Farne Islands by Bonner and Hickling (1971) and extended to North Rona by Summers *et al.* (1975) (Figure 3.3). Increased preweaning mortality at high rookery density has also been documented in the northern elephant seal (Le Boeuf *et al.*, 1972; Reiter *et al.*, 1981), Antarctic fur seal (Doidge *et al.*, 1984a), and northern fur seal (Fowler, 1987).

The effect of density on preweaning mortality can be magnified both by the topography of the breeding colony and the behaviour of adults. In grey seals, for example, the interaction of density on the breeding colony and rookery topography is clear. Hickling *et al.* (1977) reported a 47.4% mortality of grey seal pups on congested beaches of Staple Island in the Farnes while only 21.5% died on less congested areas on top of the island. Similarly, Anderson *et al.* (1979) found that even though density was similar at two sites, preweaning mortality on the steep shoreline rookeries of Ramsey Island (35%) was more than double that measured on the wide beaches of Auskerry. Pup mortality during the nursing period in northern elephant seals rose from about 14% in 1968 when only 200 pups were born on Ano Nuevo Island to over 34% in 1980 when more than 1200 pups were born (Reiter *et al.*, 1981). The authors noted, however, that this density dependence is not smoothly graded but fluctuates greatly at high densities in relation to weather and individual harem density. Much of this mortality can be attributed to the separation of mother and pup and the resulting onset of the

Table 3.4 Pup mortality in pinnipeds from birth to weaning

	Species	% Mortality to weaning	Location	Source
PHOCIDAE				
Floe-ice	Harp seal	0.34 1.1-1.4 1.4 3.6-5.4 2.8-19.5 17.0-40.0 >12	Southern Labrador Gulf of St Lawrence White Sea White Sea	Bowen (unpubl.) Kovacs <i>et al.</i> (1985) Yakovenko and Nazarenko (1971) Popov (1971) Krylov <i>et al.</i> (1980) Rumyantsev and Khryas'kin (1978) Siniiff <i>et al.</i> (1979)
	Caspian seal			Stirling (1971), Kaufman <i>et al.</i> (1975)
	Crabeater seal			Thomas and DeMaster (1983a)
Fast-ice	Weddell seal	≈5.0 3.0-16.0 >30.0-50.0 45.0	McMurdo Sound McMurdo Sound South Orkneys Pointe Geologie	Mansfield (1958a) Cornet and Joventin (1980)
	Ringed seal	9.0-40.0		Smith (1976), Stirling and Archibald (1977)
Land	Grey seal	14.5-35.0 9.8-18.6 8.8-35.1 21.5-47.4 17.6-61.0 14.3-18.4 14.6-23.2 8.0-12.5 2.1-10.0 2.0-16.0	Ramsey Is. Farme Is. Farme Is. Stable Is. North Rona Monarch Shillay Sable Is. South Georgia Macquarie and Heard Is.	Davies (1949), Anderson <i>et al.</i> (1979) Coulson and Hickling (1964) Hickling <i>et al.</i> (1977) Hickling <i>et al.</i> (1977) Summers <i>et al.</i> (1975), Baker (1984) Baker (1984) Stobo and Beck (unpubl.) Laws (1953), McCann (1982) Carrick <i>et al.</i> (1962)
S. elephant seal				

N. elephant seal	7.0-41.7	Ano Nuevo	Le Boeuf <i>et al.</i> (1972), Le Boeuf and Briggs (1977), Le Boeuf and Condit (1983), Reiter <i>et al.</i> (1981)
Harbour seal	13.0-16.0	Sable Is.	Boulva (1975), Stobo and Beck (unpubl.)
Hawaiian monk seal	16.7-21.9	Kure Atoy	Wirtz (1968), Kenyon (1980, 1981)
	39.0	Midway Is.	Kenyon (1980, 1981)
	9.0	Laysan Is.	Kenyon (1980, 1981)
OTARIIDAE			
Antarctic fur seal	6.0-31.0	Birds Is., S. Georgia	Bonner (1968), Payne (1979), Doidge <i>et al.</i> (1984a)
	3.0-6.0	Schlieper, S. Georgia	Doidge <i>et al.</i> (1984a)
	58.0	Ile Amsterdam	Paulian (1964)
Northern fur seal	4.0-22.0	St Paul Is.	Fowler (1987)
New Zealand fur seal	$\approx 40.0^a$		Mattlin (1978)
Galapagos fur seal	$\approx 20.0^b$		Trillmich and Limberger (1985)

^a To 290 days.
^b To = 365 days.

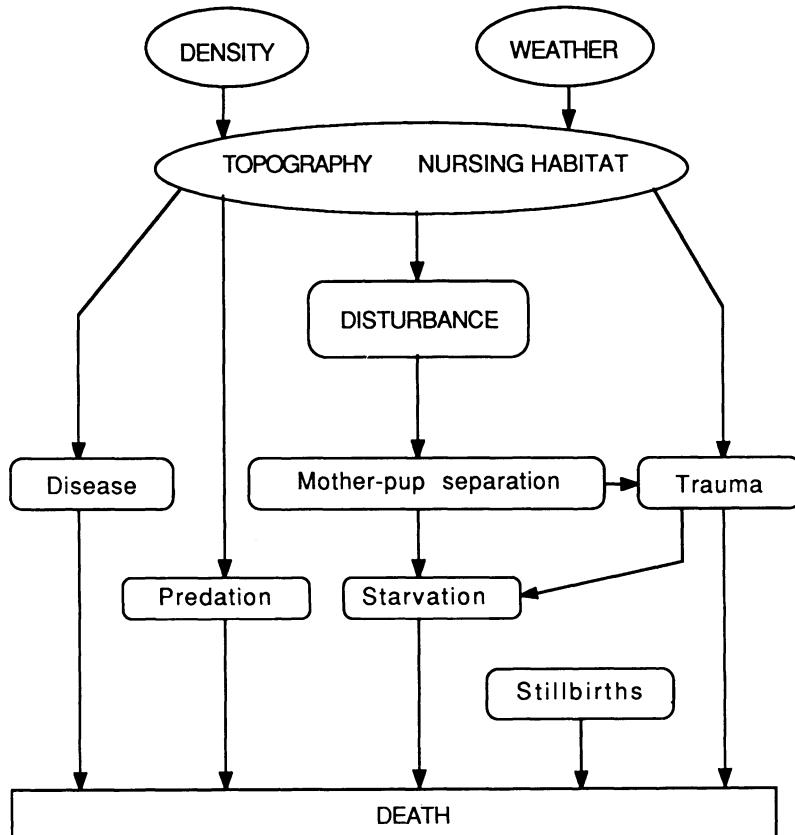


Figure 3.2 Schematic representation of the factors contributing to pre-weaning mortality in pinnipeds. The effects of the density of individuals on the breeding colony and weather on pup mortality are dependent on the type and topography of the nursing habitat.

trauma-starvation syndrome described by Le Boeuf and Briggs (1977). In both species of elephant seal, pup mortality rate is also influenced by the social status of mothers within a harem and female age (Reiter *et al.*, 1981; McCann, 1982).

Large scale environmental variation can have equally dramatic effects on pup mortality during the nursing period. The strongest El Niño-Southern Oscillation event in this century took place between August 1982 and July 1983. The El Niño is an irregular climatic variation that results in increased sea-surface temperatures and correlated decreases in zooplankton and fish abundance in the eastern tropical Pacific (McGowan, 1984; Barber and Chavez, 1983). Two species of pinnipeds were particularly affected by the 1982-83 El Niño: the Galapagos fur seal and sea lion. As a result of longitudinal studies, Trillmich and Limberger (1985) showed that the survival of fur seal pups dropped from about 80% over the first year

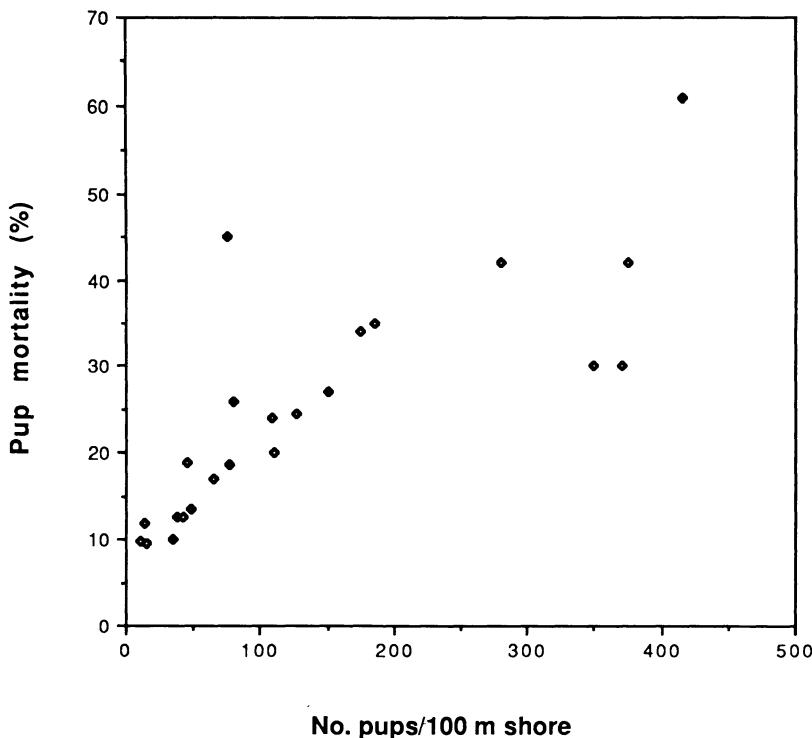


Figure 3.3 Effect of pup density, expressed as number of pups/100 m of shoreline, on pre-weaning mortality in grey seals. Data from Coulson and Hickling (1964), Bonner and Hickling (1971), and Summers *et al.* (1975).

of life in the year preceding the El Niño to 0% after 5 months in 1982. In the case of the Galapagos sea lion, survival decreased from about 95% over 7 months in 1977 (a non-El Niño year) to about 14% to 5 months of age in 1983 and overall pup production was down by 70%. As expected, starvation was the single greatest source of mortality in both species. Further north, the effects of the 1982-83 El Niño were also felt. Storm-driven waves resulted in dramatic pup losses as illustrated in northern elephant seals. In January 1983, high surf flooded nurseries at the height of the pupping season, dragging pups into the sea, hurling them onto rocks or separating them from their mothers. Pup mortality on Ano Nuevo was 70% of the 975 produced in 1983 compared to a mortality of less than 10% of pups born in uncrowded harems and less than 35% in crowded harems (Le Boeuf and Condit, 1983). California sea lions (*Zalophus californianus*) breeding on San Nicholas Island also suffered increased pup mortality (Ono *et al.*, 1987). Mortality of marked pups between late May and early August was 0% in the year preceding the 1982 El Niño, 10.9% in the 1982 and only about 2% in the following two years.

Other causes of preweaning mortality have been studied in a number of species. Predation by polar bears and arctic foxes appears to be a significant source of pup mortality in the ringed seal and the single largest source of deaths in fast-ice breeding habitat (Smith, 1976; Stirling and Archibald, 1977). Polar bears are also known to take small numbers of harp seal pups and occasionally adults, off northeastern Newfoundland (W. D. Bowen, unpubl.; B. Bergflot, pers. comm.) and in the Jan Mayen whelping concentrations (B. Bergflot, pers. comm.). Leopard seals are thought to be an important predator of both the crabeater and Weddell seal, but actual mortality estimates are not available (Stirling, 1969a, 1970; Siniff *et al.*, 1979). Walrus predation on ringed, bearded, and larga seals appears to be common and according to Lowry and Fay (1984) could have an impact on these species in some areas. Shark predation has been reported in several species and is thought to be a significant source of mortality in the Hawaiian monk seal (Wirtz, 1968; Kenyon, 1980, 1981). On Sable Island, Brodie and Beck (1983) reported that shark predation resulted in 6-7% mortality of harbour seal pups during the lactation period. According to Rumyantsev and Khyras'kin (1978), wolves accounted for a significant fraction of the 17-40% preweaning mortality observed in the Caspian seal.

Several detailed studies have been conducted on the causes of preweaning pup mortality in the grey seal. Anderson *et al.* (1979) compared mortalities at two sites: Ramsey and Auskerry. At both sites infections such as septicaemia and peritonitis accounted for about one-third of the 57 pup deaths examined. Starvation was the cause of death in 28.1% and 8% of deaths on Auskerry and Ramsey respectively. Drowning, trauma, non-viable and stillborn pups accounted for 25% and 40% of deaths at the two sites. Baker (1984) studied the cause of preweaning mortality on three islands in the Outer Hebrides: North Rona, Ceann Ear, and Shillay. On North Rona, starvation (28.6%) and peritonitis (25.7%) were the major causes of mortality in 69 pups examined, whereas on Monach Island washing-off drowning (46.7%) and starvation (25%) were the principal causes of death of 92 pups studied. At Shillay, infections accounted for more than 40% of deaths in 16 animals examined on the inland sites, whereas starvation (33%, $n = 18$) was most important cause of death on beaches.

Although mother-pup separation is a significant underlying cause of pup mortality in many pinniped species, the importance of trauma leading to starvation is much more evident in otariids and in the more colonial species of phocids. In these species, adult and juvenile males often seriously injure pups which have been separated from their mothers. Le Boeuf and Briggs (1977) stated that most pup mortalities in the northern elephant seal result from a complex set

of interacting factors which result in mother-pup separation, trauma and starvation. They referred to this set of interacting factors as the trauma-starvation syndrome. Trauma inflicted by adult males is also an important source of pup mortality in southern elephant seals (Laws, 1953; McCann, 1982) and in the Antarctic fur seal (Bonner, 1968; Dodge *et al.*, 1984a).

3.3 THE LACTATION PERIOD

3.3.1 Postparturient behaviour

Delivery appears to be rapid in most pinnipeds (Table 3.5). From the time the pup's head first appears to delivery averages about 6 min for cephalic births and 19 min for breech births in the six species of otariids that have been studied. Sufficient quantitative data are available in only two species of phocids to enable comparison of the time taken for cephalic and breech births. Le Boeuf *et al.* (1972) reported no significant difference in the time taken for cephalic deliveries (6.8 min) compared to breech births (8.8 min) in the northern elephant seal. However, in the southern elephant seal breech births took about twice as long as cephalic deliveries (Carrick *et al.*, 1962) (Table 3.5). Delivery in some phocids (e.g. harp, grey and harbour seals) can be extremely rapid, taking only 20–30 s. Existing data suggest that cephalic and breech births occur with equal probability in pinnipeds (χ^2 , $p > 0.05$ for all species where $n > 10$, Table 3.5).

In most species there is little advanced indication that delivery is imminent, except that females tend to become more restless and may move off somewhat from other females (e.g. harbour and grey seals). The sequence of behavioural events immediately following birth is similar in all pinnipeds. Data on 20 of 34 species indicate that the umbilical cord is usually broken during delivery or when the mother turns to investigate her pup within seconds after birth. If it is not ruptured during delivery, pups immediately struggle to free themselves from the amnion. Mothers have not been observed to assist the pup in freeing itself from the amnion except on two occasions in the Antarctic fur seal (Bonner, 1968).

In most species, the mother sniffs and noses her pup's face and body within minutes of birth (Table 3.5). At about the same time, pups of all species begin to utter mother-attraction calls (Stirling, 1971), described as a bleating 'mwaa' in most species, and either move toward, in the case of phocids, or are drawn by the mother to her side, as in most otariids.

Harp, hooded, grey and harbour seal mothers do not vocalize to

Table 3.5 Delivery time and post-parturient behaviour of pinniped mothers and neonates

Species	Delivery (min)			Time to Sniff/ Touch			Vocalization			Source
	Cephalic	\bar{X} cephalic and Breech	Breech	% cephalic ^a	Pup (min)	Mother	Pup			
PHOCIDS										
Hooded seal	-	-	-	0.3 (2)	< 1 (2)	N	Y			Bowen (unpubl.)
Harp seal	-	-	-	< 0.5 (5)	< 10 (6)	N	Y			Stewart <i>et al.</i> (1981), Bowen (unpubl.)
Grey seal	-	-	-	14.0 (4)	Imm	Y	Y			Fogden (1971), Burton <i>et al.</i> (1975)
Weddell seal	7.0 (2)	-	-	40.3 (190)	44	Imm	Y, 0.2-3 min	Y, 0.1-2.4 min		Stirling (1969b), Mansfield (1958a), Tedman and Bryden (1979)
S. elephant seal	22.0 (87)	-	-	8.8 (11)	62	Imm	Y, Imm	Y, Imm		McCann (1982), Carrick <i>et al.</i> (1962)
N. elephant seal	6.8 (18)	-	-	3.5 (1) ^b	-	Imm	N	Y		Petrinovich (1974), Le Boeuf <i>et al.</i> (1972)
Harbour seal	2.6 (4)	-	-	-	< 5	Y	Y	Y		Lawson and Renouf (1985)
Hawaiian monk seal	-	-	-	-	-	-	-	-		Kenyon and Rice (1959)

OTARIIDS	Antarctic fur seal	2.0 (3)	5.0 (2)	< 1	Y	Y, Imm	Bonner (1968)
	Northern fur seal		20.0 (40)	Imm	Y	Y	Macy (1982)
	Steller's sea lion	16.0 (26)	39	0.7	Y	Y, 1.25 min	Gentry (1970)
	New Zealand fur seal	0.5 (4) 2.0 (13)	30 4.0 (1) 6.5 (11)	46	Imm Imm	Y Y, < 30 min	Sandegren (1970) Stirling (1971) McNab and Crawley (1975) Bester (1977)
Subantarctic fur seal					Y	Y, Imm	
	Cape fur seal	11.2 (11)	60.6 (6)	Imm	Y, Imm	Y, Imm	Rand (1955)
	California sea lion	3.0	16.1	63	Imm	Y, < 30 min	Odell (1972), Peterson and Bartholomew (1967)
					-	Y	Trillmich (1981)
Galapagos sea lion		-	-	-	-	Y, < 30 min	
	Galapagos fur seal	-	-	< 1	Y	Y, Imm	Trillmich (1981)
	Australian sea lion	(2)	12-170	Imm	Y, Imm	Y, Imm	Marlow (1975)
	Hooker's seal lion	(8)	7-125	Imm	Y, Imm	Y, Imm	Marlow (1975)
S. American fur		2	(6) (8)	50	-	Y, Imm	Vaz-Ferreira (1975)

^a For $n \geq 10$.

^b One transverse birth took 21 min.
^c Time of first vocalization postpartum.

Imm = immediately after birth.

their pups at birth or throughout lactation, whereas, Weddell, southern and northern elephant, and Hawaiian monk seal mothers and all otariid females do (Table 3.5). Although data from more phocid species are required, it appears that the mothers of floe-ice-breeding species and the harbour seal, all of which have relatively short lactation periods, do not vocalize to their pup, whereas mothers that give birth in more stable habitats (land or land-fast ice) and have longer nursing periods do. From this we should expect that bearded, larga, and ribbon seal mothers should be silent. Because the pups of ringed seals and the Baikal seal are reared in protective snow lairs, long distance communication is unlikely to be required and so we might expect the mothers of these species to be silent as well, even though they have long lactation periods and use stable nursing habitat. The lack of pup-attraction calls by many phocid mothers means that pups of these species have potentially less information that can be used to re-locate their mothers should they become separated, placing the responsibility for maintaining mother-pup contact mainly with the mother.

3.3.2 Recognition

In many colonial species of pinnipeds, mothers regularly leave and return to their own pups after several days at sea. Even when the period of absence is only a matter of hours, as in the harp seal, the ability of mothers to relocate their pup on moving pack-ice is remarkable. The first few hours postpartum is widely regarded as an important period in the development of the mother-pup bond and the ability of the mother to recognize her pup. Odour appears to be universally important as a means by which pinniped mothers confirm the identity of their offspring at close range, whereas, the vocalizations of mothers (pup-attraction calls) and pups (mother-attraction calls) are more important at greater distances.

The use of the pup's individual odour in recognition is probably established early as evidenced by the frequency with which the mother sniffs her pup in the first few minutes following birth (Table 3.5). Burton *et al.* (1975) found that grey seal mothers ($n=6$) sniffed and touched their pups with their nose an average of 15 times in the first 10 min postpartum but that this behaviour occurred only twice in the next 10 min period and only once between 41 and 90 min after birth. Similar behaviour has been reported in the southern elephant seal (McCann, 1982), the harp seal (Kovacs, 1986), the New Zealand fur seal (McNab and Crawley, 1975), and the California sea lion (Peterson and Bartholomew, 1967). Further evidence for the importance of odour in pup recognition comes from the observation that mothers invariably sniff the face of pups upon reunion or prior to

allowing a pup to suckle (Rand, 1955; Popov, 1966; Bonner, 1968; Kaufman *et al.*, 1975; McNab and Crawley, 1975; Burns and Frost, 1979; Kovacs, 1986; Godsell, 1988). Although there can be little doubt that mothers rely on the odour of their pup in individual recognition, it is important to recognize that experimental studies have yet to be conducted.

There is stronger evidence that pinniped mothers can distinguish their pup's vocalizations from those of other pups. In all species for which data are available, newborns begin to call shortly after birth and continue to be quite vocal throughout the lactation period (Table 3.5). McNab and Crawley (1975) found that New Zealand fur seal pups began to call within 30 min of birth and called several hundred times within the first few hours postpartum. In this species, pup calls appeared to be spontaneous rather than in response to calls from the mother. Galapagos fur seal newborns begin to call immediately after birth and call more on the first day than at any other time during lactation (Trillmich, 1981). Further, the observation that in a number of species, pups cease to vocalize when they are weaned suggests that these calls are designed for use by mothers and their suckling pups.

Limited experimental evidence supports the mother's use of pup vocalizations in individual recognition. In a series of playback experiments, Petrinovich (1974) found that 11 of 14 northern elephant seal mothers responded with pup attraction calls significantly more often to their own pup's call than to calls from strange pups. However, two mothers did not respond to any of the recorded pup calls and one mother responded more often to calls from alien pups than to her own pup. Renouf (1984) found that the calls of harbour seal pups could be distinguished on the basis of fundamental frequency and that a 7-year-old female could be trained to discriminate pairs of pup calls in the laboratory (Renouf, 1985). More recently, Perry and Renouf (1988) have reported that although airborne and underwater versions of harbour seal pup calls were different from one another, they were distinct for each pup on the basis of several physical parameters, particularly the frequency of the major harmonic. The characteristics of pup calls also depended on the distance between the pup and its mother, on whether or not the mother's head was submerged, and on the mother's response to their calling pups; further suggesting that there may be information in the call that is used by the mother to recognize her pup. Nonetheless, experimental studies are still needed to verify the function of pup vocalizations in mother-pup recognition.

Many authors have argued that the mother plays the more active part in recognition and that pups react indiscriminately to any female approaching the pup (Fogden, 1971; Wilson, 1974; Petrinovich, 1974; McNab and Crawley, 1975; Roux, 1986). Others suggest that the pup

also plays an active part in ensuring the integrity of the mother-pup association (Peterson and Bartholomew, 1967, for older pups; Rand, 1967; Sandegren, 1970; Renouf *et al.*, 1983; Lawson and Renouf, 1987; Perry and Renouf, 1988). In a series of playback experiments, Trillmich (1981) found that Galapagos fur seal (aged 10 days to 2 years) and sea lion (aged 10 to 31 days), pups responded significantly more often to the pup attraction call of their mothers than to that of strange mothers, indicating that pup-attraction calls likely convey sufficient information to allow pups to identify their mothers.

The ability of mothers and pups to recognize one another and the relative contribution of each in recognition may differ in different species depending on both social and ecological factors. In species where the mother is continuously present during lactation and the risk of separation is low (as in cases where the density of mother-pup pairs is low), mother-pup recognition may be less well developed. This may account partly for the relatively high frequency of fostering observed in species such as the Hawaiian monk seal (see Section 3.3.5). On the other hand, the ability of mothers and pups to recognize each other should be greatest in colonial species where separation is frequent and high densities of mother-pup pairs are regularly encountered, such as most otariids. In this regard, it is significant that in otariids where mothers and pups are regularly separated for days and in the highly colonial elephant seals, both mothers and pups exhibit calls which appear to contain information which could be used to reunite mothers and their pups. This difference is also consistent with the greater risk of the pup being prematurely separated from its mother in these high-density colonial species and the consequences of such a separation.

3.3.3 Behavioural changes over the course of lactation

Although the general features of pup behaviour are known for a number of species, there are a few quantitative studies of the overall behavioural development of pinniped neonates. Many of the existing studies have focused attention on single elements such as suckling (see Section 3.3.4) or play (Farentinos, 1971; Gentry, 1974; Wilson, 1974; Renouf and Lawson, 1986, 1987). Within the Phocidae, the overall behavioural development of pups has been described quantitatively in just five species: the harp seal (Stewart, 1983; Kovacs, 1986), the grey seal (Kovacs, 1986), the northern elephant seal (Rasa, 1971), the Weddell seal (Tedman and Bryden, 1979), and the harbour seal (Sullivan, 1982). Quantitative studies have been published on only four species of otariids: the northern fur seal (Macy, 1982), the California sea lion (Ono *et al.*, 1987; Ono and Boness, *in press*), the Steller sea lion (Gentry, 1970; Higgins, 1984; Higgins *et al.*, 1988) and

the Galapagos fur seal (Arnold and Trillmich, 1985; Limberger *et al.*, 1986).

Pinnipeds are among the most precocial mammals. Pups are born with their eyes open. They begin to utter mother-attraction calls, are capable of following their mothers over short distances, and suckle for the first time often within minutes after birth. The precocial nature of these young mammals is illustrated in the harbour seal, where within an hour or less of birth pups are able to swim with their mothers at sea (Newby, 1973; Lawson and Renouf, 1985), often in response to rising tides, and in the hooded seal where pups are weaned in just four days (Bowen *et al.*, 1985).

Differences in female attendance of pups among pinniped species have led to some basic differences in the behaviour exhibited by offspring. Perhaps because phocid mothers tend not to leave their pups during lactation (Table 3.6), pups in these species rarely interact with individuals other than their mothers. When such interaction does take place it is generally limited to brief agonistic displays directed toward neighbouring mothers and/or their pups (Rasa, 1971; Reiter *et al.*, 1978; Sullivan, 1982; Kovacs, 1986). Movement by the pup away from the birth site also tends to be limited in most species. This lack of movement by the pup may simply reflect the almost constant presence of the mother or it may be an adaptation which makes it easier for mothers to re-locate their young after brief periods of absence.

Although most phocid pups are relatively sedentary during the lactation period, the harbour seal and Weddell seal are exceptional in this regard. In these two species, pups spend a considerable amount of time in the sea with and without their mothers prior to weaning and as they get older they tend to move some distance from the birth site (Lindsey, 1937; Kaufman *et al.*, 1975; Sullivan, 1982; Thomas and DeMaster, 1983b). Tedman and Bryden (1979) observed that Weddell seal pups, after entering the water with their mothers, sometimes hauled out on the ice up to 65 m from the original site of entry. These independent movements by pups were more frequent during the second half of the nursing period. It is perhaps significant that the distance between Weddell seal mothers is usually more than 80 m when their pups are born and that the density of mother-pup pairs is low in the species thus minimizing the chances of mother and pup becoming separated by other females.

Otariid mothers and their pups also tend to be relatively sedentary until mothers leave for their first foraging trip at sea, about one week after birth in most species (Gentry *et al.*, 1986). However, after mothers leave the colony to feed at sea, in the following species pups typically gather in pods near the periphery of the colony apparently to avoid attack from suckling mothers and adult males: northern fur

Table 3.6 Development of behaviour in pinniped neonates

		% mother with pup during lactation	Age (d) pup first enters water	Time spent with mother	Change with pup age	Pup movement	Time in water	Source
PHOCIDAE	Floe-ice	Hooded seal Harp seal Grey seal Sable Is.	100 ≈28	5 10-12	0	0	0	Bowen <i>et al.</i> (1985, 1987) Kovacs (1986), Bowen (unpubl.)
	Monachs	Rona	100	25-30	0	0	0	Boness and James (1979), Bowen and Stobo (unpubl.)
	Isle of May	Isle of May	40-80	>17	-	n.d.	+	Anderson and Harwood (1985)
	Fast-ice	Weddell seal		8-20	-	+	+	Kovacs (1987b) Lindsey (1987)
Land	S. elephant seal	N. elephant seal	100 100	>35 ≈40	0	0	0	Kaufman <i>et al.</i> (1975) Tedman and Bryden (1979)
	Harbour seal		<1	-	-	+	+	Thomas and DeMaster (1983b)
	Hawaiian monk seal		100	<1 to 4	0	+	+	Laws (1953), Carrick <i>et al.</i> (1962) Le Boeuf <i>et al.</i> (1972), Reiter <i>et al.</i> (1978)
	OTARIIDAE	Antarctic fur seal	36	≈30	-	+	+	Bonner (1968), Gentry <i>et al.</i> (1986), Dodge <i>et al.</i> (1984b)
	Northern fur seal	S. African fur seal	27 39	-	-	+	+	Gentry and Holt (1986)
	New Zealand fur seal	Galapagos fur seal	21-28 21-28	-	-	+	+	Stirling (1971) Gentry <i>et al.</i> (1986), Trillmich (1986a)
	Galapagos sea lion		73	≈7				Gentry <i>et al.</i> (1986), Trillmich (1986b)

seal (Bartholomew, 1952), Antarctic fur seal (Bonner, 1968), Steller's sea lion (Gentry, 1970, 1975), subantarctic fur seal (*Arctocephalus tropicalis*) (Bester, 1977), and New Zealand fur seal (Stirling, 1971; McNab and Crawley, 1975). While gathered in these pods, pups engage in play which as they get older is often expressed in the form of mock-fights (Stirling, 1971; Gentry, 1974, 1975). Thus, in contrast to the neonates of phocid species, otariid pups spend a considerable proportion of the lactation period interacting with one another developing social skills and physical abilities (see Chapter 5).

Our understanding of the ontogeny of behaviour in phocid species has been substantially increased by the recent work on the harp and grey seal by Kovacs (1986; 1987a, 1987b). Observations on known-age pups of both species from birth to weaning provided an accurate time frame for the study of behavioural ontogeny (Table 3.7). Kovacs (1986) found that in both species pups spent the majority of their time asleep. In harp seals, the time spent idle was always >60% and increased from about 65% during the first several days following birth to 85% at weaning. On the other hand, the time spent idle by grey seal pups decreased with pup age from about 70–80% at birth at the inland and ledge sites but not at the beach site. Both male and female pups spent a similar proportion of their time idle at each study site.

In both species, comfort movements (low-intensity activities including stretching, scratching and rubbing) initially comprised about 15–20% of the pup's time (Table 3.7). However, the time spent in these activities declined rapidly in harp seal pups more than a few days old, but, was a relatively constant proportion of the grey seal pup's time.

Agonistic and play behaviour increased with pup age in both species, but represented a small proportion of the pup's time. The time spent by pups soliciting suckling by nosing their mothers and the time spent suckling did not vary with pup age in either species (Table 3.7). However, male grey seal pups spent significantly more time nosing their mothers and nursing and were also more aggressive than female pups. These sex-related differences, not seen in the monomorphic harp seal, are consistent with both the greater mass gain of male pups during lactation (Kovacs and Lavigne, 1986b; Anderson and Fedak, 1987) and the role aggression plays in the reproductive success of male grey seals (Boness and James, 1979).

Differences in the behaviour of male and female pups during lactation have also been reported in the northern elephant seal (Reiter *et al.*, 1978), another sexually dimorphic species. In this species, males nurse for a full day longer than female pups, are more persistent and more successful in stealing milk, and more frequently engage in mock-fight interactions (Rasa, 1971; Reiter *et al.*, 1978). Both of these

Table 3.7 Changes in percentage of time spent by grey and harp seal pups in various activities during lactation. Data from Kovacs (1986, 1987a, 1987b)

Behaviour	Harp seal						Grey seal					
	Gulf of St Lawrence			Pilgrims' Haven			Rona			Rona Rocks		
	Early	Late	Trend	Early	Late	Trend	Early	Late	Trend	Early	Late	Trend
Idle	64.0	81.0	+	70.0	70.0	0	75.0	65.0	-	77.0	72.0	-
Comfort movements	22.0	8.0	-	15.0	15.0	0	15.0	15.0	0	15.0	10.0	0
Alert	<1	1.0	0	0.4	0.4	0	1.0	5.0	+	2.0	3.5	-
Nosing	2.5	1.0	-	1.5	1.0	0	0.5	0.5	0	0.5	0.5	0
Suckling	4.0	2.75	0	3.0	3.0	0	3.5	3.0	0	1.5	2.5	0
Locomotion	6.0	5.5	0	8.3	5.6	-	5.0	7.5	0	4.0	7.5	0
Agonistic	0.0	0.5	+	0.1	0.4	+	0.1	0.4	+	0.1	0.4	+
Play	0.0	0.25	0	0.0	0.0	0	0.0	1.0	+	0.0	1.0	+

+ = increase.

0 = no change.

- = decrease.

authors concluded that the sex differences in behaviour observed in young pups are similar to those observed in adults.

As might be expected, behavioural differences between male and female pups have also been reported in otariids. Gentry (1974, 1975) found that male Steller's sea lion pups were involved in play fights five times more than female pups. Similarly, Trillmich (1981) found that male Galapagos fur seal pups played significantly more than female pups and that this difference was mainly a result of play-fighting which lasted almost twice as long in males.

As noted by Reiter *et al.* (1978), Kovacs (1987b) and others, the early differentiation of behaviour in males and females in dimorphic pinniped species is predicted by current theory on maternal investment (Maynard-Smith, 1980; Clutton-Brock *et al.*, 1981). However, general conclusions in this regard must remain tentative until more species have been studied.

3.3.4 Suckling behaviour

Given the importance of suckling to the growth and development of pinniped neonates, it is surprising how few species have been studied (Table 3.8). Further, because definitions and the precision of measurements often differ, it can be difficult to compare directly, studies on free-ranging populations (Oftedal *et al.*, 1987). Estimates of on-teat time comprise 40–68% of total session duration in three species (Le Boeuf *et al.*, 1972; Oftedal *et al.*, 1987), and thus differences between species may simply reflect differences in the definition of a suckling session used by authors. In their review of suckling behaviour in pinnipeds, Oftedal *et al.* (1987) operationally defined a suckling session as consisting of both on-teat periods and short breaks between them. I have used the same definition.

There is little information on the development of suckling behaviour in pinnipeds. Pups generally have great difficulty both in locating and staying on the teat in the first few hours postpartum. In the first few days of life, young southern elephant seals occasionally spent over an hour searching for the nipple, during which time the mother never attempted to assist in any obvious way (Bryden, 1968). Newborn harbour seals, though active, were clumsy and weak and had difficulty in locating their mother's nipples (Lawson and Renouf, 1985). Similar behaviour has been observed in 1–2-day-old harp and grey seal pups (Kovacs, 1986; D. J. Boness, pers. comm.). Tedman and Bryden (1979) described the sequence of actions during the initial suckling attempts of a newborn Weddell seal which seems to be typical of most species. The pup searched for the nipples by rubbing its mouth over the mother's abdomen. Upon contacting one of the nipples the pup sucked by pressing the abdomen for about 10–20 s

Table 3.8 Suckling parameters in pinnipeds. Number of observations are given in parentheses

Species	Geographic location	Mean suckling duration (min)	Suckling interval (h)	Daily duration (h/24h)	Change with pup age		
					Dur.	Inter.	Daily total
PHOCIDS							
Harp seal	Gulf of St Lawrence	7.3 [185] ^d	2.6 [74]	1.2	+	0	0
	Gulf of St Lawrence	9.1 [146] ^g	3.6	1.0	0	0	Kovacs [1986]
	White Sea		3-3.5		+		Yakovenko and Nazarenko [1971]
Grey seal	Isle of May	9.9 [347] ^g	3.9	1.0 (503) ^b	0	0	Kovacs [1986]
	Sable Island	10.4 ^d [20] ⁱ	3.0 (20) ⁱ	1.4	+	0	Boness [unpubl.] in Oftedal et al. [1987]
N. elephant seal	Ano Nuevo	6.7 [13] ^{h,i}	7.7 [13] ⁱ	0.5 [13] ⁱ	+	+	Le Boeuf et al. (1972)
S. elephant seal	Macquarie Is.	6.3 [48] ^{a,e}	1.7 [48]	1.5 [48] ^a	+	-	Bryden [1968]
	South Georgia		2.0	3.1	n.d.	-	McCann [1982, 1983]
	McMurdo Sound	30 [486] ^{f,g}	2.9	3.5 [486] ^f	-	-	Tedman and Bryden (1979)
	Washington State	1.2 [6] ^c	3-4	n.d.	n.d.	n.d.	Newby [1973]
OTARIIDS							
Northern fur seal		8.5 ^e	n.d.	n.d.	n.d.	n.d.	Macy [1982]
California sea lion	San Nicolas	10.7 ^d [23] ⁱ	2.4 [23] ⁱ	1.8	n.d.	n.d.	Boness [unpubl.] in Oftedal et al. [1987]
Steller's sea lion		16.2 ^d	2.7	4.6 (15) ⁱ	+	-	Ono et al. [1987]
				2.4			Sandegren [1970], Higgins et al. [1988], Higgins [1984]
Guadalupe fur seal		18.5 ^e	≈5.0	1.5	n.d.	n.d.	Pierson [1978]

Subantarctic fur seal		21.4 (15) ^d	1.2 [7] ^j		7.2	n.d.	n.d.	Bester (1977)
Galapagos fur seal		25.0 (84) ^{e,i}	2.3		4.1	n.d.	n.d.	Limberger <i>et al.</i> (1986)
ODOBENIDS					2.7 (64)			Trillmich (1986a)
Walrus	Coats Is.	11.7 (25) ^g	n.d.		n.d.	n.d.	n.d.	Miller and Boness (1983)

^a Six pups with 8 observations each.

^b Estimated from Figure 6.7.

^c Likely on-teat sessions within one suckling bout.

^d Cumulative on-teat time.

^e Not enough information given to know what duration includes.

^f Estimate from total and interval, 486 observations on 22 pups.

^g Includes off-teat time.

^h On-teat time derived as 68% of total duration (9.2 min).

ⁱ Number of pups observed.

^j 3 pups observed 7 times in total.

and then collapsed to the ice and rested for several minutes.

Several hours may pass before the newborn successfully nurses for the first time. In grey seals, Davies (1949) indicated that more than 6 h elapsed before pups nursed for the first time, although Burton *et al.* (1975) observed initial nursing by a newborn after 61 min. Kaufman *et al.* (1975) stated that newborn Weddell seals ($n=6$) nursed within the second hour after birth. In southern elephant seals, Laws (1956) reported that suckling usually occurs within 1 h of birth on South Georgia, but on Macquarie Island 3 pups attempted to suckle within a few hours of birth while another successfully suckled 3 h 20 min after birth (Bryden, 1968). Le Boeuf *et al.* (1972) found that northern elephant seal pups begin to suckle within an hour after birth, and in some cases within 15 min postpartum. Harbour seal pups also seem to begin suckling within the first hour postpartum. Lawson and Renouf (1985) observed the first successful nursing at 3 min after delivery and the latest of 9 pups at 138 min, with a mean of 40.1 min. According to Gentry (1970), suckling began an average of 31 min postpartum in the Steller's sea lion. Pups begin to feed about 30 min after birth in the Antarctic fur seal (Bonner, 1968).

Suckling may be initiated by either the mother or the pup. However, in most species (northern and southern elephant seals, Weddell seals, harbour seals, grey seals, and harp seals and New Zealand, Antarctic, and subantarctic fur seals) pups usually initiate suckling and do so by calling while approaching the female and nuzzling her until she rolls onto her side (Bonner, 1968; Bryden, 1968; Fogden, 1971; Stirling, 1971; Le Boeuf *et al.*, 1972; Bester, 1977; Tedman and Bryden, 1979; Renouf and Diemand, 1984; Kovacs, 1986). The pup initiates nursing only about 60% of the time in the northern fur seal (Macy, 1982). On the Isle of May, Kovacs (1987b) found that grey seal mothers often led their pups away from other females before nursing, suggesting that mothers may initiate this behaviour. However, D. J. Boness (pers. comm.) found that this leading behaviour on the part of the female generally occurred after the pup called and/or nuzzled the mother first.

There is little information on which of the pair normally terminates suckling. Renouf and Diemand (1984) found that harbour seal pups terminated suckling early in lactation, whereas mothers were increasingly responsible for terminating suckling as weaning grew near. In harp seals, pups ended nursing sessions 52% of the time ($n=96$) (Kovacs, 1986). According to Bester (1977) pups usually terminated nursing sessions in subantarctic fur seals, however, Bester did not indicate whether or not his observations covered the entire 10-11-month lactation period.

The method of suckling appears to vary both within and between species. In the Weddell seal, Tedman and Bryden (1979) described two

types of suckling behaviour, one consisting of a single period of continuous suckling lasting for 15–60 min and another consisting of a much longer overall suckling period (1–2 h) comprising short periods of nursing lasting only several minutes. The interrupted suckling sequence was less frequent than the continuous type. A similar pattern of continuous and interrupted suckling behaviour is reported in grey seal pups on the Orkney Islands (Fogden, 1971). Peterson and Bartholomew (1967) state that the usual pattern of suckling in the California sea lion is for the pup to nurse steadily, with short breaks. However, no supporting data are provided. Most studies indicate that pups suckle from all teats without preference (Peterson and Bartholomew, 1967; Bryden, 1968; Bester, 1977; Tedman and Bryden, 1979; Kovacs, 1986).

Suckling generally takes place on land (or ice) in all species with one exception, the walrus. In this species, rarely, do mothers nurse while floating horizontally on their backs; however, most commonly mothers bob in the water while calves nurse vertically upside-down, with only the hind flippers exposed (Miller and Boness, 1983). As expected, aquatic nursing has led to a discontinuous pattern which is characterized by nursing dives lasting an average of 1.94 min separated by surface periods of about 0.5 min.

Available data (Table 3.8) indicate that the mean duration of a suckling session, the suckling interval, and estimated total daily nursing time reflect the differing rearing strategies used by phocid and otariid mothers (Oftedal *et al.*, 1987). Several assumptions have been made to derive estimates of these nursing parameters given in Table 3.8. As noted earlier, authors are not always explicit on how the duration of a suckling session was measured. Estimates given in Table 3.8 assume suckling duration represents on-teat time. Also, estimates of total daily suckling time are based on the assumption that suckling parameters measured during the day are representative of the entire 24 h period. However, the time spent suckling in Galapagos fur seal pups decreases from 22.6% during the day to 12% at night (Limberger *et al.*, 1986). Diurnal variation in suckling duration has also been reported in Weddell seal pups older than one week of age (Tedman and Bryden, 1979).

With these assumptions in mind, it appears that the duration of nursing sessions are significantly shorter in phocids ($x = 11.4 \pm 8.36$ min) than in otariids ($x = 16.7 \pm 6.29$ min). In making this comparison, the scant data on harbour seals provided by Newby were not used. The sole member of the odobenids has nursing dives of about 2 min separated by surface periods of about 0.5 min. However, suckling bouts are approximately the same duration ($x = 11.7$ min) as those of phocids only when off-teat surface time is included. The interval between suckling sessions tends to be longer in phocids

($x = 3.4 \pm 1.76$ h) than in otariids ($x = 2.7 \pm 1.37$ h). Consistent with the greater duration and frequency of nursing, total daily suckling time in otariids ($x = 3.5 \pm 2.00$ h) is almost three times that in phocids ($x = 1.4 \pm 0.99$ h). The observed differences in suckling patterns between these two pinniped groups undoubtedly reflect the limited time that otariid pups have with their mothers between feeding trips of several days or more compared to the pups of phocid species whose mothers are continuously available to the pup or are generally absent for periods of only several hours.

Another shortcoming of the existing information on the duration and frequency of suckling is the almost total lack of comparative studies among different populations of the same species. Yet information of this sort may help us to understand observed differences in neonatal growth previously discussed (see Table 3.3). For example, it is likely that the greater daily mass gain of grey seal pups on Sable Island, compared to pups on the Isle of May, may be attributed largely to the greater time spent suckling on Sable Island (Table 3.8). Similarly, differences in the growth rate of southern elephant seal pups between Macquarie Island (Carrick *et al.*, 1962; Bryden, 1968) and South Georgia (McCann, 1980, 1982, 1983) may partly be explained by differences in the total daily duration of suckling, which may in turn be related to the greater level of disturbance of mothers in crowded harems (Bryden, 1968).

Changes in the pattern of suckling occur over the lactation period in some species but not in others (Table 3.8), as previously noted by Oftedal *et al.* (1987). An increase in the duration of suckling sessions with pup age has been reported in northern and southern elephant seals, harp seals (Stewart, 1983), grey seals, harbour seals (Boness *et al.*, unpubl.) and in the Steller's sea lion. However, Kovacs (1986) found no significant increase in the duration of suckling bouts with pup age in harp and grey seals and Tedman and Bryden (1979) found that the length of suckling session decreased with pup age in the Weddell seal. The interval between suckling periods decreases in the Weddell seal, Steller's sea lion and southern elephant seal, whereas it increases in the northern elephant seal and shows no trend over the lactation period in the harp and grey seals (Table 3.8). Ecological interpretation of changes in suckling patterns over the course of lactation are clearly hampered by the scant data available in phocids and the virtual lack of data in otariids. This is an area where research is badly needed.

In a number of pinniped species males are larger than females and this dimorphism is already evident at birth and in the nursing pup (Laws, 1953; Scheffer and Wilke, 1953; Crawley, 1975; Reiter *et al.*, 1981; Doidge *et al.*, 1984b; Kovacs and Lavigne, 1986a; Trillmich, 1986a; Anderson and Fedak, 1987; Oftedal *et al.*, 1987). Thus we

might expect to see differences in the suckling behaviour of male and female pups. Unfortunately, few studies have compared the suckling behaviour of males and females. Kovacs (1987b) studied grey seals at three sites on the Isle of May and found that male pups suckled significantly more than the slower growing female pups at the beach and inland sites. At the ledge site, the difference was not significant but male pups tended to nurse more than females. In the California sea lion, Ono *et al.* (1987) found that the larger and faster growing male pups spent a larger proportion of their time suckling (14.6%) than female pups (10.7%). Although the difference was not statistically significant, Trillmich (1986a) found that male Galapagos fur seal pups tended to suckle more than females, as expected from data on differential weight gain.

Environmental variation can also affect the suckling pattern of neonates. For example, consider the effects of the 1983 El Niño-Southern Oscillation on pinnipeds in the eastern central Pacific. California sea lion pups spent 19.2% of their time suckling in the year before the 1983 El Niño compared with only 13.5% and 12.4% during the El Niño year and the following year (Ono *et al.*, 1987). This reduction in time spent suckling was reflected in lower weight gain and increased mortality.

3.3.5 Fostering behaviour

Phocid and otariid species also differ in the extent to which pups are able to obtain milk from mothers other than their own (Stirling, 1975b). Several behaviour patterns are involved which range from orphaned pups attempting to secure milk for survival to milk stealing in fully weaned pups. Reidman and Le Boeuf (1982) consider three situations resulting in pups obtaining milk from other mothers: (1) fostering - where a mother accepts and cares for an alien pup, lasting from a nursing bout of several minutes to many days of maternal care; (2) adoption - where maternal care is given exclusively to an alien pup; and (3) allomaternal care - where a mother provides milk to an alien pup while that pup is still with its own mother. However, unless otherwise stated, in this discussion fostering behaviour is taken to mean situations in which milk is given to a pup in replacement of that given by its mother.

Fostering behaviour has been reported in a number of pinnipeds, but is common only in phocids. Reidman and Le Boeuf (1982) found that from 1976 to 1980 about 18% of the marked northern elephant seal mothers at a mainland colony adopted an alien pup. At the crowded Point Harem on Ano Nuevo, between 14.8% and 18.9% of the pups born from 1976 to 1979 were permanently separated from their mothers and became orphans. Of the fostering behaviour

observed in this crowded harem, the most common form involved a mother that had lost her own pup and adopted a single orphan (58.5%, $n=82$). However, at least 14 pupless mothers (17.0%) adopted a pup while it was still with its mother and some pupless mothers aggressively attempted to steal a pup from its mother. About 7% were involved in the adoption of a normally weaned pup, whereas in 13.4% of the cases an allo-mother shared the care of a pup with its natural mother. Even though fostering behaviour is common in this species, between half and two-thirds of orphans died at the Point Harem during the 4 years of the study from a combination of injuries inflicted by nursing mothers, males, and starvation.

Fostering behaviour is also common in the Hawaiian monk seal (Kenyon and Rice, 1959). Working at the French Frigate Shoals, Boness (in press) found that 87% of 30 marked mothers cared for one or more alien pups, spending an average of 15.6 days or 38% of the lactation period with 2.3 alien pups. About 70% of fostering resulted from squabbles between neighbouring mothers which resulted in the separation of mother and pup. Although most mothers in this population accepted alien pups, there was still a risk to the pup of becoming separated from its mother as 5 of 52 pups born during the study died following separation.

According to Carrick *et al.* (1962), southern elephant seal mothers in the latter stages of lactation are tolerant of strange pups and it is common to see two pups of different ages nursing from the same female. However, Bryden (1968) also working on Macquarie Island observed only one instance of fostering and McCann (1982) reported only two instances in over 1200 observations of suckling behaviour at South Georgia.

Fostering behaviour has been reported in several ice-breeding species, but it does not appear to be common. Tedman and Bryden (1979) observed fostering in only 2 of 486 suckling periods by 22 Weddell seal mothers. Kovacs (1986) saw only one brief instance of fostering in harp seals which was quickly terminated when the foster mother's own pup vocalized. In three seasons at the White Sea, Popov (1971) did not observe a single instance of fostering in harp seals. Burns *et al.* (1972) experimentally induced a free-ranging female larga seal to adopt a strange pup, however, the incidence of fostering in this species in an undisturbed situation is unknown.

Fostering is reported to be common (approximately 44–77% of mothers observed) in grey seals at Orkney and Rona colonies (Smith, 1968; Fogden, 1968, 1971; D. J. Boness, pers. comm.). However, Fogden suggested that human disturbance contributed to the high incidence of fostering in Orkney. On the Isle of May, females suckled their own pups exclusively at an inland and ledge colony, and only 3 mothers at the beach site permitted foreign pups to suckle (Kovacs,

1987b) and fostering has not been observed on Sable Island (D. J. Boness, pers. comm.).

Fostering has been observed in the harbour seal on Sable Island (Boness, Bowen and Oftedal, unpubl.) but human disturbance may have been a factor in some cases. Finch (1966) and Bishop (1967) also observed adoptions in the moderately gregarious harbour seal, *P. v. richardsi*, but in both studies quantitative data are not available.

Fostering has also been reported in a number of otariid species, but in contrast with phocids it appears to be uniformly rare, perhaps because individual recognition by mother and pup is better developed in this pinniped family. In most species, unattended or orphaned pups which attempt to steal milk are often threatened and sometimes savagely attacked by nursing mothers, causing serious injury. Isolated cases of adoption or brief fostering have been observed in the following species: South African fur seal (*Arctocephalus pusillus pusillus*) (Rand, 1955), northern fur seal (Bartholomew, 1959), Australian sea lion, *Neophoca cinerea* (Marlow, 1972), Sub-Antarctic fur seal (Roux, 1986), Galapagos fur seal (Trillmich, 1981), Steller's sea lion (Pitcher and Calkins, 1981), and California sea lion (Ono *et al.*, 1987).

3.4 WEANING

Weaning occurs when offspring transfer their nutritional dependence from milk to solid food. In pinnipeds this process may involve an abrupt cessation of suckling by the pup, a gradual reduction in suckling duration and/or frequency before solid food is taken, or a gradual shift from milk to solid food, such that during the transition both milk and solid food may be found in the stomach at the same time. There are several ways one might go about determining that weaning has occurred. Weaning might be determined from longitudinal data on suckling behaviour for a sample of mothers and their pups. This method should be reliable when weaning involves the abrupt cessation of suckling but may be less reliable when suckling becomes less frequent as weaning approaches or involves a gradual transition to solid food, given the difficulty in observing foraging at sea. Changes in pup mass may also be used to determine when weaning has occurred on the assumption that a decrease in mass indicates that the suckling period has ended. Again this method will only provide precise data when weaning results from the abrupt cessation of suckling, as in the case of the hooded seal (Bowen *et al.*, 1985) and has the further requirement that animals be frequently recaptured. In situations where recapture is feasible, in addition to mass, stomach intubation and the opacity of blood serum can also provide useful

information on the timing of weaning (Bowen *et al.*, 1985; Muelbert and Bowen, unpubl.). However, the disturbance caused by frequent recapture of pups may result in premature weaning. Unfortunately, no single method will be suitable for all species, thus reported species differences in both timing and how weaning is achieved may depend on which of these methods is used. In most situations, the best approach will be a combination of longitudinal behaviour observations with data on mass change, stomach contents, and other measures which might indicate suckling or independent feeding such as the remains of solid food in scats. To date, however, few studies have attempted to collect this type of information.

It appears that weaning is abrupt in phocids, but gradual in most otariids (Table 3.1). Typically in floe-ice breeding species such as the harp seal and hooded seal, there is no change in the behaviour of the mother to indicate that weaning is imminent; the female quite simply abandons her pup seemingly without warning (Kovacs, 1986; W. D. Bowen, unpubl.). The same is true of the grey seal in land-based colonies (Kovacs, 1986), and is likely the case in ice-breeding grey seals, but this has not been investigated. In crabeater seals, weaning is abrupt and appears to be initiated when the male becomes dominant and drives the mother from her pup (Siniff *et al.*, 1979). Preliminary field observations suggest the male may play a similar role in the weaning of hooded seal pups (W. D. Bowen, D. J. Boness and O. T. Oftedal, unpubl.). However, in both species insufficient data are available to permit firm conclusions.

Thomas and DeMaster (1983a) suggest that weaning in the fast-ice breeding Weddell seal is probably gradual with mothers leaving their pups for increasingly longer periods during the sixth week of lactation and then finally not returning. The gradual nature of weaning in the Weddell seal was also implied by Tedman and Bryden (1979) in their statement that the pup learns to swim and catch food before weaning; however, supporting data were not provided.

In northern and southern elephant seals, weaning is abrupt and initiated by the mother. On the day of weaning, northern elephant seal mothers begin to move slowly through the colony, a process which may take several hours, to a point where they depart to the sea. The pup may or may not follow and the mother may start her move while the pup is sleeping (Reiter *et al.*, 1978). Condy (1980) reported that 6 southern elephant seal pups suckled only 2 h before their mothers departed to sea.

The situation is less clear in the Hawaiian monk seal and the harbour seal in which pups spend considerable time in the water prior to weaning. According to Wirtz (1968), nursing is ended in the Hawaiian monk seal when the pup departs to sea. Kenyon and Rice (1959) on the other hand suggest that the mother slips away and

deserts her pup while it is sleeping. Boness (in press) reported also that monk seal mothers terminated lactation abruptly by leaving the island and not returning. In harbour seals, Renouf and Diemand (1984) and Lawson and Renouf (1987) observed a decrease in the mother's willingness to suckle her pup as weaning approached, indicating that the mother controlled the timing of weaning. Nevertheless, on Sable Island the transition from milk to solid food by harbour seal pups is abrupt (Muelbert and Bowen, unpubl.).

Little is known about how weaning occurs in most otariids. Considering the long lactation period within this family, this lack of data is not surprising, though it does limit our ability to do comparative analysis. Weaning is abrupt in the northern fur seal and appears to be so in the Antarctic fur seal - two species with relatively short lactation periods inhabiting polar waters (Table 3.1). However, unlike phocid species, it is the pups of these two otariids rather than the mothers which apparently initiate weaning (Macy, 1982; Doidge *et al.*, 1986). Macy (1982) followed 39 northern fur seal pups from birth to weaning. Of these, 30 pups self-weaned; that is, they did not return to the colony after the last mother-pup reunion, but their mothers did and waited ashore often 4 or 5 days. In the other 9 cases, the mother initiated weaning only twice and weaning was a mutual process seven times.

Information on the nature of weaning in other species of otariids is practically non-existent. Stirling (1971) observed that in *A. forsteri* weaning was forced on the pup by the mother not returning to it. Similarly, Rand (1955) reported that South African fur seal pups were weaned in September and October when most mothers left the colony to feed. In the Galapagos fur seal, Trillmich (1986a) argued that gradual weaning buffers young from the effects of seasonally reduced food supply which makes it difficult for yearling and 2-year-olds to secure sufficient food independently or may reduce risk of predation by lessening the time juveniles must forage alone. Weaning is also a gradual process in the Galapagos sea lion. Trillmich (1986b) found that all pups regularly suckled when they were 6 months old, but also began to eat solid food about this time as evidenced by the changing consistency of their scats. Sea lion mothers appear to determine weaning, since yearlings and even some 2-year-olds would continue to suckle if females failed to give birth that year. On Santiago Island, only 8 of 40 mothers (20%) were still accompanied by older pups when giving birth again. Of these, in 5 cases the older pup was driven off by the mother; however, in two cases the yearling and its younger sibling suckled simultaneously for at least one year.

3.5 BEHAVIOUR AND DIET OF WEANED PUPS

Our knowledge of the behaviour of weaned pups is scanty. Logistic difficulties and cost of studying pups after they leave the rookery (many species become largely pelagic at this time) have contributed to this lack of knowledge. I could find published information on only five species of otariids. Although there is information on 12 phocid species, relatively little of this is quantitative.

A striking contrast at this stage of development is the difference in the timing of independent feeding by the pups of phocid and otariid species. Although not all species have been studied, available data suggest that all phocid pups undergo a post-weaning fast of 1.5-12 weeks depending on the species under consideration (Table 3.9). With few exceptions, estimates of the duration of the post-weaning fast are imprecise, particularly in ice-breeding species. These are typically based on cross-sectional observations of mass loss in pups and stomach content data indicating when solid food is initially taken. However, Muelbert and Bowen (unpubl.) have found that in harbour seals the loss of body mass by weaned pups is not a reliable measure of the length of the post-weaning fast. On Sable Island, longitudinal studies revealed that weaned pups began to take solid food within 10 days of weaning, but continued to lose mass for another 3 weeks. Using the above criterion, we would conclude erroneously that the post-weaning fast in this species lasts for about four times longer than is actually the case. This may account for the discrepancy between the duration of the post-weaning fast in harbour seals reported by Muelbert and Bowen and Drescher's (1979) estimate (Table 3.9). The extent to which estimates for other phocids suffer from this type of error cannot be judged at this time. However, it is likely that current values for all species, excepting those for the elephant seals, overestimate the duration of the post-weaning fast.

Given the lack of data for a number of species and the uncertainty associated with the estimates for others, it is premature to draw conclusions about the ecological significance of the apparent differences in the duration of the post-weaning fast. However, I suggest that the duration of the post-weaning fast will depend mainly on the availability of appropriate food and the ability of pups to capture it. It is perhaps significant that one of the most precocial phocids, the harbour seal, has among the shortest post-weaning fasts (Muelbert and Bowen, unpubl.). The greater behavioural and motor development of this species may enable harbour seal pups to capture prey at an earlier age than most other species. If indeed the ability of newly weaned pups to capture food is related to the proportion of time spent developing swimming skills during lactation, then we should find that the Hawaiian monk seal and Weddell seal also have

Table 3.9 Duration of post-weaning fast in phocids

<i>Species</i>	<i>Post-weaning fast (weeks)</i>	<i>Source</i>
Hooded seal	≈ 4 ^a	Bowen <i>et al.</i> (1987)
Harp seal	≈ 4 ^a	Sergeant (1973), Stewart and Lavigne (1980), Bowen (unpubl.)
Grey seal	~ 1.5 ^b Sable Is. 1–4 ^c North Rona	Beck (pers. comm.) Fedak and Anderson (1982)
Ribbon seal	2–3 ^a	Burns (1981)
Largha seal	≈ 2 ^a	Naito and Nishiwaki (1972)
Ringed seal	≈ 4–6 ^a	Smith (1987)
S. elephant seal	5–7 ^c Macquarie Is. 1–1.5 ^a Marion Is.	Bryden (1968), Carrick <i>et al.</i> (1962) Condy (1980)
N. elephant seal	8–10 ^c 8–12 ^a	Ortiz <i>et al.</i> (1978) Reiter <i>et al.</i> (1978)
Harbour seal	1.4 ^d Sable Is. ≈ 4 ^a Germany	Muelbert and Bowen (in prep.) Drescher (1979)

^a Based on mass loss in weaned pups.^b Based on stomach content data from weaned pups.^c No data to support estimate given.^d 20 weaned pups followed longitudinally.

relatively short post-weaning fasts. However, the short post-weaning fast of the southern elephant seal on Marion Island (Condy, 1980) and grey seals is not explained by this hypothesis.

The amount of energy stored during lactation and the rate at which it is spent by the weaned pup may also play a role in determining the duration of fasting. In the case of ice-breeding seals, yearly variation in the availability of ice suitable for hauling out might also influence the duration of post-weaning fasting by forcing pups to spend more time in the water thus increasing the rate of energy expenditure and accelerating the need to develop effective foraging skills. Worthy and Lavigne (1987) argued that energy use during the post-weaning fast reflects species adaptations to different fasting environments. Data on mass loss and energy use during the post-weaning fast suggest that species that fast on land (e.g. grey seals, northern and southern elephant seals) derive most of their energy from blubber, whereas those that may have spent much of their time in cold water such as the harp seal and hooded seal utilize core tissues (both protein and fat) early in the post-weaning fast thus maintaining effective insulation.

Differences in the duration of the post-weaning fast between two populations of the southern elephant seal further suggest that the amount of energy stored during lactation may influence the duration of the post-weaning fast. According to Condy (1980), pups fast for

only 6–10 days on Marion Island, whereas those at Macquarie Island fast for about 7 weeks (Carrick *et al.*, 1962; Bryden, 1968). It may be that the slower growing (2.6 kg/day, Table 3.3) and smaller elephant seal pups on Marion have less stored energy and therefore must begin to feed sooner than the larger and faster-growing (3.6 kg/day) pups studied on Macquarie by Bryden (1968).

In contrast to phocids, otariid pups begin to consume solid food prior to being weaned (Trillmich, 1981; Shaughnessy, 1982). Thus, they are able to develop foraging skills more gradually than in the case of most phocid pups, during a time when they still have mother's milk as a supplementary food source.

Phocid pups consume a considerable proportion of the energy stored during nursing and during the post-weaning fast (Ortiz *et al.*, 1978; Stewart and Lavigne, 1980; Kovacs and Lavigne, 1985; Bowen *et al.*, 1987; Worthy and Lavigne, 1987; Muelbert and Bowen, unpubl.) and their survival depends on having developed the ability to successfully catch food before these stored resources are exhausted. Given differences in the development of feeding behaviour, we might expect to find that phocid pups would feed initially on slow moving prey near the surface, whereas the pups of otariid species may have developed their foraging skills to the point where faster and perhaps somewhat larger prey could be efficiently captured at weaning. Unfortunately, at present we have virtually no information on the initial diet of otariid pups. However, present information on the initial diets of phocid pups indicates that small pelagic crustacea appear to be an important early food in all species for which there are data (Bertram, 1940; Sivertsen, 1941; Gol'tsev, 1971; Sergeant, 1973; Lowry *et al.*, 1980a; Foy *et al.*, 1981; Kato, 1982; Bowen *et al.*, 1987; Muelbert and Bowen, unpubl.).

Fay (1974) noted the association between food supply and sea ice in ice-breeding species. After being abandoned by their mothers, the pups of floe-ice breeding species tend to remain with the disintegrating ice until it disappears. In doing so these young pinnipeds appear to be taking advantage of rich concentrations of zooplankton such as euphausiids which are often found under ice floes (McRoy and Goering, 1974; Harner, 1976).

In the northwest Atlantic, the distribution of weaned harp and hooded seal pups reflects initial differences in the location of whelping concentrations with harp seals being found throughout the interior and middle of the floe ice, while hooded seals are located on the outside edge of the ice field off northeastern Newfoundland (W. D. Bowen, unpubl.). In both species, small crustaceans form an important component of the diet when feeding commences after the post-weaning fast of about 4 weeks. Sivertsen (1941) has also noted the importance of pelagic crustaceans such as *Anonyx nugax*,

Thysanoessa inermis and *T. taschii* in the diet of weaned harp seals in the White Sea population.

Lowry *et al.* (1980b) examined the diet of bearded seals and found that newly weaned pups fed mainly on a variety of small shrimps, the isopod (*Saduria entomon*), brachyuran crabs, and fish, including saffron cod (*Eleginops gracilis*) and sculpins (Cottidae).

In the larga seal, two pelagic euphausiids (*Thysanoessa inermis* and *T. raschii*) accounted for 95.5% of the diet by weight of recently weaned pups (Kato, 1982). Decapods, including *Pandalus borealis*, contributed 2.7% and fish such as *Theragra chalcogramma* made up about 1% of the diet of these pups. Gol'tsev (1971) found that larga seal pups began to feed at about 5 weeks of age on small amphipods such as *Nototropis* sp. and *Anonyx nugax*. By 7–8 weeks of age pups were feeding on decapods such as *Spirontocaris macrarozi*, *Eualus fabricii* and *E. gaimardi*, and sand lance. By the end of June, at 10 weeks of age, larger flounder and navaga (*Eleginops navaga*) were found in the diet.

Several studies have documented the importance of crustaceans in the diet of ringed seal pups during their first summer. Lowry *et al.* (1980a) examined the stomach contents of 21 pups from the Bering Strait and found that crustaceans comprised 97% of the food by volume. In the Eastern Arctic, Bradstreet and Finley (1983) estimated that crustaceans contributed 22–47% of calories consumed by pups while *Boreogadus* accounted for 41–68%. They also found that pups took significantly smaller *Boreogadus* (mean length = 8.6 cm, $n=22$) than did older seals (10.9 cm, $n=182$).

Although near-surface crustaceans are certainly an important food when feeding begins, the pups of several species soon become capable of diving to considerable depths in search of food. Kooyman (1968) showed that a 7-week-old Weddell seal was capable of diving 91 m. Gol'tsev (1971) reported that at the beginning of independent feeding, larga seal pups can dive 80 m. 8 to 10-week-old grey seals have been incidentally drowned in fixed fishing gear at depths ranging from 60 to 120 m on the Scotian Shelf off eastern Canada (B. Beck, Bedford Institute of Oceanography, pers. comm.).

Finally, there is some evidence to suggest that pups may often forage in different areas from that used by older animals. For example, Thomas and DeMaster (1983b) found that Weddell seal pups hauled out on ice over water which was an average of 39 m deep compared to 137 m used by mothers. Also pups tended to stay near the fast ice at the birth site where they may be less vulnerable to predators. Smith (1987) reported that pups tend to move westward in early autumn perhaps to avoid competition with older ringed seals. In the northwest Atlantic harp seal population pups migrate to West

Greenland whereas older animals tend to forage in waters off the eastern Arctic (Sergeant, 1965).

3.6 Discussion

Phocids are primarily ice-breeding species whereas all otariid species give birth on land. This fundamental difference in habitat selection has had a profound influence on maternal pup rearing strategies of pinnipeds (Bonner, 1984; Oftedal *et al.*, 1987). Phocid mothers typically fast or markedly reduce food intake during an abbreviated period of lactation in which they rarely leave their pup for more than several hours. In contrast, otariid mothers alternate between extended periods of feeding at sea and visits to the rookery to feed their young over periods of a year or more. The selection of pup rearing habitat and the resulting differences in patterns of maternal attendance of pups can account for the major features of the behavioural ecology of phocid and otariid neonates.

Phocid pups typically fatten rapidly, are relatively sedentary and interact mainly with their mothers until they are abruptly weaned. In these species, pups spend most of their time resting. Play behaviour tends to be infrequent and solitary. In monomorphic species such as the harp seal there is no evidence of sexual differentiation in the behaviour of neonates. However, in sexually dimorphic species, like the grey seal and northern elephant seal, sex-specific differences in behaviour are observed in the nursing pup. Pups spend surprisingly little time suckling presumably due to the high energy content of their mother's milk (Oftedal *et al.*, 1987). Phocid pups commonly attempt to suckle from foreign mothers, although their success varies widely and is frequent in only three land-breeding species. In most species, newly weaned pups fast for a period of weeks before successfully feeding independently. Crustaceans appear to play an important role in the initial diet of phocid pups.

The behaviour of otariid pups is in many ways similar to that observed in phocids during the first week following birth before the mother leaves the rookery on her first of many feeding trips. Like phocid pups, otariid newborns rarely leave their mothers during the first few days following birth. Given the colonial nature of most otariids, a pup which is separated from its mother at this age risks serious injury from neighbouring females and juvenile and adult males. When mothers leave the rookery to feed, however, the behaviour of the two families diverges with otariid pups aggregating at the periphery of the colony perhaps to reduce the risk of injury from other mothers and males. In these groups, pups socialize and play with one another. A common feature of play, especially among

male pups, is mock-fighting in which from an early age elements of the adult postures are apparent (Gentry, 1975). Unlike most phocids, otariid pups generally enter the water early in lactation and begin to feed independently prior to weaning. Thus at weaning, otariids are behaviourally more developed than phocids.

Phocid and otariid pups appear to differ in their ability to recognize their own mothers. This conclusion is consistent with general differences in the social organization of phocids and otariids on the breeding grounds, which reflect adaptations to breeding on ice versus land, and with several other lines of evidence, but experimental studies are lacking. By its very nature ice is an unstable and unpredictable environment in which space is not limiting. Thus in contrast to land-based rookeries, the density of mother-pup pairs in ice-breeding species is low. Furthermore, mothers in these species rarely leave their offspring for more than several hours. Under these conditions of low density of mother-pup pairs and almost constant attendance of the pup by the mother, recognition may not have been strongly selected. On the other hand, in many otariid species and highly colonial phocids such as the elephant seals, the high density of individuals at breeding colonies results in frequent disturbance which often leads to separation of mother-pup pairs. This, coupled with the mobility of otariid pups when mothers go to sea on feeding trips, would provide a selective advantage to pups that could recognize their mothers. This is particularly important in otariid species as pups which are separated from their mothers have essentially no opportunity to obtain milk from strange mothers. Finally, there is the observation that in highly colonial pinniped species both mother and pup exhibit vocalizations during the lactation period that could be used in recognition, whereas in ice-breeding phocids mothers are generally silent during lactation, thus reducing the kinds of sensory information that could be used by pups to recognize their mothers, particularly at long distances.

Given its importance to the survival of the pup, the paucity of studies of suckling behaviour is surprising. Quantitative data on age-related changes in suckling parameters over the course of lactation are lacking for most species. This is particularly true in the Otariidae. Yet suckling parameters ought to reflect pups' energy demands and the females' ability to meet these demands and thus should provide a powerful tool for comparative analysis of maternal care. For example, the longer the duration of suckling sessions, the shorter the inter-suckle interval, and the greater the total daily suckling time in otariids compared to phocids is likely an adaptation to the relative availability of otariid and phocid mothers. However, only when data are available for more species will we be able to address hypotheses concerning the ecological factors influencing pup development and maternal care.

The frequency of fostering also differs within and between pinniped families. Despite the high density of otariid rookeries, fostering is rare and therefore pups which become prematurely separated from their mothers early in lactation face a certain death. However, the situation is more complex in phocids. In at least three land-breeding species (the northern elephant seal, the grey seal, and the Hawaiian monk seal) foster behaviour is common, but in ice-breeding species it appears to be rare. Although density is assumed to have an important influence on the frequency of fostering in the grey seal and the northern elephant seal (Fogden, 1971; Reidman and Le Boeuf, 1982), it cannot account for the level of fostering observed in the monk seal where average nearest neighbour distance is 14 m (Boness, in press).

It seems that poorly developed mother-pup recognition, coupled with frequent disturbance by males and other females leading to separation of mother and pup, play critical roles in the incidence of fostering.

Quantitative studies on the ontogeny of pup behaviour are needed on a broad range of species. Species differences in the proportion of time that pups spend in various activities are likely to provide additional insight into the behavioural adaptations of pups to differences in breeding habitat, environmental variation, the density of individuals in breeding colonies, and maternal attendance. Of particular interest will be comparative studies on different populations of the same species in different environments, such as the grey seal which breeds on land and floe ice. Such studies are required if we are to answer questions such as what is the relative importance of energy intake and behaviour on the growth rate of pups in different species, are differences in the behaviour of male and female pups found only in sexually dimorphic species, and what determines the duration of the post-weaning fast.

Several authors have reviewed the contrasts between phocid and otariid maternal rearing strategies (Oftedal *et al.*, 1987). However, these two patterns are clearly extremes at either end of a continuum. Within both families convergent solutions to the potential conflict between maternal foraging and nursing (Oftedal *et al.*, 1987) have evolved. For example, after a period of fasting, both harbour seal and Galapagos sea lion mothers begin to alternate between daily feeding trips at sea and nursing (Bowen and Oftedal, unpubl.; Trillmich, 1986b) to support the energy demands of lactation. Is there evidence of convergence in the behaviour of pups in these phylogenetically distant species that reflect the similarity in maternal strategies? Integrated quantitative studies of the behaviour of neonates, their mothers, and the energetics of lactation will provide valuable insights into these and other questions about the factors which have influenced the evolution of pinniped life histories.

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4

Communication in pinnipeds, with special reference to non-acoustic signalling

Edward H. Miller

4.1 INTRODUCTION

Communication is complex and variable in long-lived and adaptable species. In such species, communication is shaped by learning, personal histories, variable social and ecological circumstances, and bonds between individuals. It is also often extremely subtle, especially in highly social species, in which individuals continually appraise and respond to the general social setting and to features of others around them: movements, activity levels, distances, postures, sounds, smells, and appearance. Much communication therefore takes place through unspecialized and undirected signals – sources of information that have not specially evolved or developed to be informative. In pinnipeds, the processes of communication are complicated further because all species communicate in both air and water. These media have different effects on sensory and motor abilities, and on physical aspects of signal transmission (Hopkins, 1987; Rogers and Cox, 1987; see Chapter 7).

How does communication function and how has it evolved in the face of such diverse and variable circumstances? Pinnipeds are good models to answer such questions. Many species can be observed in great detail at close range in the wild and in captivity, and they employ numerous conspicuous, frequently used communication patterns that are easy to describe and quantify. Furthermore, in many situations it is possible to obtain long-term observations (even over

years) of known individuals. Important and topical kinds of studies, such as of development or combat behaviour, can therefore be carried out. Many pinniped species have broad geographical and ecological ranges, so comparative intraspecific studies are possible. Finally, there is a variety of closely and distantly related pinniped species that offer opportunities for studying trans-specific trends in communication.

In this chapter I consider pinniped communication from several perspectives, with emphasis on signal structure and variation (Section 4.2), general processes of communication (Section 4.3), and ecology and evolution (Sections 4.4, 4.5). I begin by discussing signals that range from being completely unspecialized to highly specialized for communication (Section 4.2.1). With such a broad range, signal forms need to be well described, so I summarize some ways to describe and categorize motor patterns (Section 4.2.2). Further, variation in the structure of signals is important at all levels from individuals to species; I therefore discuss quantitative structural variation in signals, and repertoire organization (Section 4.2.3). After this treatment of signal structure and variation I introduce general characteristics of the communication process, with particular reference to W. J. Smith's model (Section 4.3), using external appearance of pinnipeds as an example (Section 4.3.2). Combat behaviour and the communication of threat are strongly developed in many species of pinnipeds; I treat those topics in Section 4.4, with special reference to games theory. In Section 4.5, I consider some ecological topics (time/activity budgets and rhythms), then in Section 4.6 discuss differentiation (species differences in signals, relationships of communication patterns to phylogeny, and geographic variation). I conclude with some recommendations for future research (Section 4.7).

Most behavioural research on pinnipeds has been carried out on the Otariidae, because otariids are much easier to observe over long periods than are the Odobenidae and most of the Phocidae. Thus the Otariidae and land-breeding phocids dominate the examples I use. Previous reviews of pinniped communication include Poulter (1968), Evans and Bastian (1969), Winn and Schneider (1977), Krushinskaya and Lisitsyna (1983), and Watkins and Wartzok (1985).

I follow nomenclature used in Ridgway and Harrison (1981a, 1981b) except for several species with more interesting common names: Steller sea lion (not northern sea lion) (*Eumetopias jubatus*), and Hooker sea lion (not New Zealand sea lion) (*Phocarctos hookeri*). I also follow Oliva (1988) in the use of *Otaria byronia* (not *O. flavescens*) for the southern sea lion, and Bonner (1988) for the spelling of the specific epithets *weddellii* and *rossii*.

4.2 SIGNAL STRUCTURE AND VARIATION

In this section, I introduce some concepts and terms in communication research, then discuss structure and variation in motor patterns. Many examples refer to general behaviour that is not specialized for communication, but the principles are equally applicable to specialized communicative behaviour.

4.2.1 Formalized and unformalized signals

Communication as a class can be loosely characterized as a process by which one animal's behaviour influences the behaviour of another, usually by just altering the likelihood of what a recipient will do next. Obviously, individual signalling events need not do this in all cases (Altmann, 1967). Behaviour that is evolutionarily specialized to communicate has traditionally been called *display* behaviour: probably all kinds of pinniped vocalizations are displays, for example (Moynihan, 1970). A single kind of display is often received by several sensory channels, and may use special structures like glands, ruffs, crests, coat patterns, or cephalic adornments. Displays have evolved from unspecialized behaviour and structures through an evolutionary process termed *ritualization*. The ontogenetic counterpart to ritualization, which also leads to formalization of signals, can be termed *conventionalization* (Smith, 1977; Morris (1957: 1) refers to it as *stylization*). Highly formalized behaviour is typically complex, stereotyped, and species-specific. Formalized signalling behaviour tends to be striking and predictable, particularly during breeding activities and intense competition by males for mates or territory (Krushinskaya and Lisitsyna, 1983). Thus formalized signalling, especially display behaviour, has been the most intensively studied and is the best-known kind of communication.

Research on displays has been strongly biased toward displays that are specialized in form, whereas they may often be unspecialized in form but specialized in other ways. For instance, displays may be evolutionarily specialized in temporal patterning (e.g. in being rhythmic or bouted),* or in being closely tied to particular contexts. In addition, a particular kind of behaviour can be used in both specialized and unspecialized ways, at different times or in different contexts (Baerends, 1975; Popp, 1987). An example of general

* Such specializations can occur in qualities that are independent of the physical specializations of the basic display units themselves (Smith, 1986a; see p. 159). For example, specialization of signalling through temporal properties is seen in barking sequences of the black-tailed prairie dog (*Cynomys ludovicianus*; Smith *et al.*, 1977), and specialization through sequencing occurs in the song of the yellow-throated vireo (*Vireo flavifrons*; Smith *et al.*, 1978).



Figure 4.1 Alarmed female and calf Pacific walruses (*Odobenus rosmarus divergens*) fleeing to the water. In the foreground two females are guiding their calves toward the water. This is an example of communication between females and calves involving little or no use of displays, taking place through their reactions, physical contact, movements, orientations, and so on. Photograph by L. M Shults; from Fig. 121 of Fay (1982).

behaviour that is communicatively significant when tied to a specific context is illustrated by sexual receptivity in female otariids: they become languid when they enter oestrus, and also stop resisting male approaches. Passivity by itself appears to be sexually stimulating to male pinnipeds, as seen in the remarkable observations of males defending, attending or copulating with dead individuals – even dead males of other species (Sivertsen, 1941; Carrick *et al.*, 1962; Peterson and Bartholomew, 1967; Miller, 1974; Wilson, 1979; Best *et al.*, 1981; Alcorn, 1984; Hawke, 1986). A second example of general behaviour that is specialized by being used in a particular context is that of female northern elephant seals (*Mirounga angustirostris*) resisting copulations with subordinate males, thereby alerting nearby dominant males, inciting competition among them, and increasing the likelihood that a resisting female will be fertilized by the locally dominant male (Cox and Le Boeuf, 1977; Cox, 1981; see also Boness *et al.*, 1982).

Ritualized display behaviour and accompanying morphological specializations abound in pinnipeds (Section 4.4). However, much or most communication occurs by means of relatively simple behaviour that is not specialized as displays and that has other functions in addition to communication (Moynihan, 1982; Figure 4.1). For example, female harbour seals (*Phoca vitulina*) in labour engage in

'frequent apparently aimless movements' (Lawson and Renouf, 1985: 396; Knudtson, 1974, 1977), which can provide socially useful information to nearby seals. Also in that species, females and pups maintain proximity to one another by mutual watchfulness and subtle dynamics of following and distance reduction (Lawson, 1983; Renouf *et al.*, 1983; Renouf and Diemand, 1984; Eliason, 1986). Intriguingly, female harbour seals do not vocalize to their pups, in contrast to related species (Fogden, 1971; Kaufman *et al.*, 1975; Riedman and Le Boeuf, 1982). Other excellent examples of unspecialized signalling are given by Sullivan (1979, 1982). The continuum joining unspecialized signals and displays in pinnipeds can be well illustrated by tactal communication through body contact, which I discuss next.

Passive body contact varies greatly among species in the extent to which it is tolerated or sought. In the bearded seal (*Erignathus barbatus*), leopard seal (*Hydrurga leptonyx*), Hawaiian monk seal (*Monachus schauinslandi*) and New Zealand fur seal (*Arctocephalus forsteri*) body contact is not tolerated except between females and pups, during fights, in precopulatory behaviour, in play, and in copulation; sleeping individuals that even casually touch one another with a flipper will withdraw it (Gwynn, 1953; Kenyon and Rice, 1959; Miller, 1971, 1974; Stirling and Warneke, 1971; Burns and Frost, 1979; Stirling, 1983; Fig. 4.2A). Incidental contact is tolerated within the dense breeding aggregations of northern fur seals (*Callorhinus ursinus*) and by resting harbour seals (Fig. 4.2B,F). More extensive contact occurs in the Australian/African fur seal (*Arctocephalus pusillus*), elephant seals (*Mirounga*), and all species of sea lions; an extreme occurs in the walrus (*Odobenus rosmarus*) (Bartholomew, 1952; Fay and Ray, 1968; Stirling and Warneke, 1971; Gentry, 1975; Marlow, 1975; Salter, 1980; Krushinskaya and Lisitsyna, 1983; Stirling, 1983; Trillmich and Trillmich, 1984; Warneke and Shaughnessy, 1985; Figure 4.2C-E).

More elaborately structured tactal communication (conventionalized or ritualized, or both) occurs in special circumstances, as when young walruses or harbour seals ride on the backs of their swimming mothers, when the mothers hold them between the fore-flippers while swimming, and during resting or nursing (Scheffer and Slipp, 1944; Fisher, 1952; Venables and Venables, 1955; Hewer, 1974; Wilson, 1974a; Sullivan, 1979; Fay, 1982; Miller and Boness, 1983; Eliason, 1986; Fig. 4.3A,B). Elaborate tactal communication occurs during agonistic encounters between walruses in striking with tusks and in the use of flippers (Fig. 4.3C); it is also an important component in pinniped copulation as animals lie in extensive contact, when males engage in neck-biting, and when female otariids 'resist' near the end of copulation (Hamilton, 1934; Laws, 1956; Le Boeuf, 1971; Le Boeuf *et al.*, 1972; Miller, 1974; Marlow, 1975; Krushinskaya and

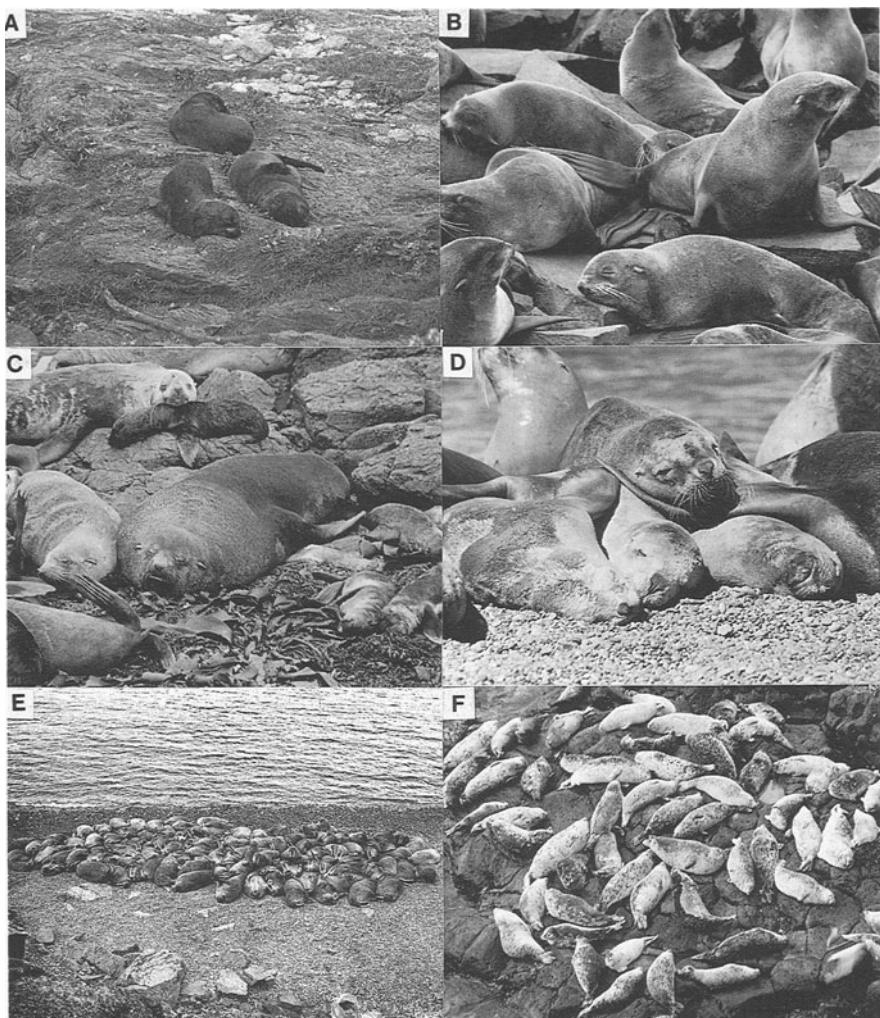


Figure 4.2 Examples of spacing and body contact (tactual communication) that are not evolutionarily specialized as displays. A - Typical spacing in a pod of pups of the New Zealand fur seal (*Arctocephalus forsteri*). B - Incidental contact between breeding female northern fur seals (*Callorhinus ursinus*); such tolerated contact would be exceptional in *A. forsteri*. C - Moderate contact between breeding male and female Australian fur seals (*Arctocephalus pusillus doriferus*). D - Typically extensive contact among pre-breeding southern sea lions (*Otaria byronia*). E - Typically extensive contact among summering male Pacific walruses (*Odobenus rosmarus divergens*). F - Incidental contact between resting harbour seals (*Phoca vitulina*) during the breeding season.

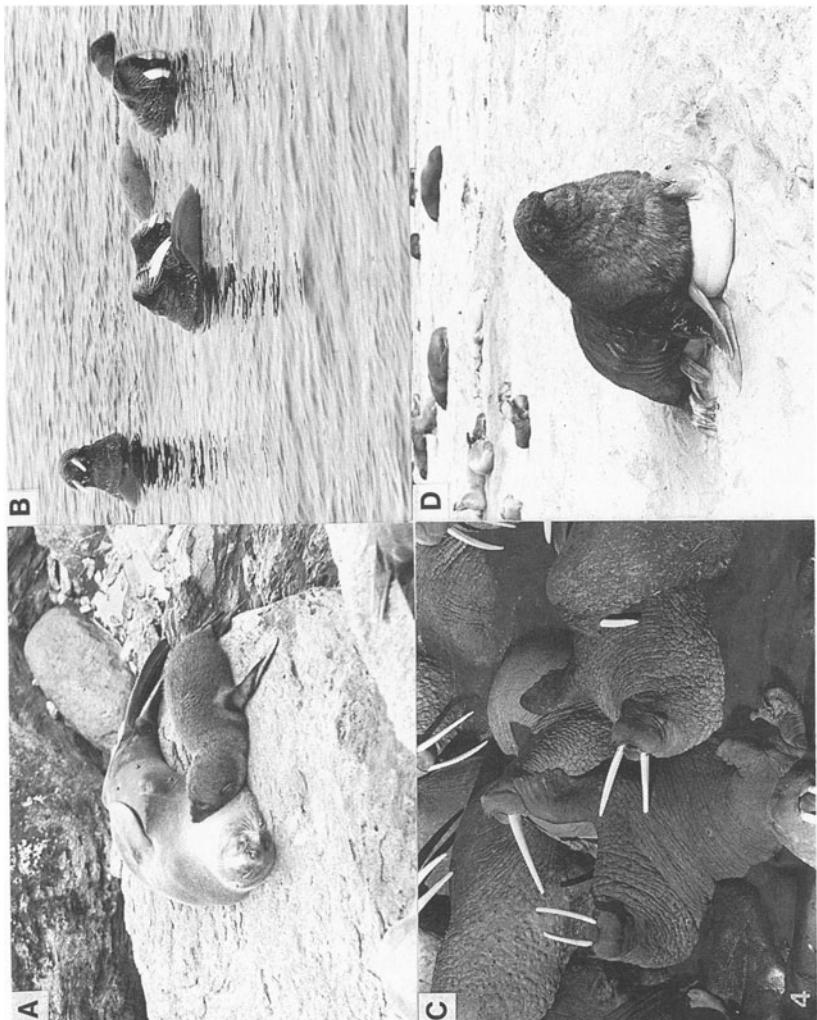


Figure 4.3 Examples of formalized tactal communication. A - Young pup New Zealand fur seal (*Arctocephalus forsteri*) resting against its mother. B - Calf Atlantic walrus (*Odobenus rosmarus rosmarus*) nursing while vertically upside down against its mother's ventral surface. C - Male Pacific walrus (*Odobenus rosmarus divergens*) using flipper during an agonistic interaction. D - Female Hooker sea lion (*Phocarctos hookeri*) biting male's chest near the end of copulation (photograph by H. A. Best). B is from Fig. 4 of Miller and Boness (1983).

Lisitsyna, 1983; Figure 4.3D). Juvenile grey seals (*Halichoerus grypus*) solicit play by laying the head over the back of another individual (Wilson, 1974b). Elaborate, dynamic tactal communication occurs in aquatic social 'rolling' behaviour in the harbour seal, which can last for several hours (Venables and Venables, 1955, 1957, 1959; Sullivan, 1979, 1981; Thompson, 1988; also Beier and Wartzok (1979) and Gailey-Phipps (1984)). Sandegren (1976b: 161) described similar interactions between male and peri-oestrous female Steller sea lions: 'in the water, male and female may tumble about in the most gracious manner for 10-15 minute periods and longer, more or less continuously touching each other' (see also Sandegren, 1975).

Nuzzling, which has tactal and olfactory components and employs the strongly developed mystacial vibrissae, occurs between females and pups of all pinniped species (Miller, 1975a; also Ling (1966, 1972), Stephens *et al.* (1973), Dykes (1975) Fay (1982), and Kastelein and van Gaalen (1988); Figure 4.4A,B). New Zealand fur seal females often press themselves repeatedly on top of their newborn pups (Miller, 1971; McNab and Crawley, 1975; Figure 4.4C,D), and otariids generally show mouthing and lifting of newborn pups by their mothers (Miller, 1974; Krushinskaya and Lisitsyna, 1983). A remarkable form of tactal communication is that of male crabeater seals (*Lobodon carcinophagus*) consorting with females: they 'maintained almost constant physical contact ... through a number of typical postures. These postures included lying perpendicular to each other, with the male's head resting on the female's side; lying back to back; and lying with the male's chest over the female's back, with his foreflipper extended over her side' (Siniff *et al.*, 1979: 2249; see their Fig. 6). Hamilton (1934: 300) described tactal communication between male and female southern sea lions: they 'sit facing one another and with snaky movements twist their necks from side to side, thus caressing one another on the front and sides of the neck and occasionally rubbing their mouths together, while the cow at times grips the neck of the male in her teeth but does not bite.' I have seen similar behaviour in the Australian fur seal (*A. pusillus doriferus*), and Lisitsyna (1976) described it for the Steller sea lion (for a comprehensive description of patterned tactal communication during 'courtship' in the latter species, see Sandegren (1975, 1976b); see also Krushinskaya and Lisitsyna, 1983).

Tactal communication thus illustrates the continuum that exists between unritualized and highly ritualized signals: these do not simply form two distinct classes of communicative behaviour (Gautier and Gautier, 1977). Tactal signals (and signals in general) that differ in their extent of ritualization can be associated and combined in diverse ways. Thus, in the harbour seal, eight behavioural patterns occur frequently in agonistic interactions on the

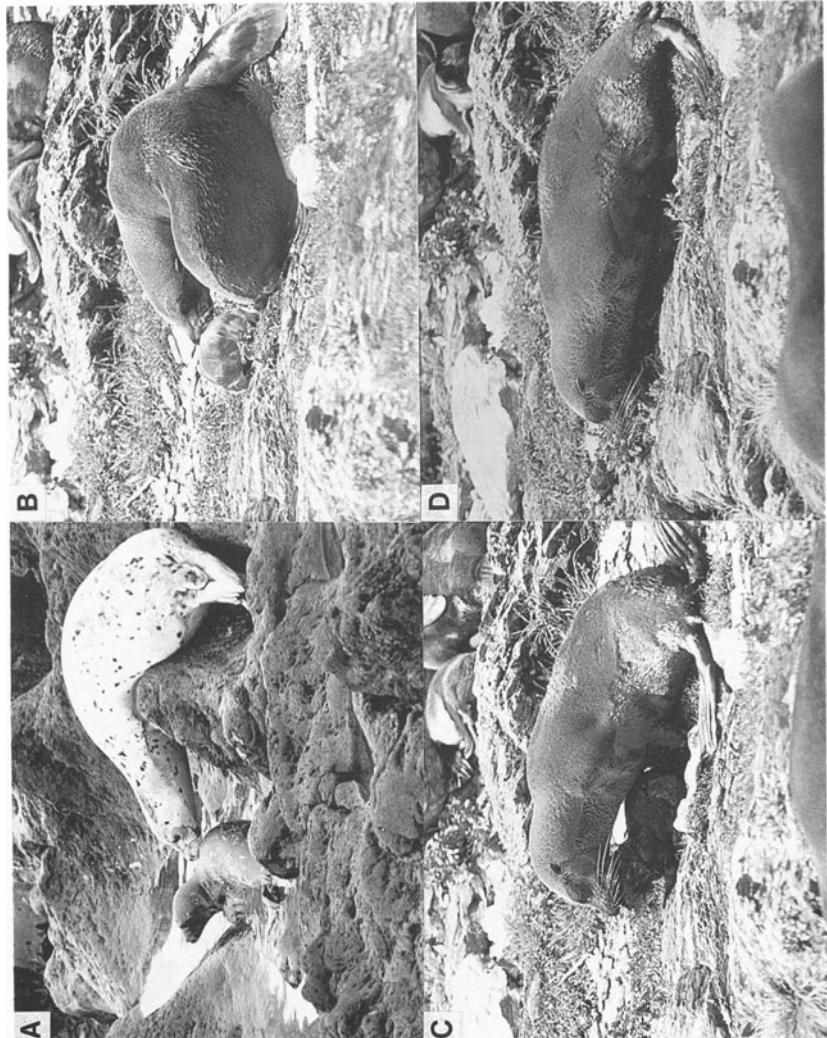


Figure 4.4 Examples of formalized tactual communication between females and newborn pups. A - Female harbour seal (*Phoca vitulina*) nuzzling her pup. B - Female New Zealand fur seal (*Arctocephalus forsteri*) nuzzling her pup, still encased in the amniotic sac. C, D - Sequence showing same female lowering herself (C) then pressing herself down on her pup, presumably to stimulate it.

Table 4.1 Occurrence of behavioural patterns alone and in combination with others, for agonistic interactions of the harbour seal (*Phoca vitulina*) on hauling ground^a

a Head-up stare	27						
b Close-mouthed head thrust	8	269					
c Open-mouthed head thrust	5	35	190				
d Foreflipper scratch	3	13	43	308			
e Foreflipper wave	7	51	15	135	223		
f Foreflipper erect	2	0	0	0	34	27	
g Growl	16	25	125	19	13	0	12
	a	b	c	d	e	f	g

^a Data are from Table 6 of Sullivan (1979; see also Sullivan, 1982). Entries on the main diagonal indicate the number of times that each pattern occurred alone in interactions; thus, growl (g) occurred alone 12 times. Other entries represent the total occurrences over more complex interactions. For example, the g-b entry of 25 is the sum of g-b ($n = 20$ interactions) and g-b-c ($n = 5$). The total of the entries is greater than the number of interactions, because complex interactions are represented in several different cells.

hauling ground (Sullivan, 1979, 1982). These include displays such as growling, and holding erect or waving the foreflipper, plus simple unritualized signals like lifting the head and looking directly at another seal. In his study, Sullivan (1979) observed that about 30% of the seals' responses involved two or more behavioural components (excluding the category 'moving away'), and that components overlapped extensively in occurrence (Table 4.1). Composite signals are widespread in pinnipeds, as in mammals generally (Altmann, 1967).

Signals and signalling behaviour are clearly complex and subtle, and differ importantly across species. To appreciate signal function and functional differences it is essential to have clear detailed descriptions of signalling behaviour. I discuss some approaches to description in the following section.

4.2.2 Describing, naming and categorizing motor patterns

(a) Description

Signalling behaviour is difficult to describe because it is variable and multidimensional, has an enormous range of relevant temporal characteristics, and can be described in many different ways. Some can be described and quantified relatively easily and in standardized ways [e.g. acoustic signals; see Watkins (1967, 1974), Greenewalt (1968), and Marler (1969)], but even those descriptions are beset with problems of establishing and classifying meaningful categories. In studies on communication, descriptions of general motor patterns as well as those of specific display types should be done, because any

kind of behaviour can be socially informative and thus important in a species' communication system (Kiley-Worthington, 1976, 1979; Smith, 1977).

Comprehensive general-purpose descriptions of motor patterns provide essential benchmarks for comparative studies (e.g. Mori, 1984; de Waal, 1988). Such comprehensive descriptions, or *ethograms*, are generally prepared for individual species, though they can also be developed for other classes of interest such as genera, populations or particular age groups (Miller, 1988; Immelmann and Beer, 1989). Ethograms should be as complete as possible. They should include detailed written descriptions, illustrations, and quantitative measures (on durations, frequencies, rates, etc.), and should use several 'frames of reference' (Golani, 1976; Miller, 1988). The latter include description of the positions and movements of body parts in relation to:

1. A fixed frame of reference that is external to the animals (Figure 4.5A);
2. Specific stationary or fixed features of the environment (Figure 4.5A);
3. Other body parts (Figure 4.5B); or
4. Non-stationary features of the environment (especially biotic features, like conspecific individuals; Figure 4.5C).

One goal of studies on pinniped communication should be to establish baseline descriptions of signalling movements and postures within a continuous spatiotemporal framework (Sheets-Johnstone, 1983). This goal can be met by illustrating positions and postures at known time intervals (e.g. Figure 4.6A), or by abstracting chosen features of position and displaying them graphically with temporal variables shown or built in (Figure 4.6B). Key features of motor patterns used by communicating pinnipeds are often three-dimensional and have important temporal characteristics, so more complete systems for recording movement over time are called for. Promising applications lie in the Eshkol-Wachmann movement notation, promulgated by Golani and others (Figure 4.6C,D; Golani, 1976; Golani *et al.*, 1979; Pellis, 1982a, 1982b; Eilam and Golani, 1988). In this system, movements of chosen body parts are described over time within one or more prescribed frames of reference (absolute, body-wise, partner-wise; see Figure 4.5). Analysis of videotape or movie film is generally necessary, and in its most complete applications the Eshkol-Wachmann system is labour-intensive. However, it is also adaptable and versatile, objective, repeatable, and applicable to complex motor patterns like those used in agonistic encounters. Furthermore, specific kinds of quantitative and graphical features can be emphasized or isolated from it (e.g. Eilam and Golani, 1988).

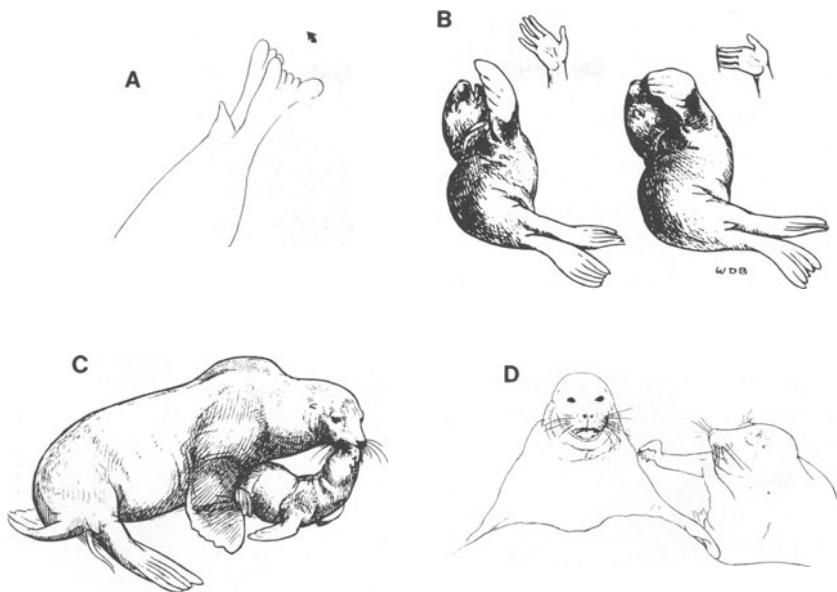


Figure 4.5 Examples of different frames of reference in behavioural description. A - 'Lobtailing' harbour seal (*Phoca vitulina*) can be described within an 'absolute' frame of reference, for example by the angle relative to the horizontal (here approximated by the water surface), and by reference to the external environment, here the water surface (e.g. by length of body out of water). B - Pup Steller sea lion (*Eumetopias jubatus*) performing foreflipper 'exercise' can be described by reference of body parts to one another ('bodywise' frame of reference); description could also be with reference to the horizontal or the substrate. C, D - Female and pup Steller sea lions rubbing noses (C) and foreflipper scratch by harbour seal (D) can be described with reference to the interactants' positions, distances, and orientations to one another (within a 'partnerwise' frame of reference). A is from Fig. 19c of Sullivan (1979); B and C are from Figs 36 and 23 of Sandegren (1970); and D is from Fig. 24 of Sullivan (1979) (= Fig. 1b of Sullivan, 1982).

In preparing ethograms, as in behavioural descriptions generally, categories must be defined (Altmann, 1967; Hinde, 1982). Several problems attend the establishment and naming of behavioural categories. First, is a category discrete, or does it grade into others? To what extent is a category comparable with that in another species? What are the hierarchical relationships among behavioural categories? What roles should structural and functional characteristics play in recognizing and naming categories (see Section 4.2.2(b))?

The establishment of categories begins with recognizing distinctive, discrete kinds of behaviour. It is not always feasible to describe behaviour in quantitative terms, but a quantitative example can serve for discussion here. Consider the angle of a seal's head relative

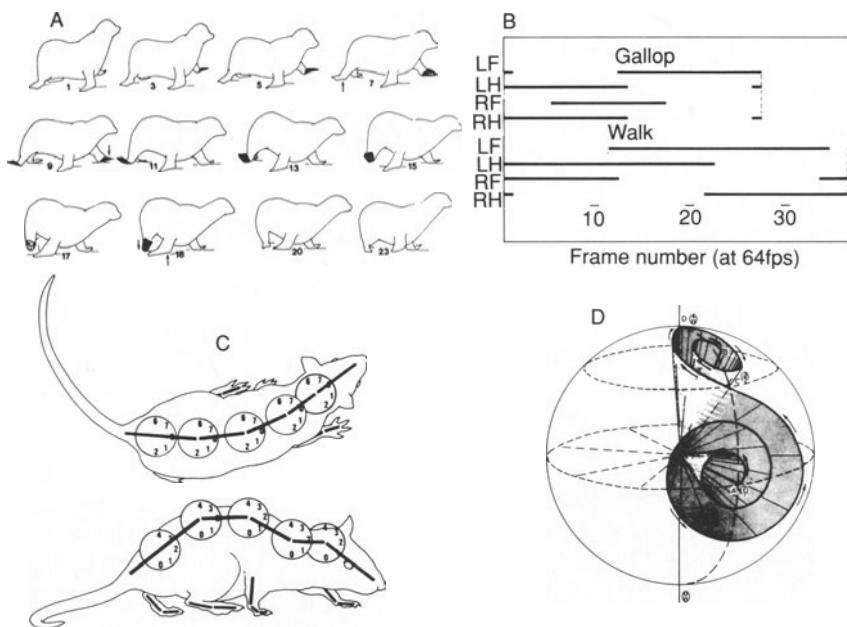


Figure 4.6 Methods of describing movement with a time base. A - Sequence of terrestrial locomotion by a California sea lion (*Zalophus californianus*). Numbers refer to motion picture frame numbers (at 64 frames per second (fps)). B - Graphical portrayal of 'gallop' and walk by a California sea lion. Contact of left and right (L, R) front and hind flippers (F, H) with the substrate are represented by horizontal lines. Numbers refer to motion picture frame numbers (at 64 fps). C - Dorsal and side views of Norway rat (*Rattus norvegicus*) during locomotion. The bars represent segments whose positions can be recorded over time. As depicted, movements of segments relative to one another would be recorded ('body-wise' frame of reference). The coordinate system used is shown by circles and numbers. For example, the rat's head position as seen from the side would be recorded as '1' relative to the neck segment. D - The extremity of a segment (e.g. limb) moves on the surface of an imaginary sphere. The trajectory shown here could be that described by the rat's head segment relative to its neck segment, with the sphere being centred on the 'joint' between the two segments. A is from Fig. 8a of English (1976) (= Fig. 7 of English (1974)); B is from Fig. 7 of English (1976) (= Fig. 5 of English (1974)); C is from Fig. 1 of Golani *et al.* (1979); and D is from Fig. 2 of Golani (1976) (= Fig. 9 of Golani *et al.* (1979)).

to the horizontal, with a range from 0 (with the seal's head horizontal) to 90° (with the seal's head at the upright, which is often called bottling; Figure 4.7). A random sample of angles could reveal a clear unimodal frequency distribution, which suggests that only one behavioural category should be recognized (Fig. 4.7I). In contrast, clear bimodality could be found, suggesting two behavioural categories (Figure 4.7 IV). But if many observations occur at

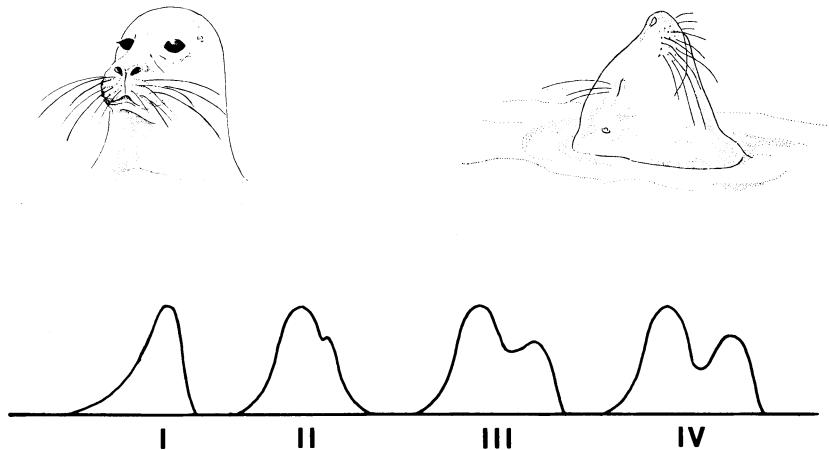


Figure 4.7 Hypothetical example of harbour seal (*Phoca vitulina*) head angle relative to the horizontal, to illustrate problems in delimiting behavioural categories. The frequency distribution of head angles (from 0 to 90°; the latter is often referred to as bottling) could range from clear unimodality (I) to clear bimodality (IV) (see text). From Figs 17 and 18 of Sullivan (1979) (top), and Fig. 3 of Miller (1988) (bottom).

intermediate values, should one or two categories be recognized (Fig. 4.7 II–III)? The answer to this question depends upon a study's purposes and upon other kinds of information. In a purely descriptive and quantitative analysis, and with no other information, there is no basis for judging whether modes are 'real' because they have no particular biological significance. We might recognize two modes on structural grounds alone if they seem distinct enough, but we must be cautious in doing so because of the influence of sampling biases and of different frequencies of occurrence of behavioural acts. Say that one of two modes is over-sampled, perhaps because bottling tends to occur mainly offshore, where we sample less often. Alternatively, two modes may occur naturally at very different frequencies. In either case we could obtain frequency distributions like Figure 4.7 II or III, which need to be resolved with other information.

Several important classes of other information exist. First, the behaviour could be described in greater detail (with more information *intrinsic* to the pattern). Using the preceding example, one could note closure of eyes and nostrils, and lateral bending of the head, for example: if seals tend to close their eyes only when holding the head vertical it would be reasonable to recognize bottling as a separate category (Figure 4.8). Alternatively, or in addition, information *extrinsic* to the behaviour could be considered: gender, age, and social status; distance and orientation between the subject and other seals; or functional significance of the context in which behaviour is occurring. For example, if only reproductively active males hold the head

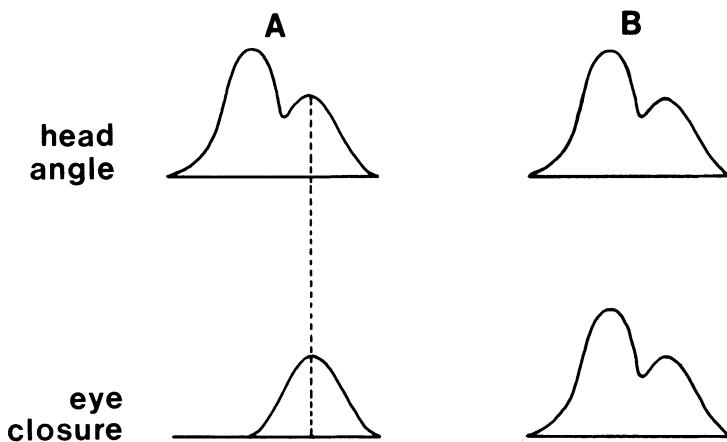


Figure 4.8 Hypothetical frequency distributions of harbour seal (*Phoca vitulina*) head angle relative to the horizontal, where eye closure occurs only when the head is held vertical (A), or varies in parallel over the whole range of head angles (B). From Fig. 4 of Miller (1988).

erect, or if the behaviour tends to follow only certain kinds of social interactions, then bottling could be considered as a distinct category.

A straightforward application of the preceding ideas could be made to the upright rest postures of otariids. These are important static-optical signals, especially during the breeding season. They are used by all age and sex classes, sometimes in highly specific contexts (Fig. 4.41). Do the postures form a structural continuum? Do they differ across age, sex, and context? Do any qualify as displays, in a strict sense?

(b) Naming

Behavioural patterns need to be named once categories for them have been established. The names chosen should not attempt to describe functions, contrary to the recommendation of Stirling and Roux (1987). In fact it is best to avoid applying functional and interpretive terms, especially to low-level behavioural categories, because they are not descriptive, they imply functions that reflect an observer's view, and they are rarely comparable across age, sex or social classes, or across species. The term 'display' should be used only in a strict sense. Even well established terms, such as the 'Boundary Display' of otariids, can be grossly inaccurate when one considers the use of common motor patterns by pups, subadults, and adult females, and by breeding males in species without rigid territorial spacing systems (e.g. Peterson and Bartholomew, 1967; Rand, 1967; Marlow, 1975; Krushinskaya and Lisitsyna, 1983; Bonner, 1984; Campagna

and Le Boeuf, 1988b; Figure 4.22, 4.23). The trumpeted roar is a widespread long-distance call used predominantly by breeding male otariids (Section 4.6). It is unquestionably homologous as a long-distance display across the species in which it occurs. Yet its attributes and functions differ, since some species use it at crowded colony sites with good visibility, where it is socially contagious (Peterson, 1965); in others, such as the Guadalupe fur seal (*Arctocephalus townsendi*), males are at much lower densities and most have no visual contact with neighbours (Peterson and Ramsey, 1969; see also Trillmich, 1984). Finally, the 'pup-attraction call' (PAC) has been used to describe a call type used by females towards their pups in species like elephant seals, where mothers and pups are in constant association, as well as in otariids, when females and pups reunite after females return from feeding trips at sea. Here the call types are neither functionally equivalent nor homologous. Eisenberg *et al.* (1975) discuss some general problems with naming acoustic displays.

(c) Categorization

Once behavioural patterns have been named, they need to be categorized. Methods for categorizing motor patterns depend upon how we view the function, causation and physiological organization of motor behaviour (Baerends, 1975; Hinde, 1982). For example, it is useful to describe and conceptualize communicative behaviour as though it were organized hierarchically, even though the neuromuscular bases of behaviour may not be organized that way (e.g. Nelson, 1985). Even so, it is difficult to establish a coherent hierarchical description based on structure over a broad range of behaviour patterns because several major kinds of behaviour typically occur simultaneously, behavioural acts can occur alone or in diverse combinations with other acts, and single behaviour patterns generally have several functions (Table 4.1). Practically, it is often best to emphasize specific structural characteristics of behaviour at low levels of a behavioural inventory (e.g. 'bark'), and general functional characteristics at high levels (e.g. 'territorial signals') - in which low-level components such as barks may occur in more than one category (Hinde, 1982). Such an approach permits motor patterns to be characterized in a flexible manner, rather than rigidly classified, and allows increasingly fine descriptions to be incorporated at lower levels. It also allows low-level patterns to be combined as necessary, as when describing composite signals. A danger to this approach lies in the assignment only of dominant functions to signal classes. If one assigned certain upright postures (termed 'full neck display' by Stirling (1970) and Bonner (1981a)) to male territorial signalling, for

example, one would be less likely to recognize the behaviour in pups, females, and other classes, where it also occurs yet clearly has different functions (Fig. 4.41; see also remarks above about 'boundary display'). There is no formula to avoid this sort of problem, except to continually improve and refine descriptions, to work progressively towards signal categories rather than start out with them, and to make explicit that functional categories categorize *only* functions – most or all displays will occur in more than one such category.

In summary, it is important yet difficult to describe behaviour rigorously, fully, variously, and in standardized ways. There are many ways to describe behaviour, depending on a study's purposes. The discreteness of behavioural categories is important to establish; the boundaries can often be clarified with additional structural and contextual information. Once established, behavioural categories are essential for comparative studies within and across species. However, behaviour is rarely comparable in structure and function (even across individuals!), so behavioural categories should be reassessed frequently (Caryl, 1979; Kroodsma, 1982). Behaviour should be described and labelled in non-interpretive ways, especially with respect to basic motor patterns.

Lewontin *et al.* (1984: 247–250) summarize some important problems and errors in the description of social behaviour: arbitrary agglomeration or division of categories; reification; inappropriate and misleading use of metaphors; and conflation of different phenomena under a single rubric. All these apply to the description of signals.

4.2.3 Signal variability and repertoire organization

(a) Signal variation and 'grading'

How and why do signals vary, and how is signal variation related to signal function and repertoire organization? Any sample of signals exhibits variation (Altmann, 1967; Struhsaker, 1967; Klingholz and Meynhardt, 1979; Figure 4.9), and it is important to fully analyse it (Green and Marler, 1979). Such analyses provide standards for comparison and reveal broad trends that may be of physiological, ecological, and evolutionary interest. For example, temporal measurements on vocalizations tend to vary more than those related to frequency, even though the latter generally have higher levels of measurement error (see Miller, 1986). Thomas and Kuechle (1982) reported data on Weddell seal (*Leptonychotes weddellii*) vocalizations that illustrate this: estimates of upper frequency for 21 call types had coefficients of variation (CVs) ranging from 0 to 59%, whereas CVs for temporal measurements on the same call types ranged from 20 to 195% (Figure 4.10). Similar trends are apparent for underwater

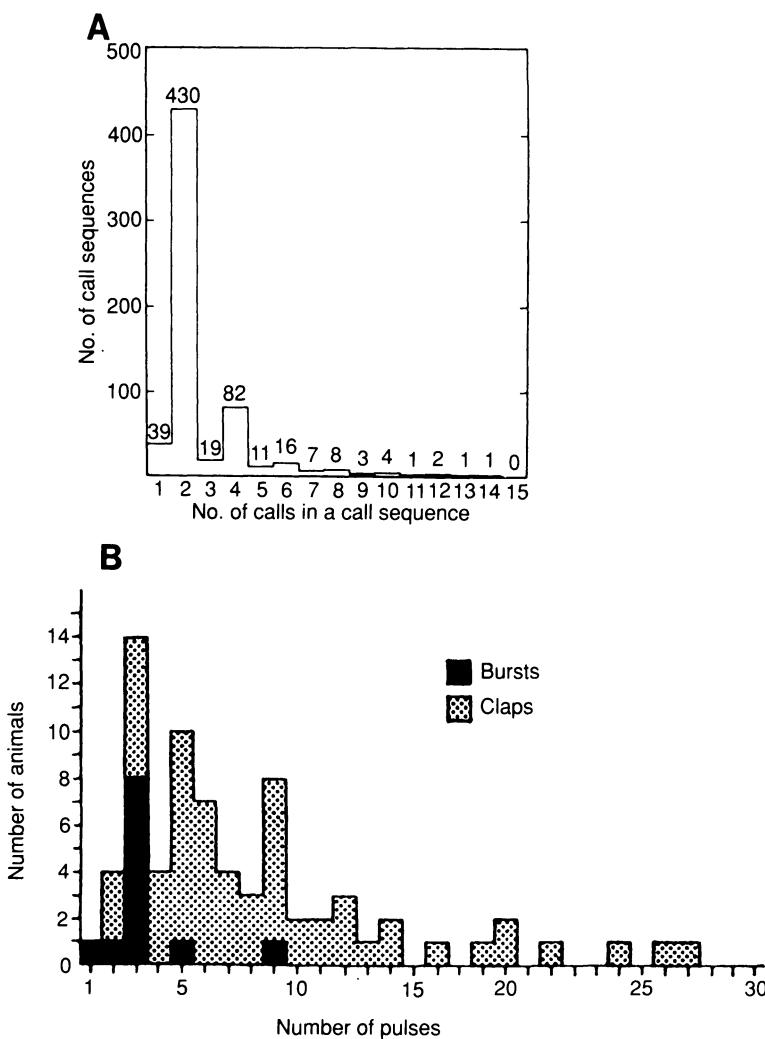


Table 4.9 Examples of structural variation in signals: variation in the number of elements per vocal utterance. A - Frequency distribution of number of calls per sequence, for underwater call sequences of harp seals (*Phoca groenlandica*) during the breeding season. B - Frequency distribution of number of pulses per call, for threat calls of male northern elephant seals (*Mirounga angustirostris*) during the breeding season (two kinds of utterances are distinguished). From Fig. 5 of Watkins and Schevill (1979) and Fig. 6 of Shipley *et al.* (1981)

vocalizations of the leopard seal, with CVs for various measures on duration, number of pulses (related to duration), and frequency averaging 39.9, 21.6, and 9.9% respectively (based on data in Table 1 of Stirling and Siniff (1979); two extreme values of 245% were excluded).

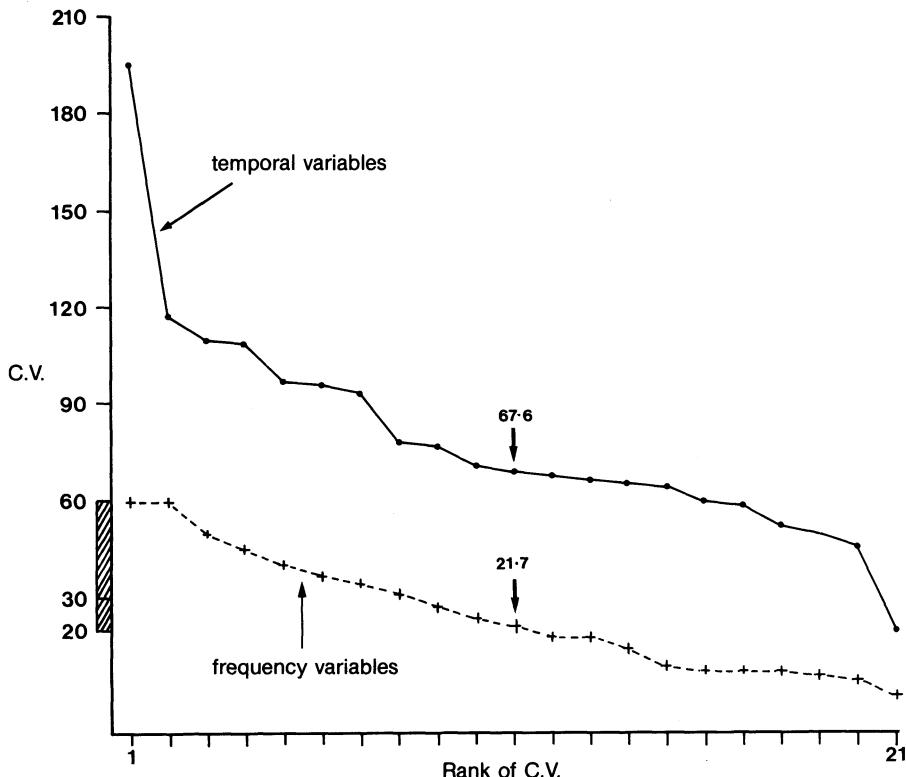
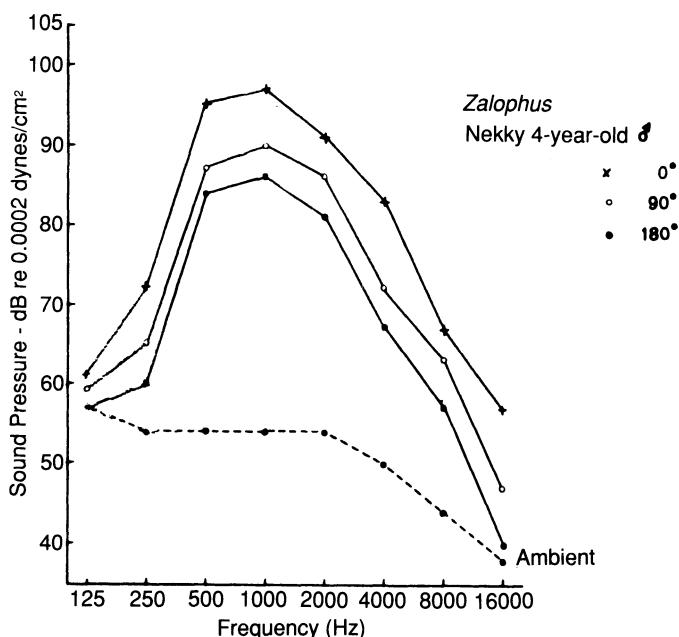


Figure 4.10 Variability profiles, showing estimates of the coefficient of variation (CV) for temporal and upper frequency measurements on 21 call types of the Weddell seal (*Leptonychotes weddellii*). The call types are arranged along the horizontal axis from most to least variable. Medians for each profile are shown. The hatched segment along the vertical axis shows overlap between CVs of frequency and temporal variables. This form of presentation is that advocated by Yablokov (1974). Data were computed from those in Table I of Thomas and Kuechle (1982), for all call types with sample sizes of 5 or more. Some of the same data appear in Table 2 of Thomas and Stirling (1983) but there are discrepancies between the two data sets; I therefore used the earlier-published one.

Such general summaries are revealing, and need to be complemented with detailed studies on signalling behaviour. The importance of signal variation at this level can be illustrated by California sea lions (*Zalophus californianus*; Peterson and Bartholomew, 1967, 1969; Schusterman 1977, 1978). Males vary their barks according to activity, location, and social circumstances. Generally, males utter more barks per series and bark more rapidly when active or interacting socially (Table 4.2). Barks are highly directional, so further information is made available to receivers simply by a sender's orientation: intensity of barks is highest when a sender is oriented

Table 4.2 Variation in characteristics of barking of two captive male California sea lions (*Zalophus californianus*)^a

<i>Nature of comparison</i>	<i>No. barks per series</i>	<i>No. barks per second</i>
Directed towards other male while stationary vs. while locomoting	6.7 9.7	- -
Directed towards other male vs. barks not directed	-	2.7 2.0
During boundary display vs. while in centre of territory	-	3.0 2.4
General undirected broadcast vs. during agonistic interaction	7.0 ^b 11.0 ^b	2.1 2.5
Underwater as general broadcast vs. during chase	-	1.0 1.4

^a Data from Schusterman (1977).^b Data on wild males from Table I of Peterson and Bartholomew (1969), in reference to 'routine patrolling' and 'threatening specific opponent'.**Figure 4.11** Relationship of the intensity of barks by a 4-year-old captive California sea lion (*Zalophus californianus californianus*) ('Nekky') to directionality and frequency. From Fig. 8.5 of Schusterman (1978).

directly towards a recipient, and a bark's intensity and frequency spectrum show characteristic differences at other orientations (Figure 4.11).

Clearly, an understanding of the behavioural significance of signal variation demands considerable information about the correlates of performance of each sort of variation and about signaller characteristics. This is not particularly true of communication over long distances, which is dominated by acoustic signals that must be simple, discrete, repetitive, and less reliant on contextual information. For short-range signalling, however, environmental interference with signal transmission is minor, several sensory channels can be used simultaneously, slight variations in signals can be introduced, and rich contextual information can be exploited. Grading refers to communication systems in which continuous variation operates (Kiley, 1972; Green, 1975; Marler, 1976; Gautier and Gautier, 1977; Marler and Tenaza, 1977; Green and Marler, 1979; Klingholz and Meynhardt, 1979; Miller, 1979; Maier, 1982; Nelson, 1985; Gyger *et al.*, 1987).

In graded communication, properties of signals can change gradually over a series, which permits a recipient to compare and contrast slight differences in successive repetitions, and to appraise longer-term trends over the series (e.g. in repetition rate, duration, or intensity). Such a graded system can be referred to as adjacent grading (Marler, 1976; Marler and Tenaza, 1977; Miller, 1979). More generally, signals that occur close together in time - not just in succession - may be more similar to one another than signals considered at random (Miller, 1979). At the opposite extreme, when recipients appraise structural variation in signals at random with respect to the temporal or sequential relationships of signals, the system can be referred to as non-adjacent grading. One problem with these appellations is that they apply only to extreme or highly specific situations. Numerous combinations are possible, involving continuous or discontinuous variation in signal structure.

In general terms, a graded system is one in which the structure of signals varies continuously, with receivers' assessments of signals, and responses to them, presumably changing accordingly (Green and Marler, 1979). However, physically different signals may be perceived to be similar, and physically similar signals may be perceived as different (a phenomenon termed categorical perception: Figure 4.12; Green and Marler, 1979).^{*} As well, any of the combinations just

* 'Categorization is a basic perceptual process by which animals recode variable stimuli into discretely different categories. This is thought to reduce neural information-processing requirements and to increase the speed and accuracy of critical perceptual judgements ... [the] process compensates for the variability [in signal structure]' (Nelson and Marler, 1989: 976).

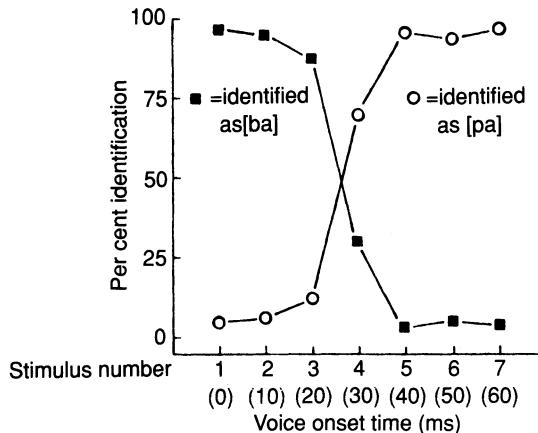


Figure 4.12. Discontinuous (categorical) perception over a continuous range of a signal's property (voice onset time). Stimuli in which laryngeal voicing starts early in the sound are perceived as the voiced consonant *b* by human listeners. Sounds with a later voicing onset are perceived as the unvoiced consonant *p*. A major discontinuity in perception occurs between 20 and 30 ms. From Fig. 9 of Green and Marler (1979).

mentioned may apply to only particular parts of a species' communication system (e.g. short-range versus long-range signalling). Thus the notion of grading is imprecise when applied to communication systems; the same weakness exists for the concept of *discrete* systems, in which different signal types are linked to discrete kinds of responses by recipients.

The notion of grading has become ambiguous for other reasons, too. First, 'grading' has become widely synonymous with 'continuous variation' in signal structure, and it is often unclear whether attributes of signals or classes of them are being referred to. Second, whether the similarity between signals is a function of their temporal proximity is not always specified. Finally, the term can refer to or confound different elements of the communication system (signal structure, context, receiver perception, etc.; Klingholz and Meynhardt, 1979). Each element of the communication system has components of variation that contribute to overall system characteristics, and these components need to be evaluated in their own right. Let me illustrate some of these points with reference to acoustic signals.

Continuous variation in acoustic structure can occur within a single continuous utterance, within a single train of utterances, or within a bout of either one of these. Physical properties commonly change gradually throughout single underwater calls of bearded seals, for example (Cleator, 1987; Cleator *et al.*, 1989; Figure 4.13G). Similarly, elements can be repeated with minor successive modifications of

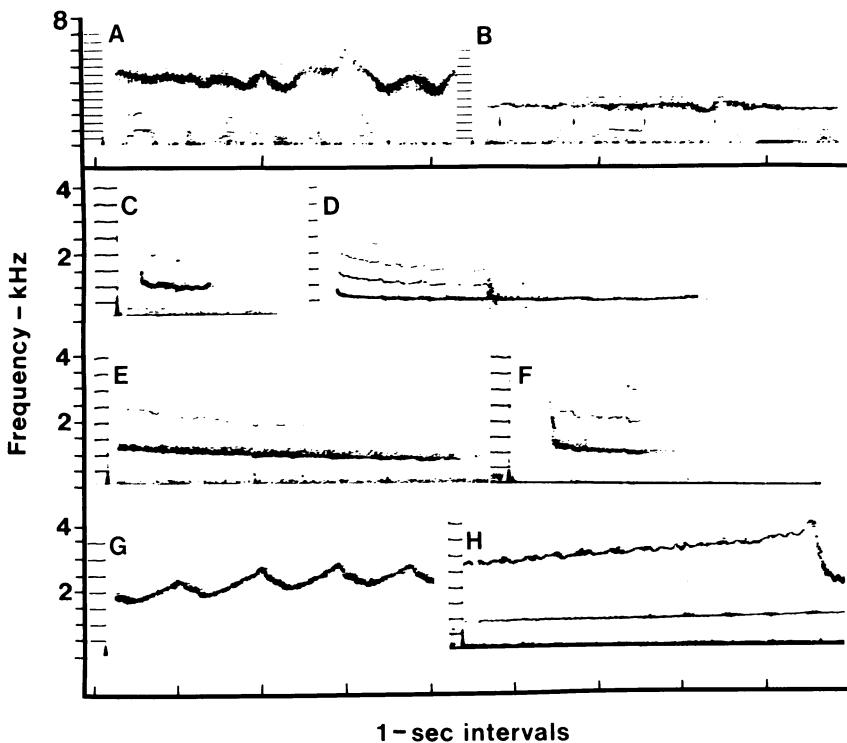


Figure 4.13 Sound spectrograms of vocalizations in the bearded seal (*Erignathus barbatus*). A - High-frequency trill; B - Ending of high-frequency trill; C - Brief descending trill; D - Low-frequency trill with several sidebands; E - Slowly descending trill; F - Rapidly descending trill; G - Trill with rhythmic, long-period frequency modulation; H - Two increasing-frequency trills, one ending with a descending-frequency portion. Analysing filter bandwidths: A and B - 45 Hz, C to H - 22.5 Hz. From Fig. 3 of Stirling *et al.* (1983).

frequency or duration, as in calls of calf walruses (Figure 4.14); Andrew (1969) and Lemon (1975) refer to this phenomenon as 'drift', and Marler and Tenaza (1977) comment on how it provides an ideal basis for listeners to detect directions and rates of change in acoustic signals. Finally, calls (or call sequences) can be organized into bouts within which they display similar trends; drift occurs at different hierarchical levels in such cases.

We can also consider structural variation without reference to the time base of a particular signalling event. For instance, physical characteristics of calls change gradually, throughout development. As walruses age, one call type becomes lower in frequency and elements in trains merge into continuous vocalizations (Miller and Boness, 1983; Miller, 1985; Figure 4.15). Shipley *et al.* (1986) have summarized age-related variation in threat calls of male northern

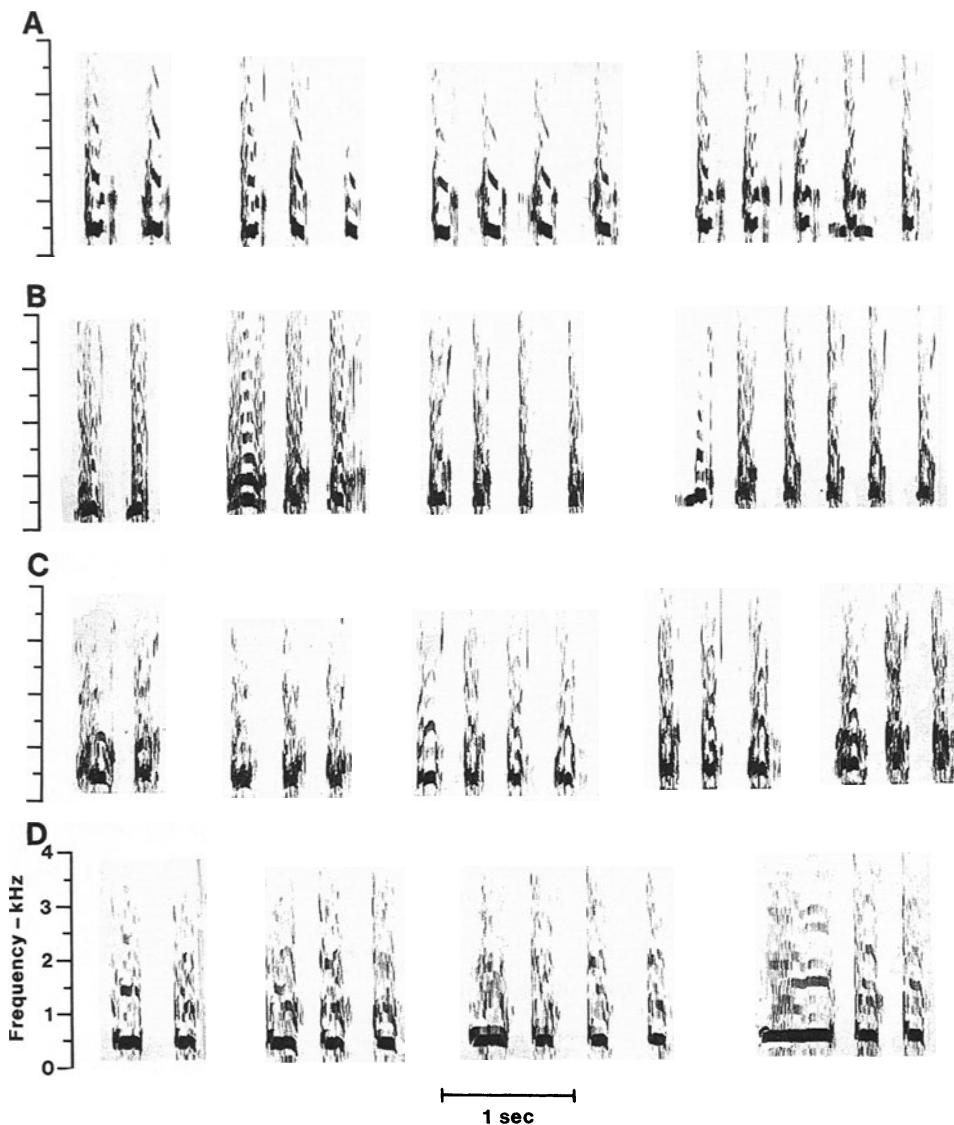


Figure 4.14 Barking by four young calves (<2 weeks old) of Pacific walrus (*Odobenus rosmarus divergens*). Barking in this species is not functionally similar to that in the Otariidae, and may not be homologous (see pages 209–211). A – Female-1: two-, three-, four-, and five-part utterances; B – Female-2: two-, three-, four-, and six-part utterances; C – Female-3: two-, three-, four-, then two more three-part utterances (the interval between the last two is natural); D – Male-1: two-, three-, four-, then another three-part utterance. Analysing filter bandwidth, 150 Hz. From Fig. 4 of Miller (1985)

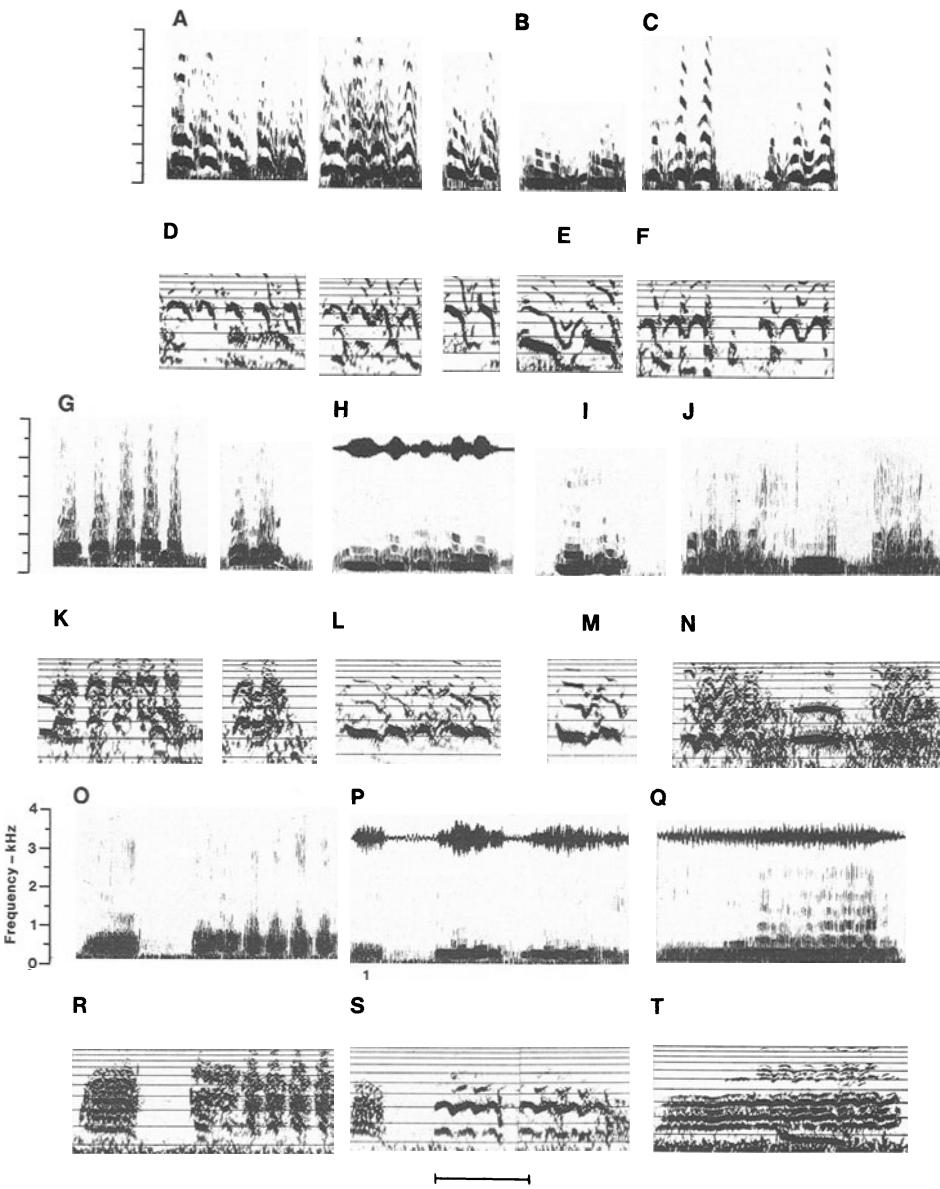


Figure 4.15 Developmental changes in barking of Pacific walrus (*Odobenus rosmarus divergens*). A - Barks (the second and third show merging) by 3- to 4-month-old calf [intervals between calls are arbitrary]. B - The last call of A, over range 8000 Hz. C - Merged barks, by same calf as in A (interval between calls is natural). D-F - Narrow-band sound spectrograms corresponding to A-C. G - Barks (the second merged) by 2-year-old (interval between calls is arbitrary). H, I - Merged barks by 2- or 3-year-old [with oscillogram above H]. J - Merged barks by 3- or 4-year-old (interval between calls is natural; the middle call is not from this animal). K-N - Narrow-band sound spectrograms corresponding to G-J. O - Long bark followed by partly merged bark by 3- or 4-year-old (interval between calls is natural). P - Sequence of roar by female in mild threat (I), then two merged barks (the first of three parts, the second of four) by 4-year-old [oscillograms are shown above; intervals between calls are natural]. Q - Long merged bark by 3-year-old [oscillogram shown above]. R-T - Narrow-band sound spectrograms corresponding to O-Q. Analysing filter bandwidths 150 Hz [A, C, G-J, O-Q], 300 Hz [B], 22.5 Hz [D, F, K-N, R-T], and 45 Hz [E]. Sound spectrograms in B and E are over range 80-8000 Hz, so time marker at the bottom represents 500 ms for them, and 1 s for the remainder. Logarithmic frequency scales are shown for D-F, K-N, and R-T, with 200 Hz markers for E and 100 Hz markers for the others. From Fig. 9 of Miller (1985)

Table 4.3 Developmental changes in threat vocalizations by males of the northern elephant seal (*Mirounga angustirostris*)^a

Characteristic of threat utterances	Juvenile			
	Young	Old	All	Adult
Incidence with short clap bursts as most common syllable type (%)	80	35	-	-
Incidence with mixed syllables (%)	-	-	41	2.9
Incidence with roar (%)	45	10	29	0.0
Coefficient of variation for intervals between syllables (%)	25	16	22	9.0
Number of syllables per utterance	-	-	4.8	6.1
Number of claps per clap burst	-	-	3.2	7.2
Syllable rate within utterance (%)	1.8	1.6	1.7	1.4

^a Data from text and Table 2 of Shipley *et al.* (1986).

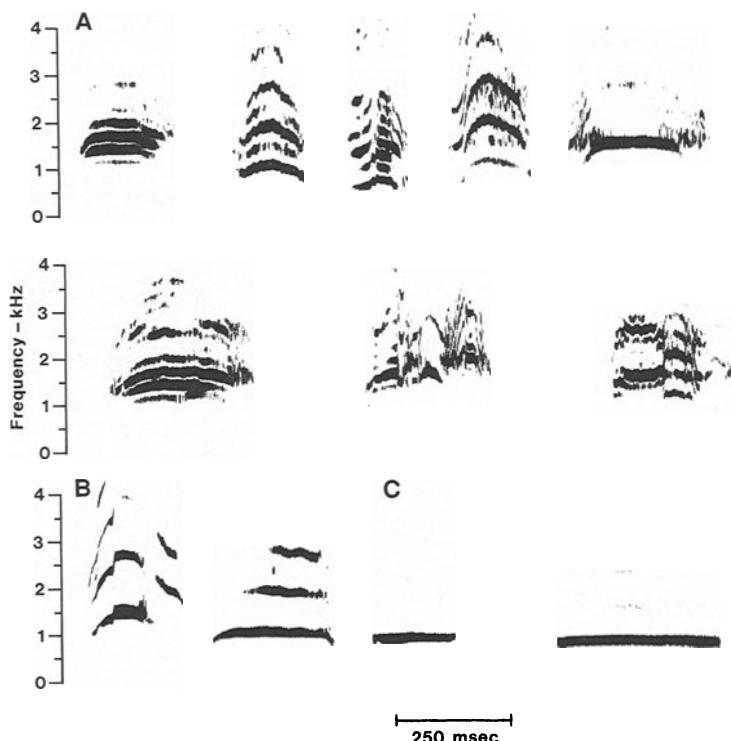


Figure 4.16 Structural variation in an acoustic display, the airborne call of a pup harp seal (*Phoca groenlandica*). Eight examples of calls from a young (<1 week old) pup are shown in A. The less variable calls of the pup's mother are shown in B (left, on ice with pup; right, in water, looking at pup from a few metres away), and C (threatening vocalizations directed at another female about 5 m away, with both on the ice surface).

elephant seals (Table 4.3).

Structural variation can be assessed without any reference to a time base, as well. Consider variation among calls of single individuals (Figure 4.16), and within samples of calling sequences from unknown numbers of individuals (Figure 4.9). Neither of these cases should be considered to exhibit grading; they simply illustrate structural diversity and variation within recognized categories of signals. Signals emitted in such a manner must be difficult for recipients to compare, unless additional cues or contextual information are used (Marler and Tenaza, 1977). Variation across categories likewise includes examples of discontinuous and continuous patterns (e.g. Eisenberg *et al.*, 1975), but the term 'grading' would be inappropriately applied to the latter (Figure 4.17). A danger here is that if classes are established according to artificial criteria, then characterization of grading may be meaningless. Thus, establishment of signal categories by a worker simply 'may be based on the more frequent usage of modal forms than of intermediates' (Marler, 1976:269; Marler and Tenaza, 1977) - yet infrequent so-called 'intermediate' forms may have distinctive significance, and might have their own category assigned by a human observer if they occurred more often. Ostensible shifts or transitions between signal classes can therefore be artefacts of the behavioural catalogue being used.

Structural variation in signals is extremely important to document for almost any kind of research on communication. Documentation needs to be quantitative and standardized. It must also be done with reference to specific levels of variation: geographic, sexual, developmental, contextual, etc. (Miller, 1986). Variation in signal structure and in contextual circumstances is central to our understanding of pinniped communication. The term 'grading' can rarely be applied to a species' communication system because of our meagre knowledge of signal processing by recipients; the term 'structural grading' is preferable for describing repertoires that show extensive continuous variation and intergradation of categories.

(b) *Repertoire organization*

Species that live at close quarters can use structurally graded signals and contextual information extensively, and often build parts of their structurally graded communication systems around 'keystone' signal types. Certain call types of the walrus (Miller, 1985) and California sea lion are examples. In the latter species, the bark appears to be the only structural class of acoustic signal employed by breeding males (Peterson and Bartholomew, 1969). In contrast, breeding male northern fur seals employ five distinctive classes of vocal display: trumpeted roar, low roar, bark, boundary puff, and whine (Peterson,

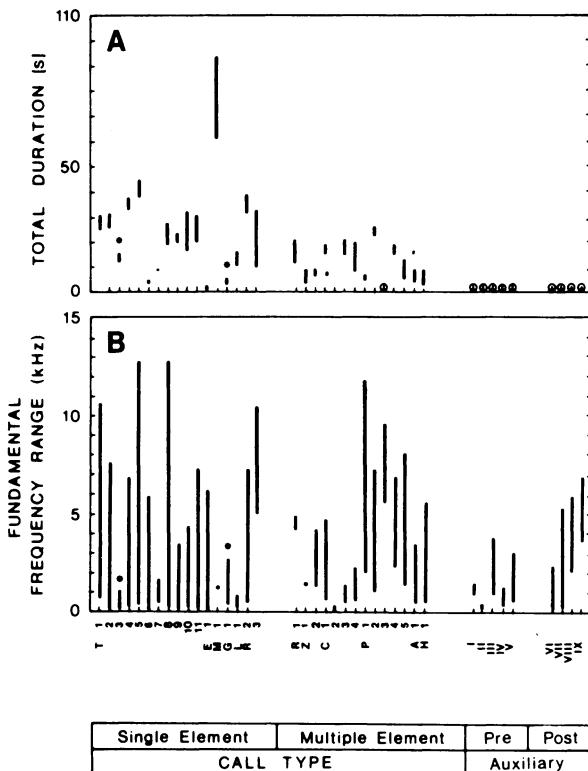


Figure 4.17 Physical diversity of underwater sounds of breeding male Weddell seals (*Leptonychotes weddellii*). Sound classes are arranged along the horizontal axis. A - Mean duration ± 1.96 S.E. are plotted for each class. Open circles represent brief sounds that could not be represented accurately on this scale. Asterisks denote sound classes that are repeated in series. B - Frequency ranges for each sound class. From Fig. 5 of Thomas and Kuechle (1982)

1965; Lisitsyna, 1973). Breeding males of the Steller and Australian sea lions (*Neophoca cinerea*) likewise employ several kinds of vocalization (Stirling, 1972; Lisitsyna, 1979). The social systems of these species are broadly similar, so males interact for roughly the same proximate and ultimate reasons. Therefore male California sea lions, by varying their barks' rhythm, intensity, duration, frequency characteristics, temporal properties, and directionality, can manage their complex interactions in ways that are comparable with the other species across the same broad range of contexts. The key to understanding the difference lies in information about the referents* of the bark, a display which occurs in all age and sex groups and is homologous throughout the Otaridae (see Section 4.6). A comparative study would yield insight into the evolution of the structurally

* See p. 161.

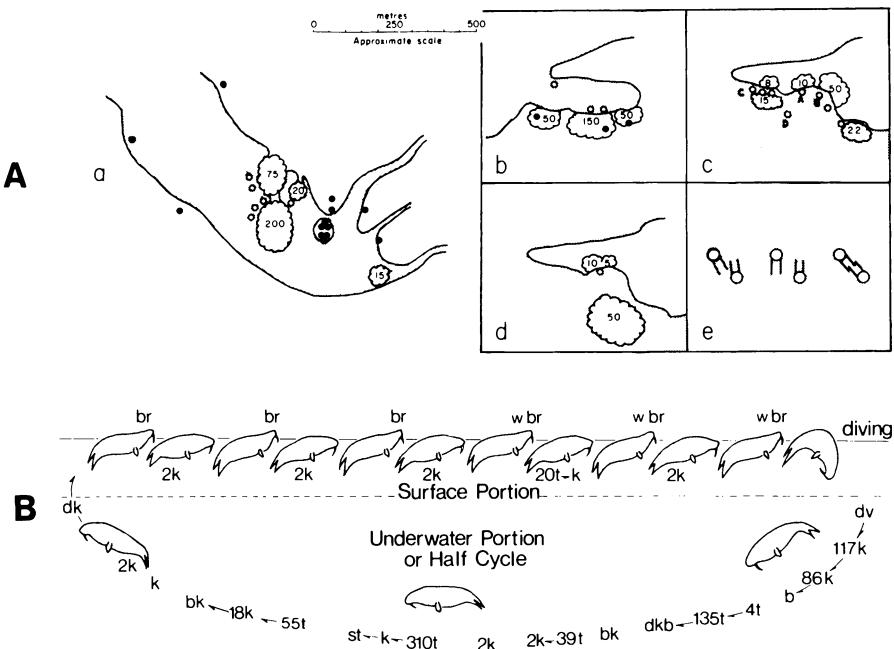


Figure 4.18 Complex displays of male walruses (*Odobenus rosmarus*) during the rut. A - Charts of the spatial arrangement of mixed herds of Pacific walruses (*Odobenus rosmarus divergens*) observed in the north-central Bering Sea in March. The number of adult females and young is shown within each herd. Circles represent bulls that were actively displaying in the water (open) and those that were inactive on the ice surface (solid). Parts a-d summarize observations on different dates; part e illustrates orientations of males in several tusk-threat displays at the water surface. Areas of open water and thin ice are shaded. B - Diagrammatic representation of a single display cycle of a male Atlantic walrus (*O. r. rosmarus*) [b, bell phonation; bk, bell-knock phonation; br, breath; dk, double-knock phonation; dkb, double-knock-bell phonation; dv, diving phonation; k, knock phonation, preceded by the number of knocks in a sequence; st, strum phonation; t, tap phonation, preceded by a number of taps in a sequence; w, whistle; arrows denote separable vocalizations that run together]. A is from Fig. 3 of Fay *et al.* (1984); B is from Fig. 1 of Stirling *et al.* (1987).

graded vocal communication system in the California sea lion, and how it functions.

At the opposite extreme from the California sea lion are the structurally distinctive underwater displays in the walrus and several species of phocids. Adult male walruses in rut engage in elaborate display sequences in water adjacent to herds containing females (Ray and Watkins, 1975; Stirling *et al.*, 1983, 1987; Fay *et al.*, 1984; Figure 4.18A). These complex but stereotyped sequences comprise several distinct, physically diverse kinds of phonations (Figure 4.18B, 4.19). Visual communication probably plays a minor role in the displays,

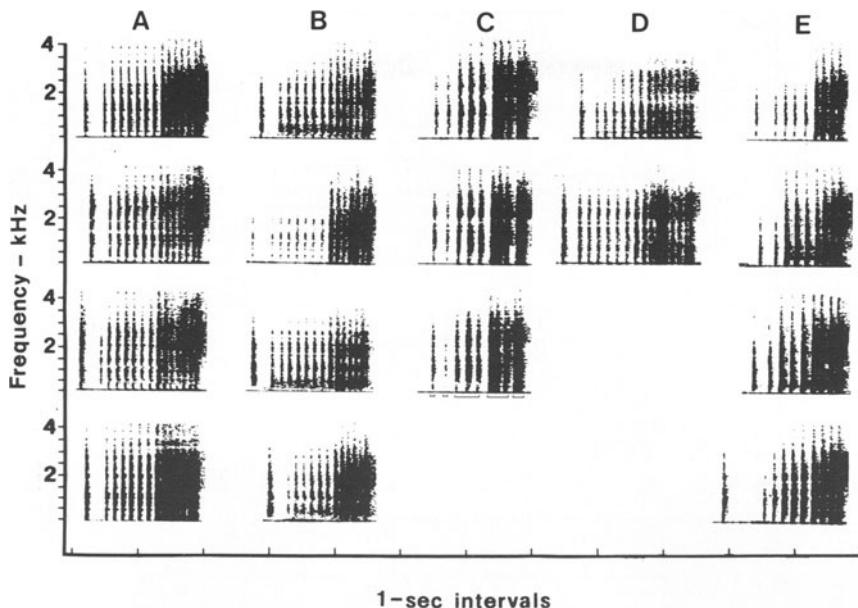


Figure 4.19 Sound spectrograms of phonation sequences by Four male Atlantic walruses (*Odobenus rosmarus rosmarus*) in nuptial display. These phonations are from the surface portion of the display cycle. A - Four sequences by a male in 1983; B - Four sequences from same male in 1984; C-E - Sequences from three other males. Analysing filter bandwidth, 150 Hz. From Fig. 3 of Stirling *et al.* (1987).

though tactual communication is significant as females contact displaying males at the surface, and probably also under water when females dive with displaying males. Long-distance underwater phonations of the bearded seal, harp seal (*Phoca groenlandica*), crabeater seal, Ross seal (*Ommatophoca rossii*) and leopard seal are also complex and diverse (Poulter, 1968; Ray *et al.*, 1969; Ray, 1970, 1981; Møhl *et al.*, 1975; Stirling and Siniff, 1979; Watkins and Schevill, 1979; Cleator, 1987; Cleator *et al.*, 1989), but the complex acoustic repertoire of breeding male Weddell seals is without peer (Thomas, 1979; Thomas and Kuechle, 1982; Green and Burton, 1988b; Figure 4.17, 4.20). The long distances over which this species communicates under water necessitate a structurally discrete arrangement of vocalizations. It is tempting to invoke sexual selection as the cause for elaboration of the repertoire, with the sounds providing information about maturity, learning skills, behavioural versatility, and responsiveness.

Display repertoires in other species of pinnipeds are more modest in both size and physical diversity. The spotted seal (*Phoca largha*) has nine major classes of acoustic display, for example, some of

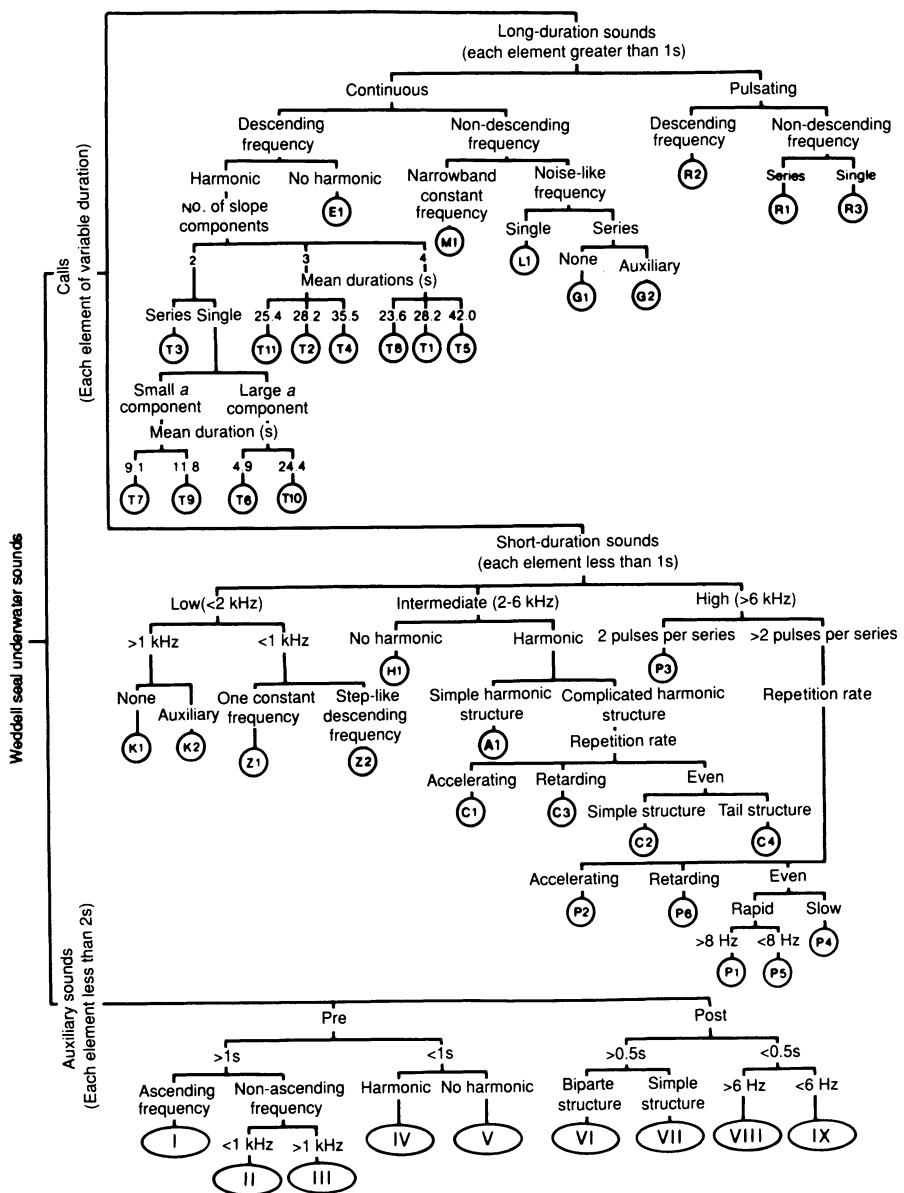


Figure 4.20 Hierarchical characterization of the repertoire of underwater sounds of breeding male Weddell seals (*Leptonychotes weddellii*). From Fig. 2 of Thomas and Kuechle (1982).

which are used frequently and others rarely (Gailey-Phipps, 1984; Table 4.4). There are also striking sexual differences in the relative use of different classes (Table 4.4). To date, our understanding of display diversity, repertoire structure and the relationship of display

Table 4.4 Relative frequency of use of acoustic displays by captive male and female spotted seal (*Phoca largha*)^{a,b}

Display class	Per cent use in repertoire of:	
	Male	Female
Growl	46	0.3
Drum	17	1.3
Bark	11	43
Slap	11	30
Grunt	10	2.3
Buzz	3.5	0.2
Gurgle grunt	1.7	2.5
Snort	0.8	21
Chirp	0.02	0.06
N	9061	5238

^a Ranked from most to least frequent for males.

^b Data from Table 3 of Gailey-Phipps (1984).

structure to function is meagre, and reflects the fact that only a few species have been studied in detail - mainly just for prominent acoustic displays used during the breeding season, though Renouf and Lawson (1986a) present some interesting data on play behaviour. Considering this, and considering the paucity of detailed observations on the behaviour of communicating, it would be premature to attempt any synthesis of repertoire size and structure at present.

I have discussed repertoires in the conventional sense. Smith (1986a) proposes several different and independent ways of viewing repertoires: a basic set; a set of qualities that can occur throughout the basic set (e.g. rhythmicity, amplitude modulation); sequences or combinations of the basic set, or of qualities; and a set of formalized interactions.

4.3 SOME CONCEPTS IN COMMUNICATION

Animal communication has been well reviewed in recent publications (Hailman, 1977; Sebeok, 1977; Smith, 1977; Green and Marler, 1979; Halliday and Slater, 1983). Here I summarize some current concepts and models in communication, with special reference to W. J. Smith's work (Smith, 1965, 1968, 1977, 1981, 1985, 1986a, 1986b, 1988).

4.3.1 Message, meaning and context

Displays and other signals make available to recipients much information about a signaller's current behavioural states and inclinations.

Information that is important for managing social interactions is also made available in non-behavioural ways, such as by appearance; examples are species identification, age and gender (see Section 4.3.2). Some non-behavioural information is fixed, some varies seasonally, and some is environmentally induced over vastly different time periods; these generalizations even apply to simple kinds of information like gender: male pinnipeds can be distinguished throughout life by their penile opening; males of many species become increasingly different from females through development (e.g. facial growth in elephant seals); and breeding males change in appearance seasonally (e.g. the mouth lining of male southern elephant seals, *M. leonina*, is brighter during rut (Laws, 1956)). Even short-lived environmentally induced states like wetness can provide useful information in a social encounter (Knudtson, 1974): wetness probably indicates that a seal has recently hauled out, which may dispose it to interact agonistically over a resting place, for example. Information from such diverse behavioural and non-behavioural sources is probably important in all social interactions of pinnipeds, especially over short distances.

All the information that a sender makes available to recipients forms the *message* about the sender and describes the sender's state(s). 'It may, for example, indicate that the individual is anxious, that it is an adult male in breeding condition or that it has just seen a predator. The *meaning* ... is what the recipient makes of the message' (Slater, 1983: 13). Methodologically, meanings are generally inferred from recipients' responses, because responses are the best indicators of a signal's significance to recipients.* Responses, in turn, are often taken as indicators of the *functions* of displays. Responses to both displays and unritualized signals are extremely variable because recipients almost always use other kinds of information as well when selecting a response. For example, a territorial male northern fur seal that has stayed 'in his territory after he has ceased any but the most perfunctory maintenance will watch with apparent unconcern while a subadult male wanders through the area which a week before he defended furiously against all intruders' (Bartholomew and Hoel, 1953: 431). Furthermore, 'responses to a single use or period of use of the display can extend over prolonged intervals, generating consequences that become interlinked with the consequences of other acts' (Smith, 1977: 271).† In any case, displays

* 'No response' is often an important kind of response by recipients, of course.

† 'Responses may be immediate or delayed; they may be vocal, postural, locomotor, or physiological. Some are discrete; others can only be described as a general shift in "arousal level" shown by an increase in exploratory or vocal activity. Their functions may have immediate consequences, such as fleeing in response to an alarm call, or may be more long term, perhaps by promoting spacing' (Gould, 1983: 280).

rarely have unitary meanings and functions: 'functions differ for different users ... differ in different kinds of events ... [and] No display that is used in more than one kind of circumstance has a single function ... [or] single meaning' for a recipient (Smith, 1977). A consistent association between a display and particular signaller characteristics across diverse situations permits us to judge those characteristics as the display's *referents*: a referent is 'anything becoming knowable or predictable through performance of a signal: who and where the signaller is, what it may be doing or about to do, aspects of its internal state, and things or events other than itself' (Smith, 1981: 273; see also Gould, 1983).

It is much more difficult to establish the meaning of a signal to a recipient than to establish a signal's message and referent. 'First, a display need not elicit an immediate, overt response from a recipient' (Smith, 1977: 265; Gautier and Gautier, 1977; Kiley-Worthington, 1979). For example, some displays are given continually (often rhythmically) and function to maintain a certain state in recipients or to inform them about the signaller's state or changes in state (Schleidt, 1973). Upright postures of breeding male otariids are one example of such tonic communication (Figure 4.41). Second, a recipient may respond to a display in different ways, any of which may be appropriate. Finally, the components of a display and the surrounding context that a recipient is responding to are difficult to determine; in natural situations with many uncontrolled variables they are essentially impossible to determine rigorously. Enquist and Leimar (1983) discuss some theoretical reasons for variation in behavioural responses (see Section 4.4).

In all social interactions, recipients of signals respond to sources of information that are separate from the signals themselves (Gautier and Gautier, 1977; Smith, 1977, 1985; Emmons, 1978; Kiley-Worthington, 1979). These other sources of information, or context, are varied and rich; they include aspects of the social and physical setting, as well as experience and motivation of the recipient.* The three main sources of contextual information are (1) communicator, (2) recipient, and (3) other features of a particular interaction (Smith, 1977: 226). Examples of each source are:

1. A harbour seal displaying with a foreflipper scratch (see Figure 4.5D) also provides important behavioural information to the recipient through other signals, for example simultaneous or

* A nice analogy is provided by words. 'The full meaning of a word does not appear until it is placed in its context, and the context may serve an extremely subtle function ... And even then the "meaning" will depend upon the listener, upon the speaker, upon their entire experience of the language, upon their knowledge of one another, and upon the whole situation. Words do not "mean" things in a one-to-one relation' (Cherry, 1978: 10).

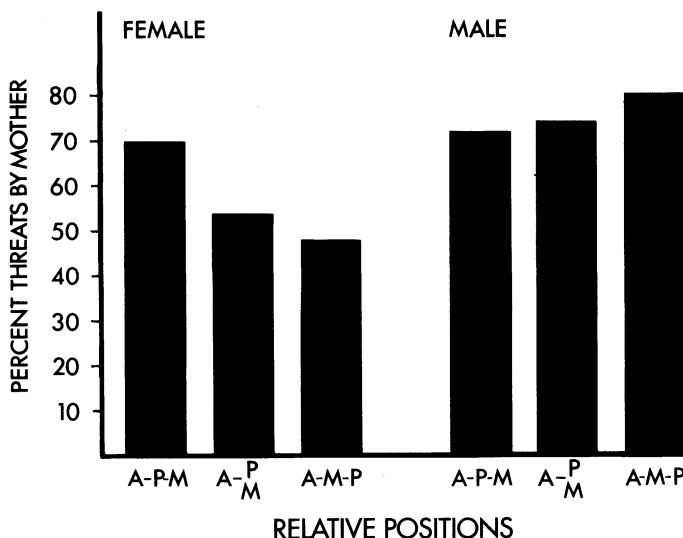


Figure 4.21 The influence of contextual features upon communication in the grey seal (*Halichoerus grypus*): the position of a pup (P) relative to its mother (M) and an approaching animal (A) affects the mother's aggressive responses if the intruder is a female, but not if it is a male. From Fig. 1 of Boness *et al.* (1982).

preceding vocalizations and postures (see Table 4.1). These other displays and unritualized signals act as part of the context that a recipient seal appraises when selecting a response to foreflipper scratch. Recipients also take account of non-behavioural kinds of information about a signaller - size and gender, for example.

2. The recipient of a signal enriches the context in important ways, notably through its own physiological state and personal experience: 'It will see any communicator as a stranger or a familiar individual with whom it may even share a social bond . . . will regard any display as expected or unexpected . . . any local environment as well known or foreign . . . , and so on (Smith, 1977: 227). Territorial male otariids reduce the frequency, intensity, and duration of threat displays towards one another over time as they become familiar with one another (see pp. 166-167).
3. Finally, the physical, biological and social settings in which signalling occurs strongly influence the course of social interactions and how recipients respond to signals. For example, aggression by female grey seals towards other adults is strongly influenced by both the position of their pups and the gender of an approaching seal (Boness *et al.*, 1982; see also Stewart (1987); Figure 4.21), and the elements of communication by threatening male New Zealand fur seals depend upon what triggers the threat (Miller, 1971; Table 4.5).

Table 4.5 The influence of contextual features upon communication in territorial male New Zealand fur seals (*Arctocephalus forsteri*): elements of communication are affected by how a threat is elicited^{a,b}

Male response	Stimulus category ^c			N (occurrences)
	TF and NBF	NB	Dist.	
Lunge-sprawl	1.26	0.64	0.53	68
Boundary display	1.16	0.92	0.46	145
Run approach	1.13	0.88	0.64	94
Walk approach	0.68	1.81	0.93	78
Lunge/swing	0.98	1.61	0.10	68
Trumpeted roar	0.50	1.41	2.33	83
Parallel broadside	0.75	1.28	1.47	40
Partial approach	0.83	0.88	1.87	54
N (interactions)	220	91	55	

^a Data from Table 27 of Miller (1971).

^b Each cell entry represents proportional occurrence of behavioural element relative to the number expected based on their random distribution across stimulus categories. Thus, in the stimulus category TF/NBF, trumpeted roars occurred half as often as expected, while lunge-sprawls occurred 26% more often than expected, and so on.

^c TF = trespass into responding male's territory by a neighbouring male interacting with a female; NBF = neighbouring male interacting with a female near common territorial boundary; NB = neighbouring male near common territorial boundary not interacting with a female; Dist. = threat to distant male.

A kind of formalized interaction in otariids, termed boundary display (BD) by Gentry (1970), illustrates some of the preceding points (see also Miller, 1975a; Miller and Boness, 1979; and Krushinskaya and Lisitsyna, 1983) (I will use this well established term here, despite my criticism of it; see p. 142). BDs involve characteristic postures, movements, and sounds of adjacent territorial males displaying with one another across a segment of their common territorial boundary (Figure 4.22). Similar displays are used by other classes of individuals in a range of agonistic contexts, though they appear to be less stereotyped in form and context (Figure 4.23). Male pups show well developed BD-play behaviour, and BDs continue to dominate play and 'practice' behaviour until males acquire breeding status (Farentinos, 1971; Gentry, 1974; Krushinskaya and Lisitsyna, 1983). The years of development provide individual male otariids with rich experiences in the use of BDs (motor patterns, interaction dynamics, eliciting and terminating stimuli, and so on). Breeding males engage in hundreds or thousands of BDs over each breeding season, many with the same neighbours. In addition, males may occupy the same territory in consecutive breeding seasons and so encounter some of the same neighbours over several years (Peterson, 1965, 1968; Trillmich, 1984). Gisiner (1985) found that 36 of 102

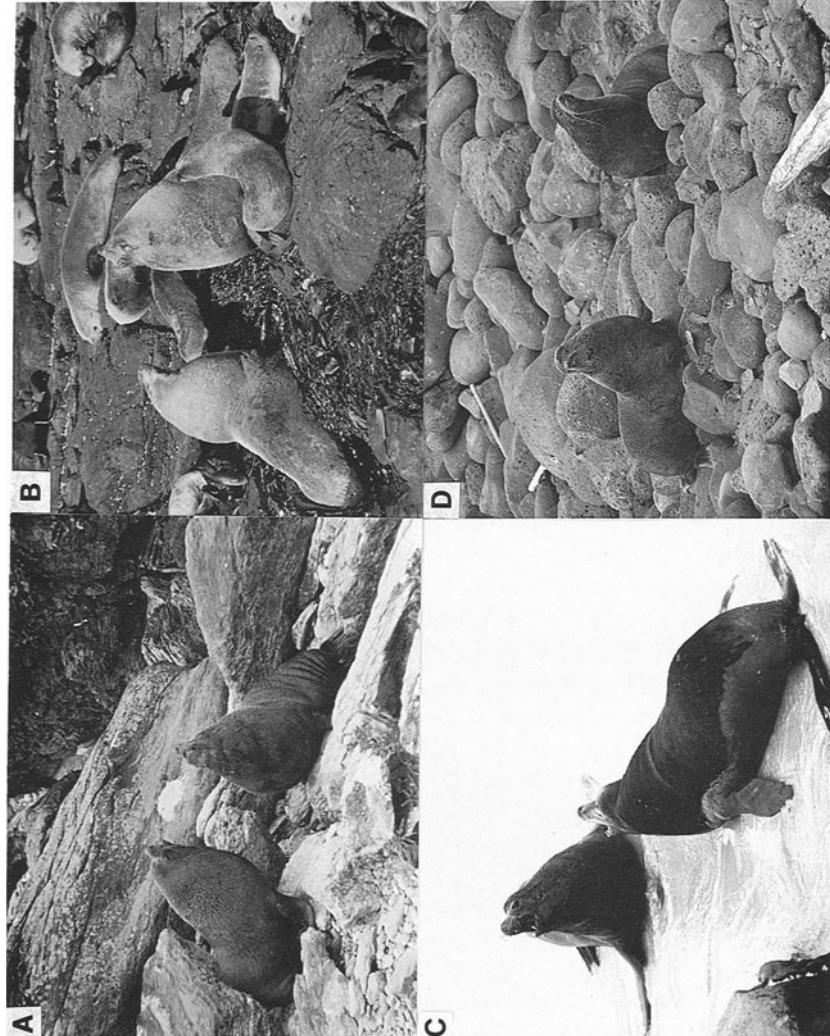


Figure 4.22 Boundary displays by adjacent territorial male otariids. A - New Zealand fur seal (*Arctocephalus forsteri*). B - Australian fur seal (*Arctocephalus pusillus doriferus*). C - California sea lion (*Zalophus californianus*) (photograph by R. L. Gentry). D - Northern fur seal (*Callorhinus ursinus*), facing-away phase at end of boundary display (compare Figure 4.23D).

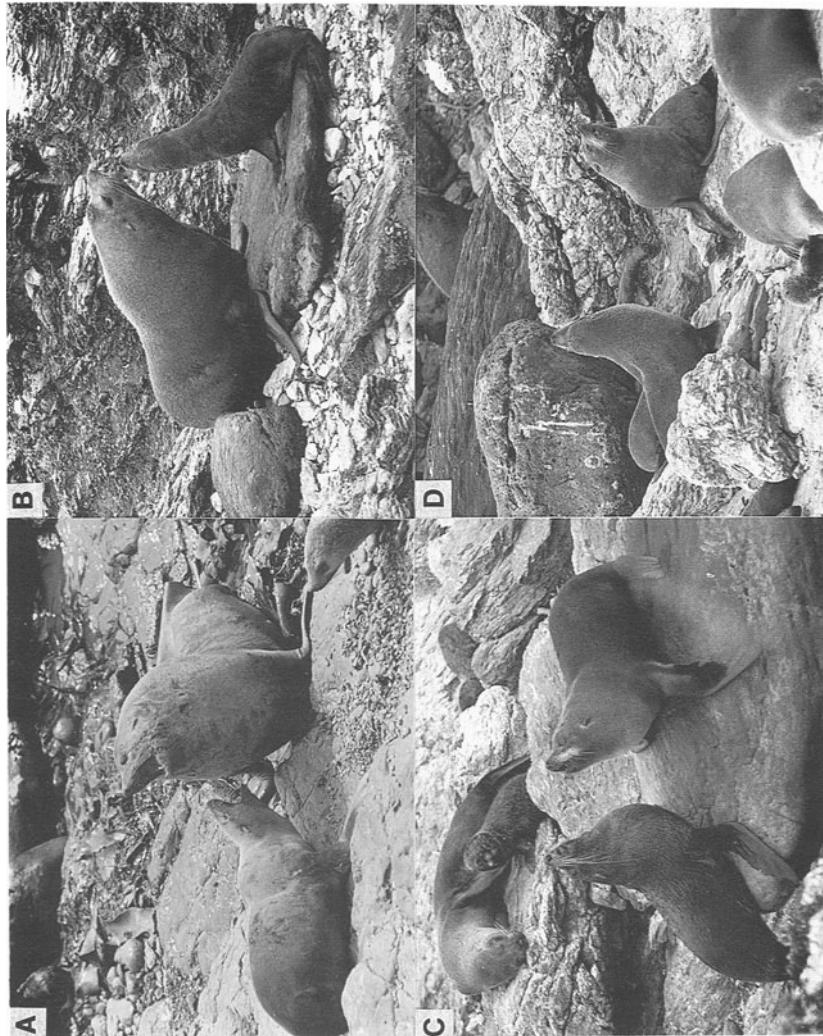


Figure 4.23 Threat displays by otariids, showing motor patterns like those in male-male boundary displays (see Figure 4.22). A - Threat between adult male and adult female Australian fur seal (*Arctocephalus pusillus doriferus*). B - Threat between adult male and young female New Zealand fur seal (*Arctocephalus forsteri*). C - Threat between adult female *A. forsteri*. D - Threat between adult female *A. forsteri*, showing facing-away phase at end (compare Figure 4.22D).

dyads of territorial male Steller sea lions shared a common territorial boundary for two or more years. All these experiences contribute to the context of BDs, and all significantly influence interactants' responses to one another, often in different ways according to each male's motor skills, memory, physical prowess, aggressive inclinations, etc. A simple illustration of the influence of context lies in the changing nature of BDs between the same territorial males as their familiarity with one another increases within a single breeding season: BDs decline in duration, rate of occurrence, incidence of biting, and in other ways (Miller, 1971, 1975b; Gentry, 1975; McCann, 1980; Figure 4.24A-C). Another relevant aspect of context is topography of the display site, because certainty about where a territorial boundary is located depends upon how well marked it is; in turn, males recognize intrusions and retaliate most often against them over topographically well-marked boundaries (Miller, 1975b; Figure 4.24D). In Steller sea lions, territorial males display and fight most frequently with one another in their first season together as neighbours (Gisiner, 1985). Such factors, in combination with others like the nature and frequency of eliciting stimuli, and the length of a common boundary, lead to great variation in the form, significance, and frequency of occurrence of BDs even within a single colony; in my study of New Zealand fur seals, for example, the rate of participation in BDs varied six-fold across 14 males, and varied from 0 to 3.6 per day even for a single male in relationship to his seven different neighbours (Miller, 1971). The responses of individual participants in BDs are thus highly variable for numerous reasons, many of which are unknowable to a human observer though important to the individuals involved. Researchers can analyse the influences of experience, topography, eliciting stimuli, and other factors upon BDs statistically, but variation across individual instances is very difficult to explain primarily because of the importance that personal experiences play, and because of inherent variability among animals.

Pinnipeds are highly individualistic because of their intelligence, behavioural plasticity, and unique developmental experiences over many years. Even particular age-sex classes are extremely variable. In the Antarctic fur seal (*Arctocephalus gazella*), territorial 'bulls are individually highly variable in their reaction to man, some allowing extremely close approach, even to the point of being touched without responding other than by turning their heads . . . while others will threaten before the observer has entered their territories' (Bonner, 1968: 40). Considering such high levels of behavioural plasticity and individuality, and the rich, complex, interacting, and dynamic sources of contextual information that surround social interactions in pinnipeds, we should expect to observe variation in the form, uses, and consequences of even highly ritualized signalling.

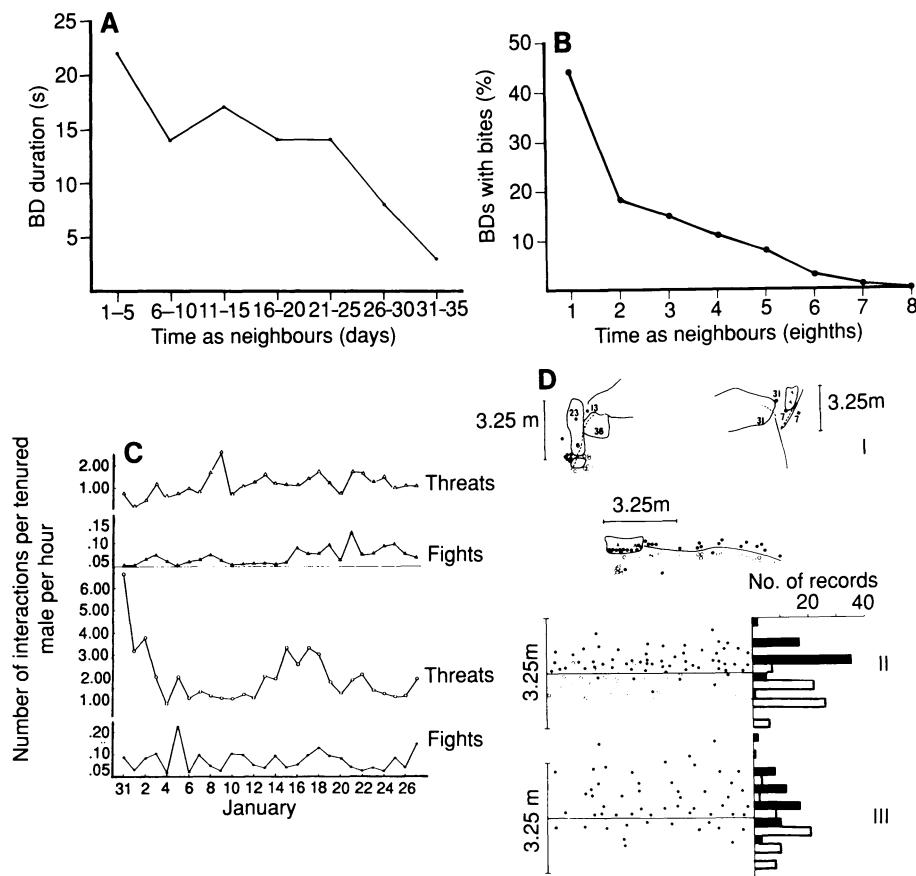


Figure 4.24 Relationship of context to the form, incidence, and location of threat displays among breeding male pinnipeds. A, B, and C - 'Familiarity' as part of context: in the Steller sea lion (*Eumetopias jubatus*), both the duration of boundary displays (BDs) (A) and the incidence of biting in BDs (B) decline the longer that males are neighbours of one another; grey seals (*Halichoerus grypus*) interact with one another most frequently in their first two days as neighbours (C - lower), and less so thereafter (C - upper), regardless of the date when they become neighbours. D - Rookery topography as part of context: BDs between male New Zealand fur seals (*Arctocephalus forsteri*) occur in fixed relation to well-marked topographical features (class I - pools and large rocks are shown in outline; numbers of records for each location are shown), but vary in location more when features become progressively less distinct (II, III). A and B are after data in Table 29 and Fig. 149 of Gentry (1975); C is from Fig. 24 of Boness, 1979; and D is from Fig. 137 of Miller (1975b).

Two points that are relevant to Smith's model of communication need to be stressed. First, in Smith's view the information content of displays is fixed (the referents of messages are fixed): variation and flexibility in the communication process result from recipients integrating and responding to information in messages *and* context (for mammals see also Kiley, 1972; Kiley-Worthington, 1976, 1979; Gautier and Gautier, 1977; Emmons, 1978; and Gould, 1983). This view contrasts with P. Marler's (and others') emphasis on recipient behaviour, with the view that displays provide rich information, which differs in different events, and from which recipients select (see Smith, 1977: 287–288). A problem with the latter view is the unrealistic assumption that a 'recipient would have to process each kind of event as a discrete unit' (Smith, 1977: 288). This problem is related to a second point: animals can 'package' information in displays only in a finite and rather limited number of ways. Otherwise, if the displays of a species were very numerous, they would be extremely similar to one another and hence might be confused by recipients. Therefore an upper limit to repertoire size must exist, with richness achieved through the use of context (Smith, 1977; see Moynihan, 1970).

Message, meaning, and context are key features of Smith's model of communication (Smith, 1965, 1968). To apply the model one begins by analysing messages, through information that signalers make available. Smith emphasizes display behaviour as a source of information. However, in the next section I illustrate his approach using informative, socially relevant characteristics of external appearance.

4.3.2 Assessing the information available from external appearance

Lavigne and Kovacs (1988) provide an excellent general account of pinniped vision (see also Jamieson and Fisher, 1972; Schusterman, 1972; Lavigne *et al.*, 1977; Braekevelt, 1986a, 1986b; Busch and Ducker, 1987; Sivak *et al.*, 1989). The large eyes of pinnipeds are adapted primarily to provide sensitive vision in low light conditions under water, at the expense of acuity and colour perception there and (especially) in air. Even so, pinnipeds can perceive fine details under high light levels in both media (especially under water) and are particularly sensitive in the blue-green part of the spectrum. Under dim light in air, pinnipeds are myopic and may also suffer from astigmatism. Limited colour vision may occur in both water and air, but is affected by the altered spectral environment in the water (with blues or greens dominating near the surface) and is reduced in dim light (see Chapter 7). Considering these characteristics, one can

predict that visual communication in pinnipeds is likely to emphasize general aspects of movement and appearance (e.g. postures and major pelage patterns) except at close range, and that colour must be less important. Stoskopf *et al.* (1985) have documented a high prevalence of eye disease in wild northern fur seals (46% of 1716 seals had clinically recognizable lesions). It is not known how typical this is for natural populations of pinnipeds, or what effects such diseases have on visual signalling, but they must increase the variation of recipient responses and thereby increase variation in communication generally.

Non-behavioural information that is important for pinnipeds in managing their social interactions lies in identifying messages, which can provide information such as the following (see Smith, 1977: 156–167):*

Population classes

- Species identification (p. 169)
- Deme identification (p. 172)
- Morph identification (p. 172)
- Individual identification (p. 175)

Physiological classes

- Age (p. 175)
- Breeding condition (p. 176)
- Gender (p. 178)
- Moult (p. 182)

These kinds of information are all made available in pinniped communication, generally through signals that have not been evolutionarily specialized as displays or display adornments.

(a) *Species identification*

All species of pinnipeds can be distinguished visually using characteristics of size, pelage, and special structures (for illustrations, see Scheffer, 1958; Backhouse, 1969; Ridgway and Harrison, 1981a, b; King, 1983; Nowak and Paradiso, 1983; Macdonald, 1984; Lavigne and Kovacs, 1988; and other general works). However, pinnipeds are not challenged in distinguishing conspecific individuals from members of other sympatric species by visual characteristics because almost all species differ substantially in appearance, habitat, and breeding chronology (for the closely related species *Arctocephalus*

* The functional importance of these classes of information to the animals themselves must obviously be considered, for their perceptual processes differ from ours. Furthermore, the evolutionary and ecological significance of the classes must vary across and even within species.

tropicalis and *A. gazella* see Condy, 1978; Payne, 1979; Kerley, 1983a, 1983b; and Shaughnessy *et al.*, 1988). A parallel can be drawn with species differences in habitat, geographic distribution, and annual cycle (Ling, 1969): ecological differences among sympatric species of pinnipeds can be parsimoniously explained by phylogeny, and it is unnecessary to invoke interspecific competition as a cause for the origin or maintenance of such differences. Similarly, morphological differences among pinniped species can be attributed to patterns of phylogeny. There is no reason to suppose that the visible differences among species have resulted from selection for species specificity, or that they have been reinforced in sympatry to facilitate identification of species or improve interspecific signalling (see West-Eberhard, 1983; Eberhard, 1985; Paterson, 1985; Butlin, 1987; Coyne *et al.*, 1988). Thus the identification of conspecific individuals based on appearance is a simple effect of phylogenetic differences among pinniped species: the differences arose as by-products of selection within species for effective and efficient communication, or for non-communicative purposes (e.g. camouflage). The differences did not evolve as isolating mechanisms adapted to protect species integrity. Information about 'species' as a class therefore has no selective basis. Unspecialized sources of information about species thus are simply adventitious, and are only used opportunistically by conspecific individuals. (Some workers argue that concepts of species should be separated from processes of speciation; compare Chandler and Gromko (1989) with de Queiroz and Donoghue (1988).)

There are many examples of socially specialized markings and structures that are unique to different pinniped species, but all carry other sorts of information too. Both the ribbon seal (*Phoca fasciata*) and harp seal have unique and striking markings which are also informative about age and gender, for they develop with age and are most strongly expressed in males (Naito and Oshima, 1976; Burns, 1981a; Ronald and Healey, 1981; Lavigne and Kovacs, 1988). The ribbon seal has four bands, one each encircling the neck, lumbar region, and each foreflipper: '... indistinct light bands are present on some young seals by twelve weeks ... but they are usually not obvious until they moult at age one. After the third year of life males are reddish brown to almost black (reddish brown before the moult and almost black immediately after it) with light ... bands [that] increase in contrast to the dark background ... up to sexual maturity. Adult females ... are much less distinct because of a considerably lighter background coloration' (Burns, 1981a: 91). The sexes are not distinguishable until the third year, individuals vary greatly in their band characteristics, and polymorphism may exist in some characters (e.g. blending of the lumbar band with background colouration; presence of small rings on the background) (Naito and Oshima, 1976). Thus, information about

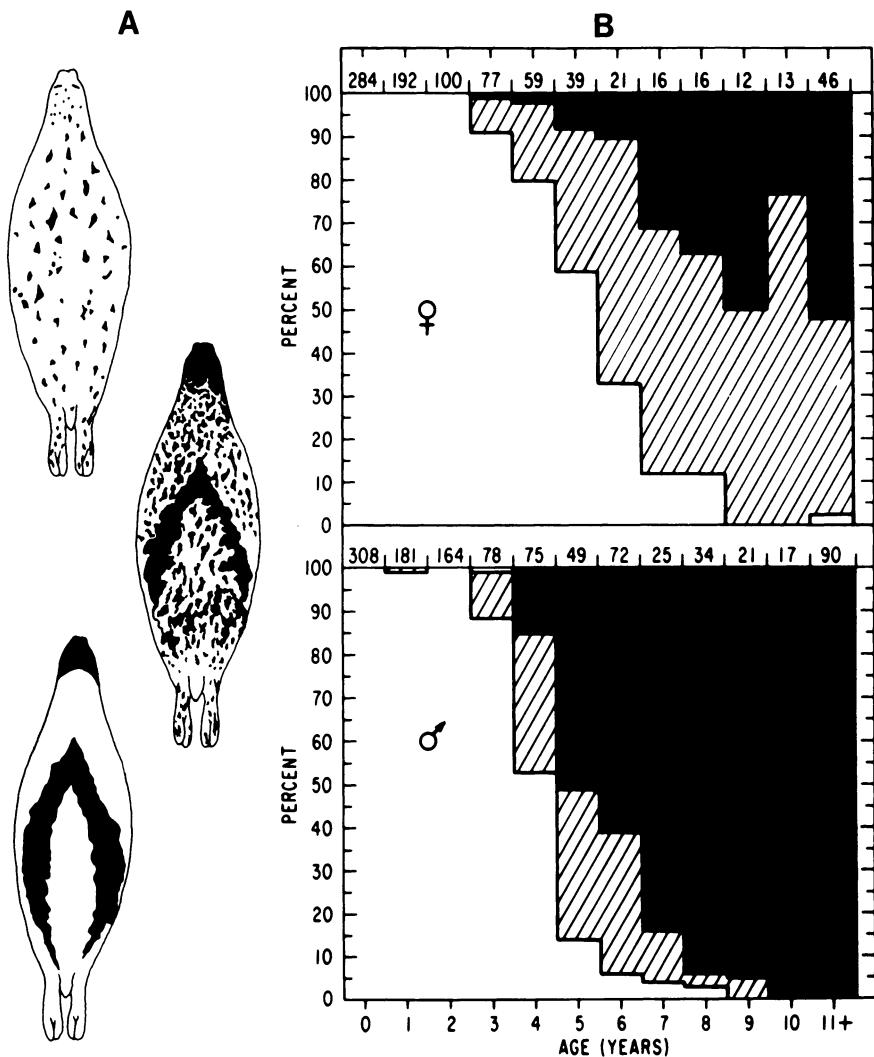


Figure 4.25 Information about age that is available from variation in pelage markings of harp seals (*Phoca groenlandica*). A - Spotted (top), spotted harp (centre), and old harp (bottom). B - Variation in pelage type with age: open = spotted; hatched = spotted harp; and solid = old harp. The numbers along the top of each part represent sample sizes for each age class. A is from p. 42 of Lavigne and Kovacs (1988); B is from Fig. 2 of Roff and Bowen (1986).

species, age, gender, individuality, stage of moult, and morph class is available in different ways and different combinations from visual appearance following the ribbon seal's post-natal moult of lanugo. Those classes of information are enriched further by contextual circumstances surrounding social interactions, as I have stressed in the preceding section.

In the harp seal, young animals are spotted but a distinctive 'harp' characterizes old seals; as for the ribbon seal, in this species such age-related characteristics also encode information about gender (Roff and Bowen, 1986; Figure 4.25).

(b) *Deme identification*

Visual characteristics signifying deme membership or origin probably have not been selected for as such. Rather, such characteristics arose as by-products of population differentiation, just as species-distinctive features have.

Pinnipeds exhibit geographic variation in appearance in several species. The striking coat patterns of harp seals differ in their relative frequencies among breeding populations of Jan Mayen, the White Sea, and Newfoundland (Yablokov, 1974). Pelage of adult harbour seals varies geographically: in eastern Canada dark pelage is more prevalent in the northern than in the southern part of the range; along the Pacific coast, light pelage characterizes the populations in southeastern Alaska and dark pelage becomes increasingly prevalent toward the range extremes of southern California and Hokkaido (Shaughnessy and Fay, 1977; Kelly, 1981; Burns and Gol'tsev, 1984; Figure 4.26). In both species, interchange of individuals among populations provides opportunities for the use of information about deme membership in social interactions. However, these and other examples of geographic variation in visual appearance (including size) concern quantitative features that differ in their incidence among populations. Therefore information about a seal's deme of origin is uncertain (probabilistic) in most cases. Also, much geographic variation in pinnipeds is disjunct so opportunities for the use of such information in social encounters must be rare (e.g. New Zealand fur seals in Australia and New Zealand (Reprenning *et al.*, 1971), and walruses in the Alaskan and Canadian Arctic (King, 1983; Fay, 1985)).

(c) *Morph and mutant identification*

'Polymorphism' refers to the 'simultaneous occurrence of several discontinuous phenotypes of genes in a population, with the frequency even of the rarest type higher than can be maintained by recurrent mutation' (Mayr, 1969: 409). 'Morph' refers to the 'genetic forms (individual variants) that account for polymorphism' (Mayr, 1969: 407). The terms 'morph' and 'polymorphism' have been used in reference to coat patterns or colours in several pinniped species, but it has not been demonstrated that polymorphisms (as defined) really exist. Instead, workers have divided continuous variables into several discrete categories. In some cases the categories may be good

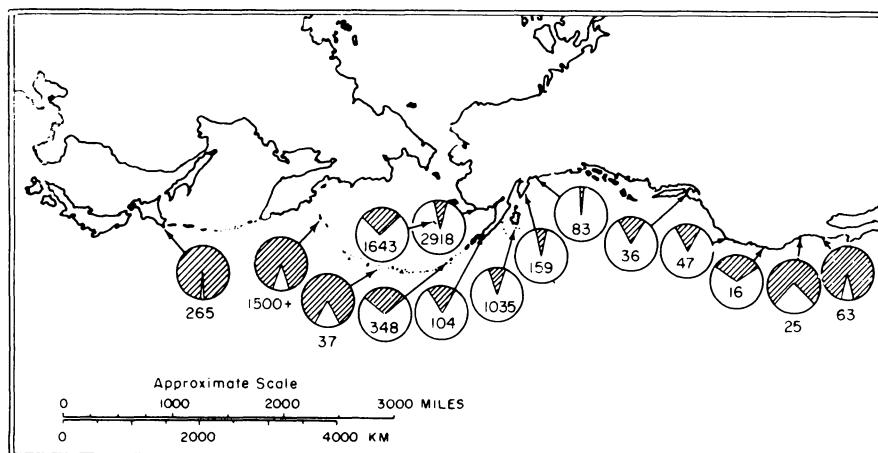


Figure 4.26 Regional frequency of occurrence of light and dark pelage of adult harbour seals (*Phoca vitulina*) in the North Pacific Ocean. Proportions of light (open) and dark (cross-hatched) are represented for each population sample, and sample sizes are indicated. From Fig. 3 of Shaughnessy and Fay (1977).

measures along a continuous scale (e.g. Kelly, 1981), but in others they clearly are not (e.g. Yablokov (1974) on harp seals).

Thus information about 'morphs', as defined above, may not be made available through pinnipeds' visual appearance. However, information about quantitatively varying features such as darkness/lightness of pelage is, and such information may be useful for social purposes much as is morph-related information. Kelly (1981) documented the incidence of light and dark pelage in Alaskan harbour seals. He classified 77-85% of seals on Tugidak Island and 77% on Otter Island as 'light' in two years. The incidence of 'light' pelage varied (generally declined) with age in all samples: pups, yearlings, and adults on Tugidak Island had incidences of 93, 87, and 81% in one year and 91, 82, and 73% in the following year; estimates on Otter Island were 80, 86, and 74%. It is not known what socially useful information can be conveyed by lightness/darkness of pelage aside from probabilistic information about age.

Discrete mutant forms occur in pinnipeds. In the northern fur seal albino, piebald and chocolate forms occur (the latter is apparent only in pups) (Scheffer, 1958, 1961; Figure 4.27A). Blonde mutants occur regularly in the Antarctic fur seal (Bonner, 1968, 1981a; Gentry and Kooyman, 1986a) and in the Juan Fernandez fur seal, *Arctocephalus philippii* (J. M. Francis, *in litt.*). Pelage variants that reflect more complex genetical control merge into such discrete mutants: Scheffer (1961: 36) described great variation in piebald northern fur seals; and the extensive variation in ribbon, harbour and harp seals described by

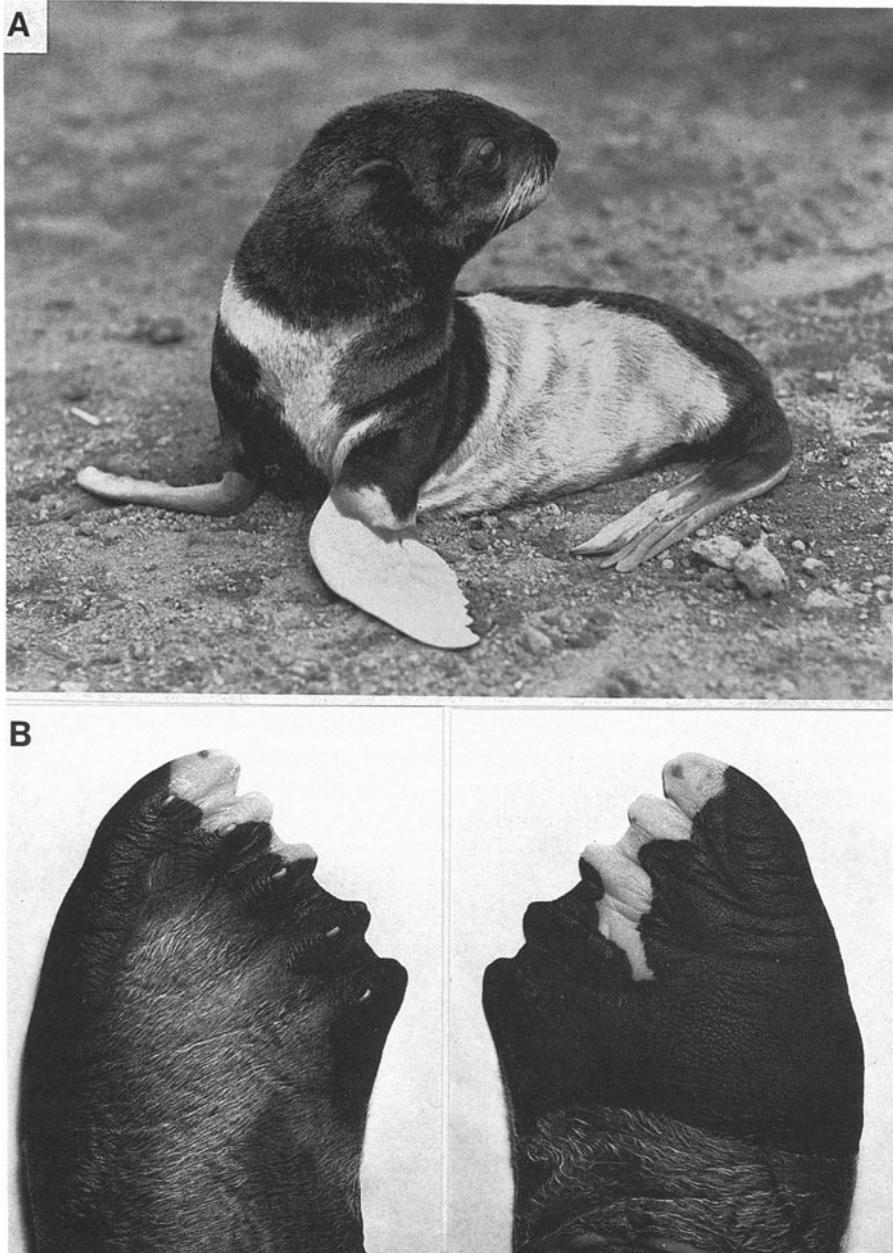


Figure 4.27 Information about 'mutant' class that is available from external appearance. A - Piebald mutant in pelage of the northern fur seal (*Callorhinus ursinus*). B - Piebald mutant of the Pacific walrus (*Odobenus rosmarus divergens*), illustrated by right foreflipper of a fetus (dorsal view on left, ventral view on right). A is from Plate II of Scheffer (1958); B is from Fig. 31 of Fay (1982).

Naito and Oshima (1976), Kelly (1981), and Yablokov (1974) typifies pelage variation in many pinniped species. Discrete mutants/morphs and genetically determined continuous variation among individuals lie along a continuum. Information about mutant/morph status must usually also encode information about individuality, especially where expression is variable as in the piebald mutants of northern fur seal pelage, Hawaiian monk seal pup pelage (Kenyon and Rice, 1959), and walrus flippers (Figure 4.27A, B).

(d) *Individual variation*

Individuality is apparent in numerous external features of pinnipeds and occurs in combination with many other kinds of information. A single yearling Steller sea lion on a portion of a breeding colony can become known as an individual to other sea lions through its age attributes (e.g. size, pelage, shape of head), for example, simply because it may be the only one present. Characteristics that identify a mutant or morph can also supply information about individual identity, especially where the condition is rare (e.g. blonde mutant form of the Antarctic fur seal) or variable (e.g. piebald mutant of the northern fur seal), as I have pointed out.

Pinnipeds can identify other individuals by a great number of visually apparent external features. Some features are strongly genetically determined and are influenced little by external factors through development; examples include pelage colour or markings that remain constant throughout life, as in harbour seals (Stutz, 1967), plus developmental abnormalities such as supernumerary tusks in walruses (Fay, 1982). Other individually distinctive features are under strong environmental control, such as injuries caused by predators (Kenyon and Rice, 1959; Laws, 1984; Figure 4.30) or intraspecific strife (see next paragraph), and effects of skin disease (Scheffer, 1961; Lauckner, 1985). As for developmentally 'closed' characteristics, some of those that result from environmental agents are rare while others occur regularly.

(e) *Age identification*

Age, like individuality, is encoded in numerous conspicuous features of appearance. General reviews of moult and pelage provide information about major developmental changes in coat colour and pattern (Ling, 1974, 1978; Ridgway and Harrison, 1981a, 1981b; King, 1983). Most age-related information that is available from external appearance is probabilistic and age categories overlap (Figure 4.25). Exceptions are the striking changes in coat appearance between the shedding of the natal pelage and the assumption of the second coat.

Thus, grey seals change from white to mottled silver-grey or black, Weddell seals moult from a greyish-brown natal coat to one that is black on white, and otariids replace their dark or black natal pelage with one that is generally grey or silver-grey. Subsequent moults result in less striking changes. In the northern fur seal underfur shifts gradually towards a darker and redder colour with age, imparting a darker and browner appearance to 2-year-olds than younger animals, and a distinctly darker appearance yet to seals older than 5 years (Scheffer and Johnson, 1963). Vibrissae of the northern fur seal and southern fur seals (*Arctocephalus*) are black for the first few years, but are white in older animals (Rand, 1956; Scheffer, 1961; Bonner, 1968; Miller, 1975a).

Environmentally induced features can provide socially valuable information about an individual's age. Fresh wounds on crabeater seals typify weanlings, which suffer intense predation by leopard seals; older animals have only scars (Laws, 1977, 1984; Siniff *et al.*, 1979; Stirling, 1983). Male elephant seals and walruses develop heavily scarred chests and necks through years of mock fighting, followed by serious fighting when they enter the breeding population (Laws, 1953, 1956; Sandegren, 1976a; Tierney, 1977; Fay, 1982); scarring also characterizes adult male harbour seals (Scheffer and Slipp, 1944; Calambokidis *et al.*, 1978), ringed seals (*Phoca hispida*; Stirling, 1977), and Weddell seals (Stirling, 1977). Female crabeater seals cause much scarring on the neck of adult males, through frequent agonistic encounters during the rut, so heavily scarred males are generally the oldest and most sexually experienced (Siniff *et al.*, 1979; Laws, 1984; Shaughnessy and Kerry, 1989). Bartholomew (1953: 487) underscores the importance of such characteristics in the social life of the northern fur seal: 'Old battered bulls missing several of their canines - a bull's primary offensive weapon - often hold territory by bluff alone. A show of force by one of these grizzled veterans is usually enough to cause the withdrawal of a more powerful but still inexperienced young male.' Sandegren (1975, 1976b) noted that male Steller sea lions are more attentive to old than to young females.

(f) Breeding condition

The reproductive state of pinnipeds is apparent from external appearance in both general and specific ways. An example of the former is the appearance of females in late pregnancy. Male otariids also show a circannual change in size, due to an annual rhythm of fattening in which they gain weight most quickly before the breeding season, even when their food intake is held constant (Howell, 1930; Rand, 1956; Schusterman and Gentry, 1971). The difference in appearance of otariid males before and after their lengthy territorial

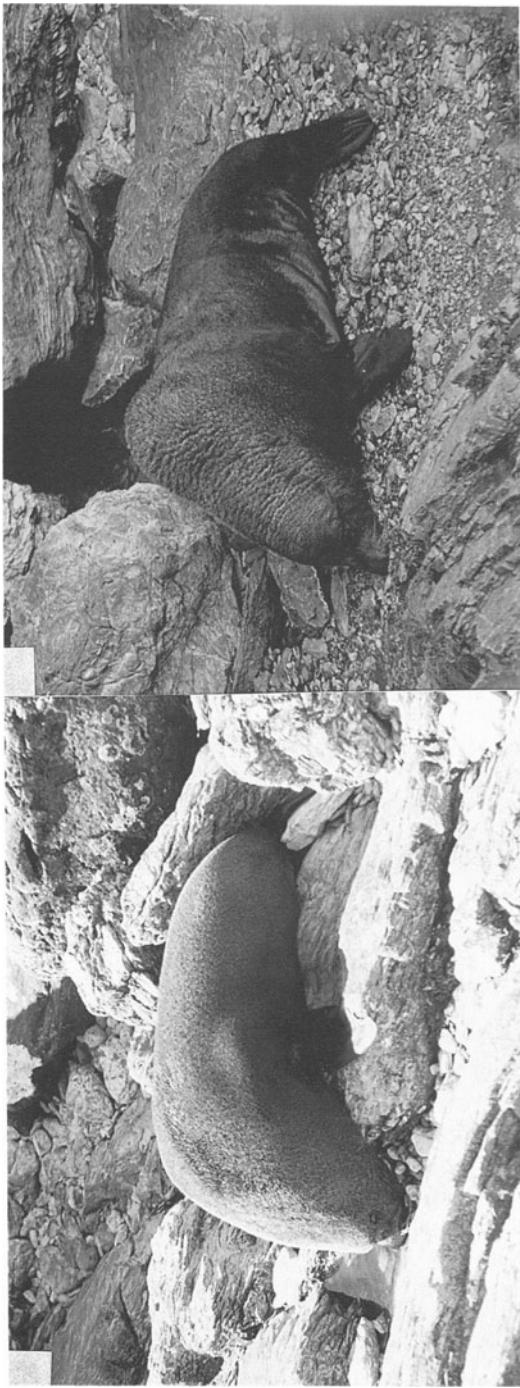


Figure 4.28 Information about condition and stage of territorial tenure that is available from external appearance. A - Male New Zealand fur seal (*Arctocephalus forsteri*) on first day of territorial occupancy. B - Same male on 63rd day of territorial occupancy. In both photographs the male is shown with face lowered to a freshwater pool.

fast is striking (Figure 4.28). Similar changes in appearance occur in fasting female grey seals between parturition and oestrus: 'indications of approaching oestrus . . . are those provided incidentally by the emaciation of the female and her relatively sedentary behaviour' (Boness, 1979: 44).

A specific example of information about breeding condition being made available by appearance is the proboscis of male elephant seals, which changes in size seasonally and is largest during the breeding season, when the mouth lining is also brightest red (Laws, 1953, 1956; Sandegren, 1976a). Male spotted seals become conspicuously swollen in the genital area in the two months before females enter oestrus (Gailey-Phipps, 1984). In sexually receptive female northern elephant seals 'the vulva becomes noticeably enlarged and swollen, particularly ventrally' (Bartholomew, 1952: 391), and between parturition and the end of oestrus in the northern fur seal 'the vulva is swollen and protruding and the vestibular mucosa and vaginal orifice are a brilliant pink'; after a female's first post-partum trip to sea the swelling is gone and the 'entire vulva appears dark brown or black' (Bartholomew and Hoel, 1953: 420).

In the Galapagos fur seal (*Arctocephalus galapagoensis*), males have highest reproductive success if they mate with virgin females or females that are attending yearlings, because females with newborns are unlikely to raise the next year's pup successfully (Trillmich, 1984); a female's reproductive status may therefore affect male behaviour and communication.

(g) *Gender*

Sexual dimorphism in size of pinnipeds has been reviewed by many authors (see Stirling, 1983; Laws, 1984). Sexual dimorphism in other features has been commented on less frequently and is badly in need of review.

I know of no secondary sexual differences in the external appearance of pinnipeds that are present throughout development, though gender may have an important influence upon communication since in some species females invest differentially in pups according to gender (Kovacs and Lavigne, 1986a; Trillmich, 1986; Anderson and Fedak, 1987a). A qualitative difference that appears early in life distinguishes male and female grey seals: following their moult of lanugo, males assume an extremely dark or black pelage, whereas females develop a grey coat (Hewer and Backhouse, 1959; Hewer, 1974; Bonner, 1981b; Figure 4.29A). This sexual difference characterizes all older age classes as well (Hewer, 1974; Bonner, 1981b). Adult males are much darker than females in the Hooker sea lion, southern sea lion (Figure 4.3D, 4.41B), Australian sea lion, and

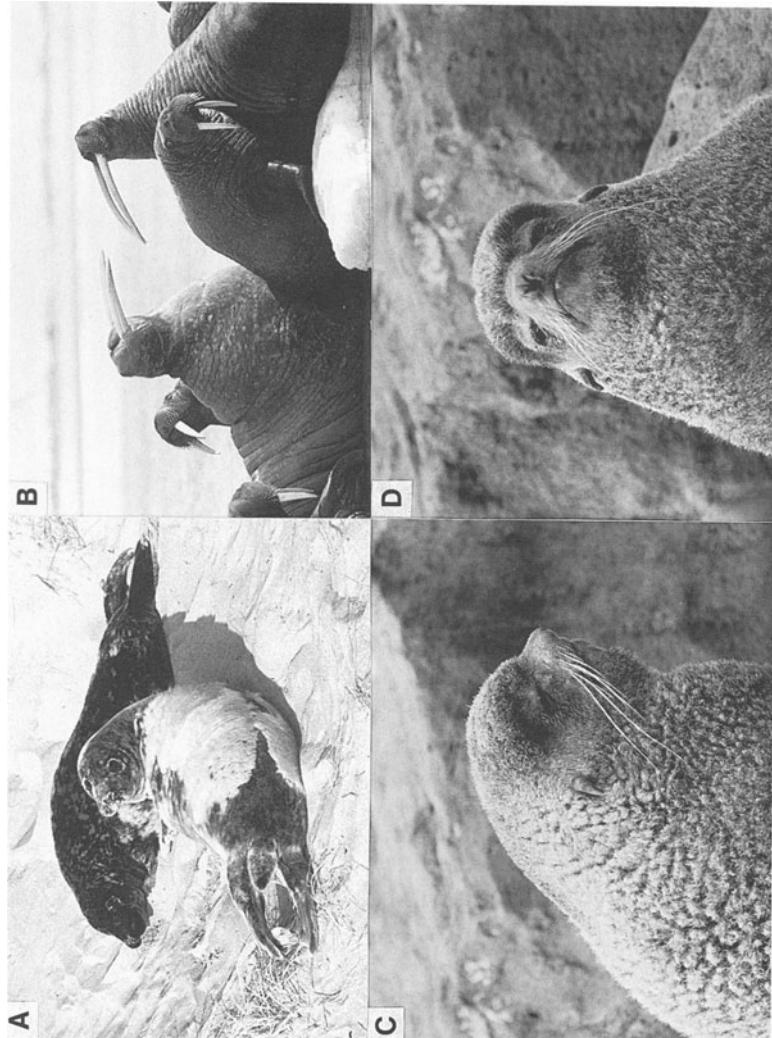


Figure 4.29 Information about gender that is available from external appearance. A - Weaned male [background] and female pup grey seals (*Halichoerus grypus*), showing the male's dark and the female's light coats. The female's white lanugo still covers most of her back. B - Adult male (left) and female Pacific walrus (*Odobenus rosmarus divergens*) threatening one another, showing larger and more robust head, neck and tusks of the male. C, D - Portraits of an adult male northern fur seal (*Callorhinus ursinus*) (compare Figure 4.2B).

California sea lion (Peterson and Bartholomew, 1967; Marlow, 1975; King, 1983). The lemon-yellow face, throat and chest of the sub-Antarctic fur seal (*Arctocephalus tropicalis*) are more extensive and intensely pigmented in males than in females (Paulian, 1964; Condy and Green, 1980; Bonner, 1981a).

Male walruses and otariids average larger and more robust than females from birth, a difference that is particularly obvious in their heads; using head features, I could visually distinguish male from female New Zealand fur seal pups when they were about 6 months old, and it is likely that the seals themselves could distinguish gender using such features much earlier (Miller, 1971). Territorial male Steller sea lions distinguish between female and male yearlings suckling their mothers, and chase male yearlings away (Gisiner, 1985). Sexual differences in facial features are apparent also in some pinniped species with little size difference between the sexes, such as the harp seal.

In the Otariidae, strong candidates as cephalic display structures are the bleached crest of mature male California sea lions and the 'topknot' on the crown of mature male sub-Antarctic fur seals (Peterson and Bartholomew, 1967; Repenning *et al.*, 1971; Condy, 1978; Bonner, 1981a). In the related Antarctic fur seal there is no 'crest of longer hair on the head but the hairs on the top of the skull are set vertically in the skin, or recurved slightly forward, and thus stand out as an apparent crest when viewed against the flattened and sleeker pelage of the sides of the skull' (Bonner, 1968: 19). However, the facial differences between males and females of other species, such as the southern sea lion and northern fur seal, are so striking that it is tempting to also interpret male features as being specially evolved display modifications (Figure 4.2B, 4.29C,D). Adult male otariids have massive necks, especially in the breeding season, and the neck hairs are longer than in females (nearly mane-like in the Hooker and southern sea lions; Hamilton, 1934; Marlow, 1975; Campagna and Le Boeuf, 1988a; Figure 4.3D, 4.41B). Cephalic display structures have evolved independently in the walrus, hooded seal (*Cystophora cristata*), elephant seals, grey seal, and the extinct desmatophocid *Allodesmus* (Miller and Boness, 1979; Kovacs and Lavigne, 1986b). In all of these taxa except the walrus, the structures have involved modification of the snout of males (e.g. grey seals: Figure 4.30). In the walrus, both sexes develop tusks (upper canines) but those of males are longer, thicker, farther apart at the base, and more divergent at the tips than are female tusks (Fay, 1982, 1985; Figure 4.29B, 4.31).

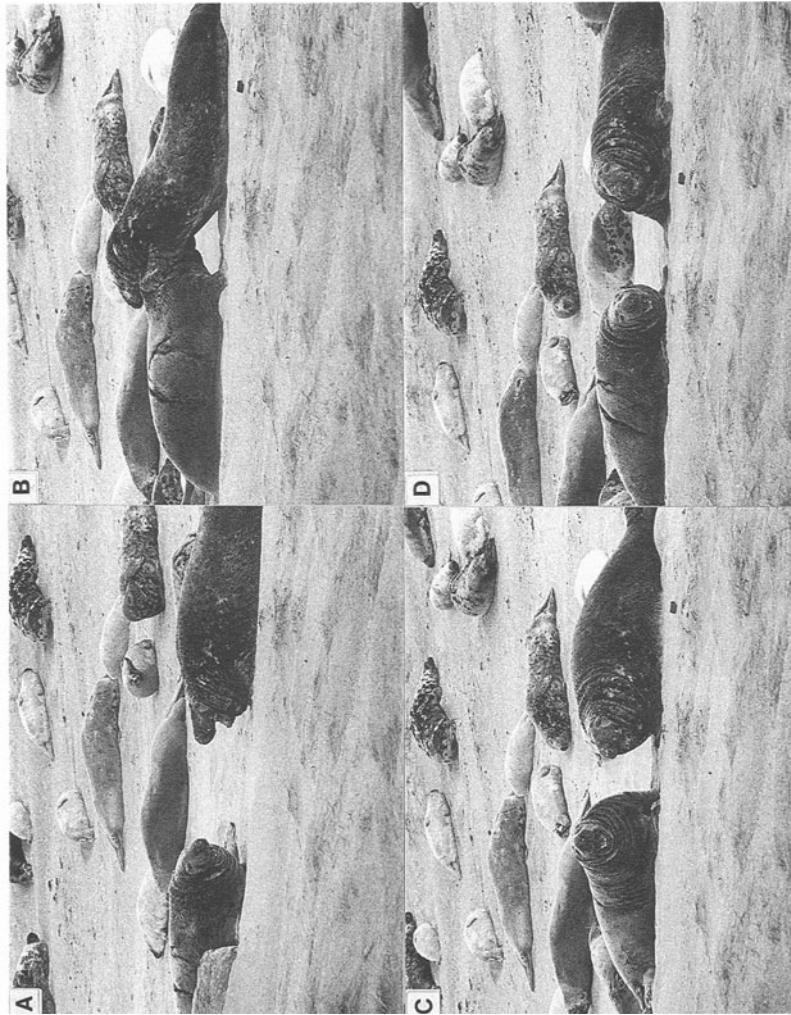


Figure 4.30 Information about gender that is available from sexually dimorphic cephalic display structures. A-D - Display sequence between breeding male grey seals (*Halichoerus grypus*) showing approach, brief fight, then close-range threat [C, D]. The sexually dimorphic snout in this species is typically displayed in oblique or broadside orientation, as in parts C and D. Note the large scars on the flank of the male on the left, possibly due to a shark attack (see p. 175). From Figs 5-8 of Miller and Boness (1979).

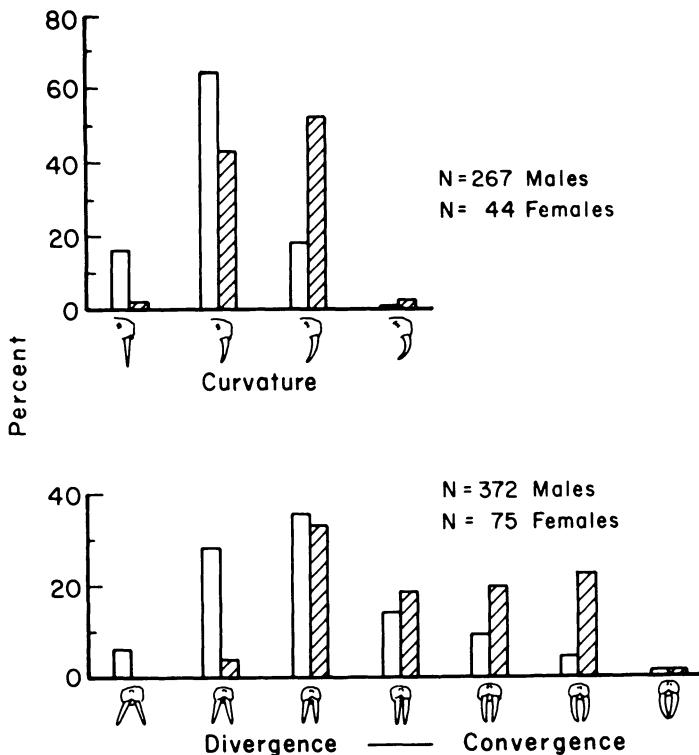


Figure 4.31 Information about gender that is available from appearance of curvature and divergence/convergence of tusks of male (open bars) and female (cross-hatched bars) Pacific walruses (*Odobenus rosmarus divergens*). From Fig. 76 of Fay (1982).

(i) Moult

Moult in pinnipeds is an important component of the annual cycle because it dictates lengthy haul-outs and is energetically demanding (Fay and Ray, 1968). Moult demands high peripheral temperatures and, because of a reduction in their resting metabolic rate, moulting pinnipeds typically fast or eat little so tend to be lethargic when hauled out (Ashwell-Erickson *et al.*, 1986). In monk seals and elephant seals sheets of cornified epidermis with the old hairs slough off, so moulting individuals are visually conspicuous (Kenyon and Rice, 1959; Ling, 1965; Figure 4.32A). Moult is also obvious in walruses (Figure 4.32B), but in most species is evidenced by the pelage simply becoming duller (often more brownish or yellow) with less distinct markings, due to the tips of the hairs splitting (Scheffer and Slipp, 1944; Scheffer and Johnson, 1963; Backhouse, 1969; Hewer, 1974; Knudtson, 1974).

Seasonal moult activity changes with age and differs between the

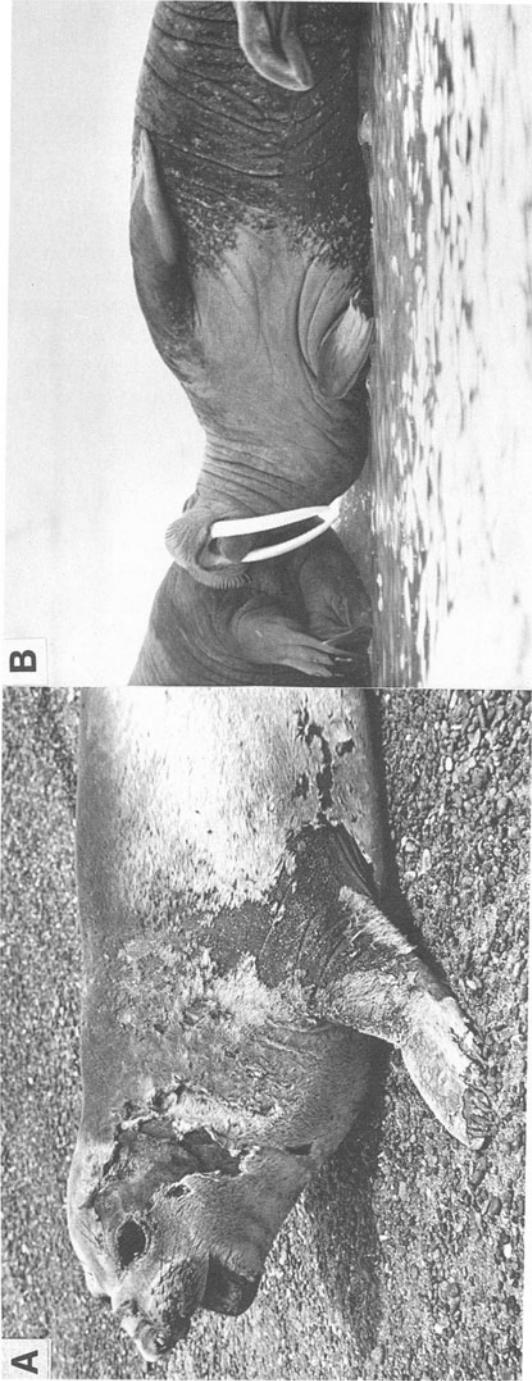


Figure 4.32 Information about physiological state [moult] that is available from appearance. A - Moulting juvenile male southern elephant seal (*Mirounga leonina*). B - Moulting adult male Pacific walrus (*Odobenus rosmarus divergens*).

sexes (e.g. Laws, 1956; Carrick *et al.*, 1962; Reiter *et al.*, 1978). In the northern fur seal moult begins later each year as animals age (on average it begins 3.4 days later each year for males and 5.5 for females), and females moult several weeks later than males of the same age (Scheffer and Johnson, 1963). Yearling harbour seals moult first; among older animals females moult about 7 days earlier than immature males, which in turn moult about 12 days earlier than mature males (Thompson and Rothery, 1987; Thompson *et al.*, 1989).

Moult is accompanied by major changes in haulout behaviour, activity levels, and behavioural dispositions: captive moulting phocids are 'listless, ill-humoured and lazy' (Mohr, quoted by Rand, 1967: 14).

(j) Summary remarks

To illustrate part of Smith's approach to message-meaning analysis I have focused on some kinds of information contributed to messages solely from external characteristics of pinnipeds. Much of this information is reliable and highly relevant to communication and social behaviour. Many of the characteristics occur at one time in an individual pinniped, and many are linked. Many change systematically over short time courses for physiological or environmental reasons; others change over long time courses because of predictable events in the annual cycle or in development, with the latter including genetically programmed attributes as well as environmentally induced ones (e.g. scarring from intraspecific combat or predators; Figure 4.30). Alone and in various combinations external characteristics can contribute extremely detailed and complex information to context and to messages. When messages are augmented further by a sender's behaviour and by external features of context, and when meanings are assigned by recipients who have their own unique attributes, experiences, and predispositions, the potential variability in pinniped communication can be seen to be staggeringly high. This is especially true of short-range interactions that characteristically involve several senses, and less so of interactions that occur over long distances, and which just involve sounds or gross visual signals. On the one hand, this should make us comfortable in documenting high variation in signalling and responsiveness in what we simplistically judge to be similar circumstances; on the other, it is notable that much pinniped communication is so strongly structured and patterned. Combat and threat behaviour provide many examples of such structured communication. I discuss them next.

4.4 COMBAT BEHAVIOUR AND THE COMMUNICATION OF THREAT

Fighting behaviour in pinnipeds can be dramatic and intense, particularly between breeding males. Males also participate in striking displays that function in spacing and in dominance relations. In this section I discuss general models of threat communication, then some aspects of combat in pinnipeds.

4.4.1 Models of threat and combat

Morphologically specialized display features seem to characterize pinniped species with fluid spacing, and which need to reaffirm social status through airborne displays at different locations or with different individuals (Miller and Boness, 1979). This hypothesis derives support from the occurrence of such features in polygynous land-breeding species that are not territorial (elephant seals, grey seal), in polygynous ice-associated species that display in air or at the water surface (walrus, grey seal, hooded seal), and in polygynous land-breeding otariids whose territorial systems are dynamic because of thermoregulatory requirements (California sea lion, southern sea lion). Less striking facial modifications occur in other, strictly territorial species however, as I have noted above (pp. 178–180; e.g. northern fur seal, sub-Antarctic fur seal).

The preceding hypothesis assumes that social morphology is important in how competing males establish and maintain social status or territory, and how they resolve disputes. Morphological features such as manes and enlarged noses can be modified in appearance, for example through the assumption of different postures or through muscular action, but they are much more constrained than is behaviour. Thus they can accurately reflect a male's growth, size, or condition, or more generally a male's resource-holding power (RHP; Parker, 1974), which can be defined as 'a measure of the capacity of an individual to hold a resource, which can be increased, if at all, only with a substantial cost in fitness' (Maynard Smith, 1982: 2; see also Andersson, 1982). Thus social morphology should generally subserve honest communication. The same generalization also applies to displays that are expensive or difficult to perform (Zahavi, 1977, 1981; Burk, 1988) though not to most kinds of threat displays, such as between equally matched contestants:

... the average costs of the display required would be equal to the average gain from victory. This is of course uneconomic. If animals indicated by the intensity of their initial display the effort they were prepared to make to win the resource, it would be less wasteful if the loser-to-be retreated immediately on

seeing that its rival had shown the more intense display. But a population of animals which took the information proffered at its face value would be open to invasion by a mutant which always displayed at the highest possible intensity, no matter what its real intentions' (Caryl, 1982: 679–680).

In brief, according to this model it is advantageous to obtain information that places an opponent at a disadvantage, but disadvantageous to communicate such information; 'threat displays should not transmit information about the cost that an individual is prepared to pay' in a particular evenly-matched contest (Caryl, 1979: 141) and recipients of threat displays should be sceptical, and should probe or otherwise assess the reliability of the information proffered (Caryl, 1979, 1982; Moynihan, 1982; Smith, 1986a). Further, when confronted with inconsistent information about a signaller's RHP and behavioural intentions, a recipient should usually 'believe the least impressive information' (Caryl, 1982: 681; Caryl, 1979), that is to say it should attend and respond to the most reliable source of information (Zahavi, 1977). Evolutionarily specialized social morphology, as well as acoustic displays, are likely to be such reliable sources in pinnipeds (Burk, 1988).

Unritualized signals cannot be used dishonestly by a signaller because they convey information regardless of costs and benefits (Caryl, 1982; Maynard Smith, 1982). If it is important for signallers to conceal their intentions (the cost they are prepared to pay) then displays should evolve towards a typical intensity (Caryl, 1979) or ambiguity (Hinde, 1985). However, predictions of ritualization towards typical intensity also follow from other theoretical assumptions (see Baerends, 1975). Zahavi (1977, 1980) argues that ritualization provides a reliable standard for comparison and hence is a result of selection for reliable information. As an analogy, he notes that a standardized race permits accurate assessment of the abilities of competitors, whereas unstandardized comparisons of speed do not. Clearly certain kinds of unritualized signals, namely those that provide reliable information to receivers, are likeliest to become ritualized, with the resulting displays encoding *more* information than their precursors – not less as originally conceived by Morris (1957; Zahavi, 1980). As an example of the process consider fighting between male pinnipeds, which promotes age discrimination. Then the evolution or exaggeration of secondary structures and display behaviour that heighten the appearance of strength or age (or both) would naturally follow (Williams, 1978).

The evidence for dishonest or manipulative communication through ritualized signalling is weak, though the logic for it is appealing (see above). The dishonest model rests on two kinds of evidence:

winners and losers often cannot be distinguished by their display behaviour; and agonistic displays are poor predictors of attack (Nelson, 1984; Popp, 1987). Both present methodological problems, and the latter makes a questionable assumption. The methodological problems are associated with the coarse level of detail of motor patterns and context that are used in most studies: behavioural components are coarsely described, contextual sources of information are ignored, and an extremely short-term view of interactions and their consequences is taken, so the data are inadequate to support the generalization (Caryl, 1979; Smith, 1986a). An important assumption relates to predicting attack - 'that agonistic displays are meant to communicate the intention to attack' (Popp, 1987: 154). There is little evidence for this. Indeed, 'if displays are often effective in causing an opponent to flee then one would not expect the display to be followed by an attack. An animal cannot attack an opponent that has fled' (Popp, 1987: 154; Paton, 1986; see also Smith, 1977). More substantially, displays *in general* do not provide a single, fixed kind of information or an unconditional prediction; thus a display 'that indicates the possibility of attack also indicates that the signaller may engage instead in alternative acts - e.g. flee, associate, or behave indecisively - and gives some information about the relative probabilities of the choices' (Smith, 1986a: 75).

The occurrence of 'manipulation' or 'deception' through display behaviour can be accommodated within Smith's (1977, 1986a) model. One extremely important kind of data needed to refine the picture will come from studies on the long-term interdependence of communicating individuals: in principle, long-term familiarity such as occurs in pinnipeds should reduce the efficacy of dishonest communication, and communication between experienced, familiar pinnipeds should be subtle and rich. Another important kind of data lies in how information is obtained by interactants: is it sequential, simultaneous, organized in rounds, etc. (Enquist and Leimar, 1983)? Finally, what roles does contextual information play in the resolution of aggressive encounters?

I agree with Nelson (1984) and Smith (1986a) that models of contest behaviour are seriously impaired by their simplicity and lack of reality. However stark the models are, many nevertheless make clear predictions about behaviour that should be tested and refined. A simple example is contest duration (reflecting 'cost'), which is predicted to follow a negative exponential distribution under the 'war of attrition' model of symmetric contests.* This model is restrictively simplistic (Caryl, 1979), but neither this nor other models can be

* Such a distribution describes many sorts of behavioural durations, however (Getty, 1981; Nelson, 1984).

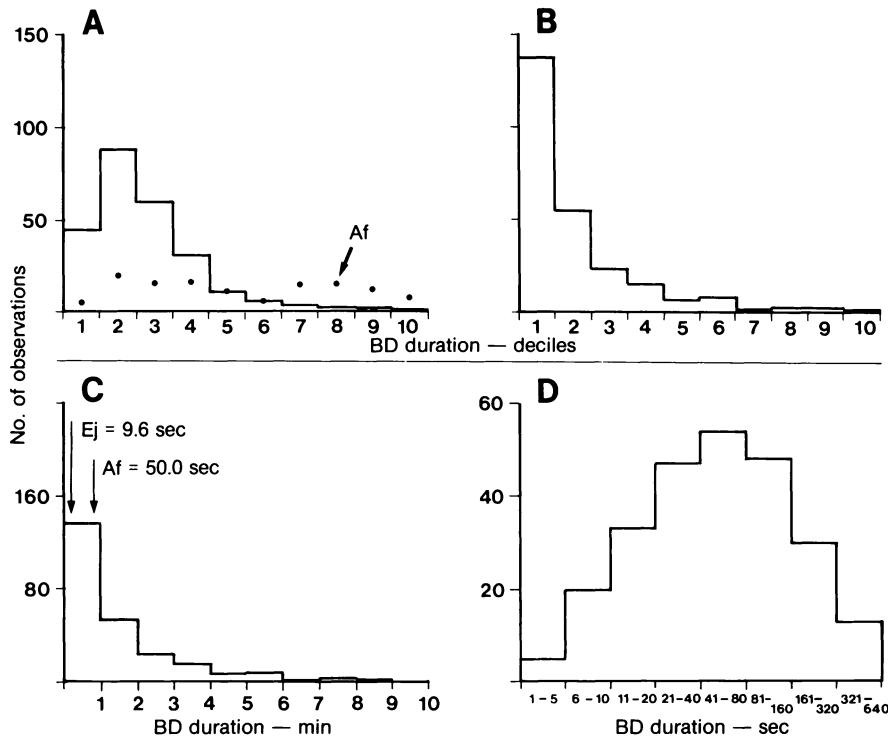


Figure 4.33 Species differences in the durations of boundary displays (BDs) between breeding male otariids. A, B - Frequency distributions of BD durations for Steller sea lions (*Eumetopias jubatus* (A) and New Zealand fur seals (*Arctocephalus forsteri* (B). Data are plotted for deciles of the range of BD durations; data for the New Zealand fur seal ('Af') are also shown on part A. Note the striking difference in shapes of the frequency distributions. C, D - Frequency distribution of BD durations for New Zealand fur seals, plotted over the range of durations on arithmetic (C) and logarithmic (D) scales; medians for Steller sea lions ('Ej') and New Zealand fur seals ('Af') are indicated on part C. This graph is based on unpublished data of R. L. Gentry.

examined using data on pinnipeds, because no relevant data have been published! Boundary Displays in otariids are a good candidate (see Figure 4.22); some data are summarized in Figure 4.33. Are such remarkable differences across species related to costs and benefits (see Figure 4.34A)? Good, detailed, quantitative and descriptive data on pinniped contest behaviour and communication generally are needed to explore such important issues.

The diversity of aggressive displays used by pinnipeds is high, as in other animal groups, and is particularly high in gregarious species (Moynihan, 1960; Baerends, 1975; Miller, 1975a; Sandegren, 1975, 1976a, 1976b; Maynard Smith, 1982; Paton, 1986; Paton and Caryl, 1986). This diversity relates to variability in displays and responses to displays. In Section 4.2, I discussed variation, and here summarize

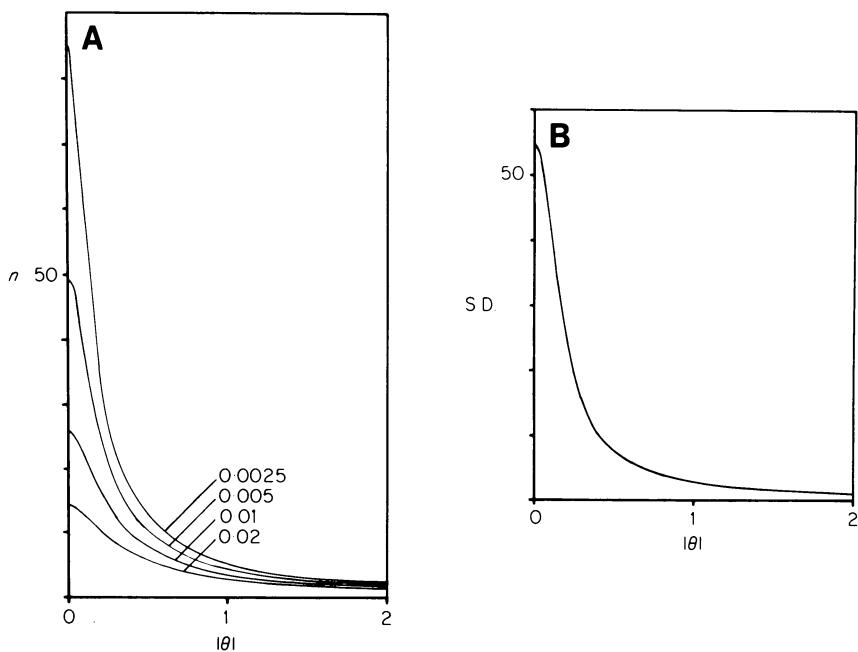


Figure 4.34 A - Average fighting times, in number of steps (vertical axis), as a function of relative fighting ability (θ) of interactants. Curves represent different costs to the interactants. B - Variation in the duration of fights, estimated by standard deviation (vertical axis), as a function of relative fighting ability of interactants. From Figs 9 and 10 of Enquist and Leimar (1983).

a few further points. First, displays provide more than one kind of information, they provide information in a probabilistic way, and they provide only partial information, thus have inherent variability (Smith, 1977, 1986b). Second, pinnipeds assess one another's behaviour dynamically in contests and naturally do so imperfectly; this leads to another source of variation in displays, even between clearly unequal opponents (Enquist and Leimar, 1983; Figure 4.34B). Third, variation is introduced by both the choice of behaviour, and the form of behaviour that is chosen (Enquist, 1985). Finally, variation in resource value and in the level of asymmetry between interactants also markedly affect the nature of their contests (Enquist and Leimar, 1987). The importance of these latter factors is obvious, and they really are just part of context in the sense of W. J. Smith.

The interplay of external and internal factors results in complex variable social interactions, excellent descriptions of which have been published for the northern elephant seal (Bartholomew, 1952; Sandegren, 1976a). In this species:

'Winning fights . . . is not easily predicted by focusing on a few variables that are easy to measure. We have seen males depose an alpha bull by challenging him immediately after he had fought and was exhausted. Some adult males sleep, avoid fights, and allow subadult males to approach nonoestrus females early in the breeding season, apparently conserving their energy for the time when females come into oestrus. The winner of a fight is not necessarily the male that does the most damage; we have seen males win fights without delivering a single butt or bite' (Le Boeuf and Reiter, 1988: 356).

It will obviously be difficult to align simple mathematical models with such typically complex observations and to make biologically meaningful generalizations, especially if year-to-year and cohort-related variation in reproductive success like that reported by Le Boeuf and Reiter (1988) is widespread.

4.4.2 Combat behaviour

In elephant seals, walruses, fur seals, and sea lions, fights between breeding males can result in severe injuries or death (Figure 4.35). In the southern sea lion, about 68% of adult males sustain punctures, wounds, or lacerations of the body, 11% lose one or both lower canines through breakage, and 6% injure a foreflipper through fights (Campagna and Le Boeuf, 1988a). Male Galapagos fur seals experience an annual mortality rate of about 30%, primarily because of the stresses and injuries involved with territorial behaviour and fights with other males (Trillmich, 1984). Walruses and elephant seals inflict injuries with the upper canines by striking forcefully downward on the opponent (Bartholomew, 1952; Laws, 1956; Carrick *et al.*, 1962; Miller, 1975c; Sandegren, 1976a). Fur seals and sea lions grasp the opponent and twist or jerk with an upwards motion, ripping with the lower canines; the lower canines develop sharp edges on the posterior surface through wear against the upper canines (Figure 4.36A, B). Bearded seals have short dull teeth, and males fight and inflict injuries with the strong sharp claws of the foreflippers (Burns, 1981b; Figure 4.36C). Combat between breeding males can also cause injuries in other phocid species (e.g. Scheffer and Slipp, 1944; Bishop, 1967; Kaufman *et al.*, 1975; Smith and Hammill, 1981; Smith, 1987), but none approaches the incidence or severity of that in elephant seals, walruses, and otariids. For example, the grey seal has a polygynous terrestrial social organization throughout much of its range, but males have short dull teeth and inflict only minor injuries on one another, despite their energetic fights (Boness, 1979; Boness and James, 1979;

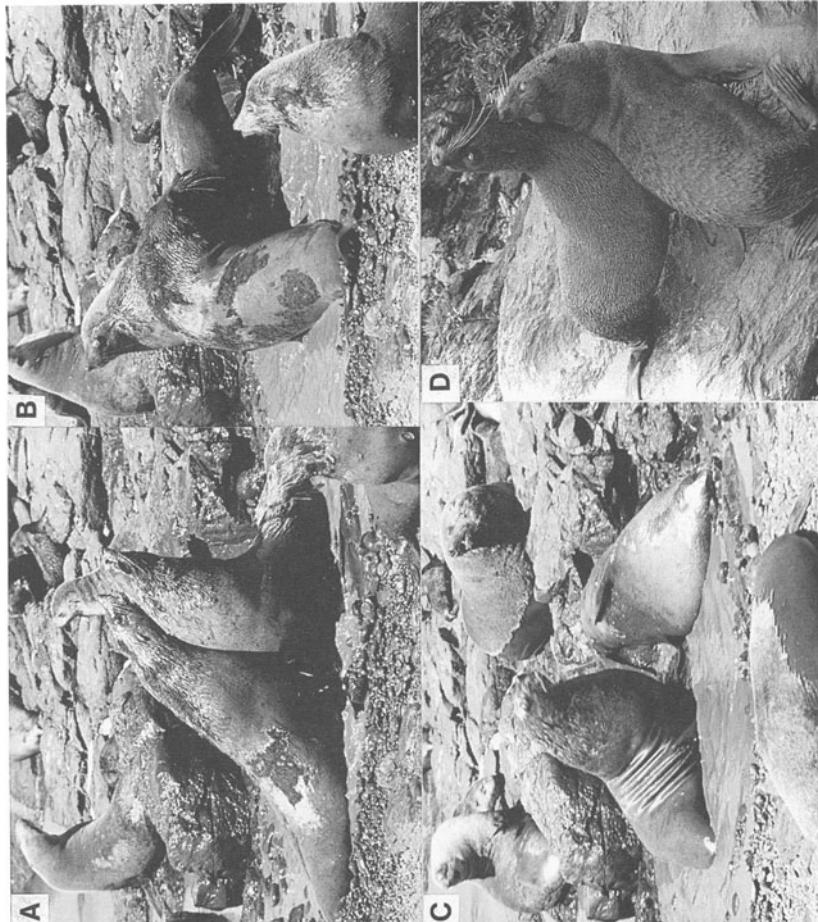


Figure 4.35 Fighting in otariids. A-C - Fight between adult male Australian fur seals (*Arctocephalus pusillus doriferus*), resulting in one's death (C). D - 'Fight' [high-intensity interaction with chest-to-chest pushing] between adult female New Zealand fur seals (*Arctocephalus forsteri*).

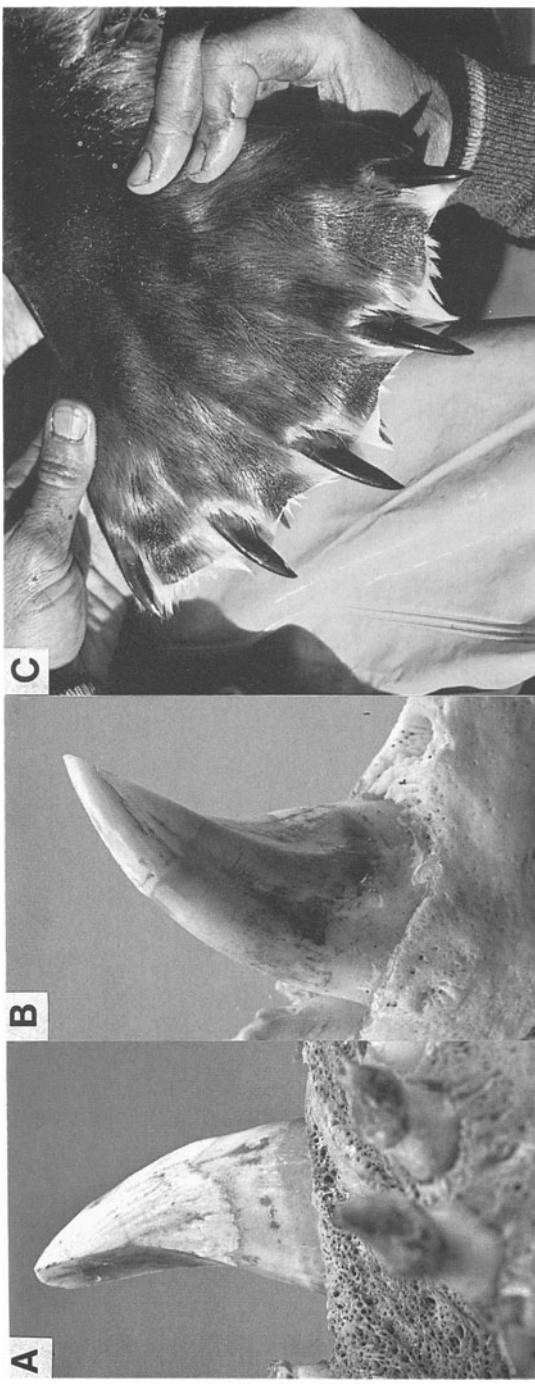


Figure 4.36 A - Medial view of the left lower canine of adult male Steller sea lion (*Eumetopias jubatus*), showing the wear on the posterior surface developed through rubbing against the anterior surface of the upper canine. B - Same tooth in left lateral view. C - Foreflipper of adult male bearded seal (*Ereignathus barbatus*), showing the strong sharp claws used in intrasexual fighting.

Miller and Boness, 1979; Figure 4.30; see also Anderson and Fedak, 1987b).

The adaptive significance of pinniped fighting behaviour is not clear. Certainly the most energetic and dramatic combats occur between mature breeding males, but such combat behaviour occurs in species that mate in association with ice (walrus, hooded seal, some populations of grey seal) as well as those that have complex land-based breeding systems (elephant seals, some populations of grey seal, fur seals, sea lions). Among the latter, serious combat occurs in species where males hold discrete territories (fur seals, some sea lions), are organized within a dominance structure (elephant seals), or exhibit flexible spacing that is strongly influenced by tide, thermal conditions, topography, or female movements (California sea lion, southern sea lion, grey seal). Combat behaviour occurs in species that have obvious display structures or weapons - which are not systematically associated with one another - as well as in species that do not. Finally, vigorous fighting between males occurs in species that are only weakly polygynous (hooded seal, harbour seal, grey seal, bearded seal) and in others that are strongly so (elephant seals, many otariids). Can any general patterns be detected within this bewildering variety?

Combat between male pinnipeds has to be viewed within the broad picture of competition for access to mates, and the costs and benefits that attend such competition. The consequences of competition for mates by male pinnipeds can be judged by the frequency distribution of copulations per male; this gives some idea about how intense sexual selection is in some species, and how much it varies within and among species (see Chapter 1). In the grey seal, females copulate several times, and many copulations are interrupted through social interactions between males; one index of male reproductive success is therefore the number of uninterrupted copulations with females that are copulating for the first time in a season. Using that measure, male grey seals on Sable Island averaged 1.6 copulations each (range 0-5), and 41% of the 34 males observed were unsuccessful (Boness, 1979; Boness and James, 1979; Figure 4.37A; see also Anderson and Fedak, 1987b). It is widely assumed that female otariids usually copulate only once per season (Miller, 1974). If the assumption is true, then the number of females with which a male copulates should be a straightforward estimate of his reproductive success. Of 71 adult male southern sea lions, 24% did not copulate, and one copulated with 18 females ($\bar{Y} = 3.5$ copulations per male; Campagna and Le Boeuf, 1988a; Figure 4.37B). In a sample of 32 territorial male New Zealand fur seals, 53% did not copulate, and one male copulated with 30 females; the average number of copulations per male was 2.6 (Miller, 1971, 1975b; Figure 4.37C). Territorial male

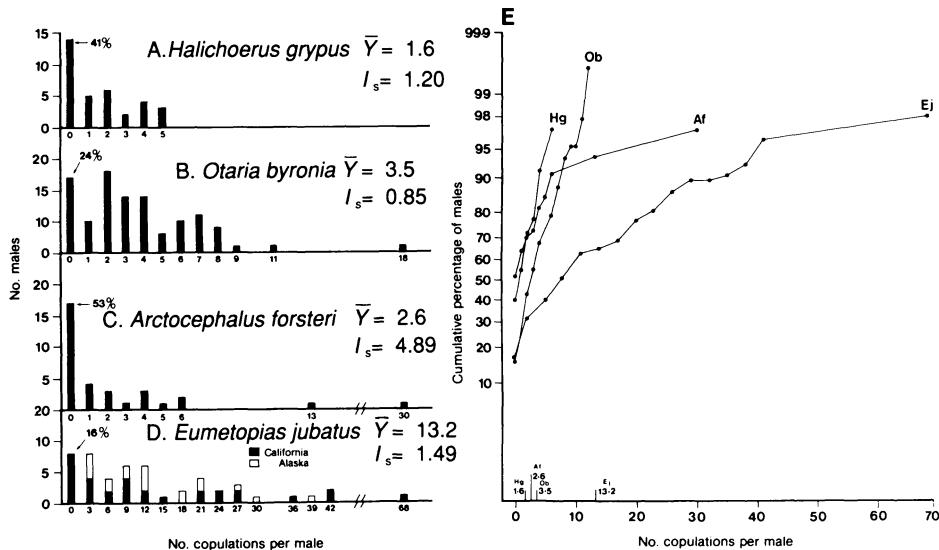


Figure 4.37 Inter- and intraspecific variation in frequency distributions of copulation frequency per male, for four land-breeding species of pinnipeds. A - Grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. Data refer to complete (uninterrupted) copulations with females that were copulating for the first time each season. B - South American sea lion (*Otaria byronia*) at Peninsula Valdés, Argentina. C - New Zealand fur seal (*Arctocephalus forsteri*) on the Open Bay Islands, New Zealand. D - Steller sea lion (*Eumetopias jubatus*) on Ano Nuevo Island, California and Marmot Island, Alaska. E - Probability plots of same frequency distributions (data were divided by $[N + 1]$ in each case, for purposes of plotting); means are indicated at the bottom left. Hg = *Halichoerus grypus*, Ob = *Otaria byronia*, Af = *Arctocephalus forsteri*, Ej = *Eumetopias jubatus*. The percentage of males that did not copulate is indicated for each species in A-D. I is a measure of the intensity of sexual selection (see text). Data sources: A - Boness (1979: lower right part of Fig. 28); B - Campagna and Le Boeuf (1988a: Fig. 4A); C - Miller (1971: Fig. 59A; 1975a: Fig. 142); D - Gisiner (1985: Tables 8 and 9).

Steller sea lions averaged 13.2 copulations per male in an Alaskan breeding colony (range 2-38), and 13.2 (range 0-68, summed over several years) in a California colony (Gisiner, 1985; Figure 4.37D). Overall, only 16% of the territorial males did not copulate.

The intensity of sexual selection, based on the copulation differential among males, can be estimated by $I_s = s_s^2 / \bar{Y}_s^2$, where \bar{Y}_s is the mean number of copulations per male, and s_s^2 is the associated variance (Ryan, 1985; but see cautionary remarks of Grafen, 1988). Using this expression, estimates of 1.20, 0.85, 4.89, and 1.49 were obtained for grey seal, southern sea lion, New Zealand fur seal, and Steller sea lion, respectively. These estimates can be compared with 19 estimates of 0.5-5.2 (mean 2.20) plus an extreme of 13.6, for 20

studies on anurans (Table 4.4.4 of Ryan, 1985). Estimates of I_s for land-breeding pinnipeds are complicated by the inclusion of males that achieve no copulations, because many males in the population are unsuccessful at penetrating the prevailing social structure so are not represented in the samples. For this reason, Boness (Chapter 1) recommends that only males that copulate be included in the estimation of I_s . In addition, the presence of such males is influenced by the size of a breeding aggregation and topography so varies from colony to colony within a species (e.g. van Aarde (1980) reported average harem size of southern elephant seals to range from 22 to 254 in different habitats on Kerguelen Island).

The contrasts apparent in Figure 4.37 span only part of the range that exists in pinnipeds. Elephant seals are certainly more extreme at the upper end of the scale (Le Boeuf, 1974; McCann, 1981; Le Boeuf and Reiter, 1988), and spotted seals at the lower (Burns, 1970; Burns *et al.*, 1972; Fay, 1974; Bigg, 1981). Over this range, determinants of male reproductive success are varied and complex. In species that are widely dispersed during the breeding season, such as the pack-ice-breeding spotted and crabeater seals (Burns, 1970; Fay, 1974; Siniff *et al.*, 1979; Bigg, 1981; Laws, 1981, 1984), sexual selection probably operates mainly through mate choice. Males consort with individual females and engage in courtship over several days around the time of oestrus. Male spotted seals give distinctive vocalizations then, and engage in stylized patterns of body contact (Gailey-Phipps, 1984). Sexual dimorphism in the spotted seal is slight, unlike the closely related harbour seal, and males engage in few fights (Naito and Nishiwaki, 1975). The means by which male spotted seals compete to consort with preferred females (e.g. females that are large, in good condition, in good habitat, or breeding at an optimal time) are unknown. Male bearded seals seem to offer an unusual example of attraction of females through long-distance acoustic displays, as in many bird species (Ray *et al.*, 1969; Burns, 1981b; Stirling *et al.*, 1983; Cleator, 1987; Cleator *et al.*, 1989; Figure 4.13). Consort behaviour has not been described in this species, but injuries caused by fights between rutting males are severe, which suggests that some sort of defence of space or clumping among males may occur, or that females vary significantly in quality. Species in which breeding females are gregarious or clumped provide the opportunity for polygyny even in species that associate with ice (Bartholomew, 1970; Stirling, 1983; Laws, 1984). In the walrus, males display in the water adjacent to mixed herds on the ice, and compete for such display space close to the herds (Ray and Watkins, 1975; Stirling *et al.*, 1983, 1987; Fay *et al.*, 1984; Figure 4.18, 4.19). In some parts of the range, ice formations are so predictable that individual males can return to nearly the same location in successive years (Stirling, 1983; Stirling

et al., 1987). Parturient female ringed seals and Weddell seals are sufficiently clumped in locally stable habitat that males achieve polygyny by holding large underwater territories (Smith and Hammill, 1981; Stirling, 1983; Smith, 1987). Females of the hooded seal are much more dispersed, but males consort with them for only a few days, so become polygynous by sequentially consorting with different females (Boness *et al.*, 1988). Extremes of polygyny occur when large aggregations occur on land. In all polygynous pinniped species male combat is pronounced but, as noted, there is no simple association between the presence or intensity of combat and the development of social morphology (see Section 4.5).

To summarize, the presence and intensity of combat in pinnipeds must be considered in light of reproductive competition. Sexual selection varies within and among species in both intensity and form and, in a few instances (e.g. spotted versus harbour seals), can explain differences in combat behaviour. Overall, however, there is only a general correspondence between severity of combat and degree of polygyny. To improve understanding, studies on the components of reproductive success in different populations of single species need to be carried out. The influences of life history and body size need to be considered in such analyses, and the nature and functioning of communication among males, and among males and females, must be documented in detail.

4.5 ECOLOGICAL VARIATION AND TIME/ACTIVITY BUDGETS

An appreciation of how communication operates within a species demands detailed behavioural observations over a range of ecological and environmental factors such as seasonal and diel changes, year-to-year variation, population densities and dispersion characteristics, geographic variation, and habitat characteristics. No research addressing all these factors has been carried out on a pinniped species, but some general characteristics can be deduced from specific studies. In this Section I discuss some general ecological and social influences on communication and the amount of time spent communicating.

4.5.1 Environmental variability

Spatial and temporal variation profoundly affect opportunities and characteristics of social communication, and account for many species differences (Figure 4.38). Consider the range of communication possible, the functions of communication, and the distances over which it occurs, as numbers and proportions of different social classes change over a typical annual cycle of breeding in any species,

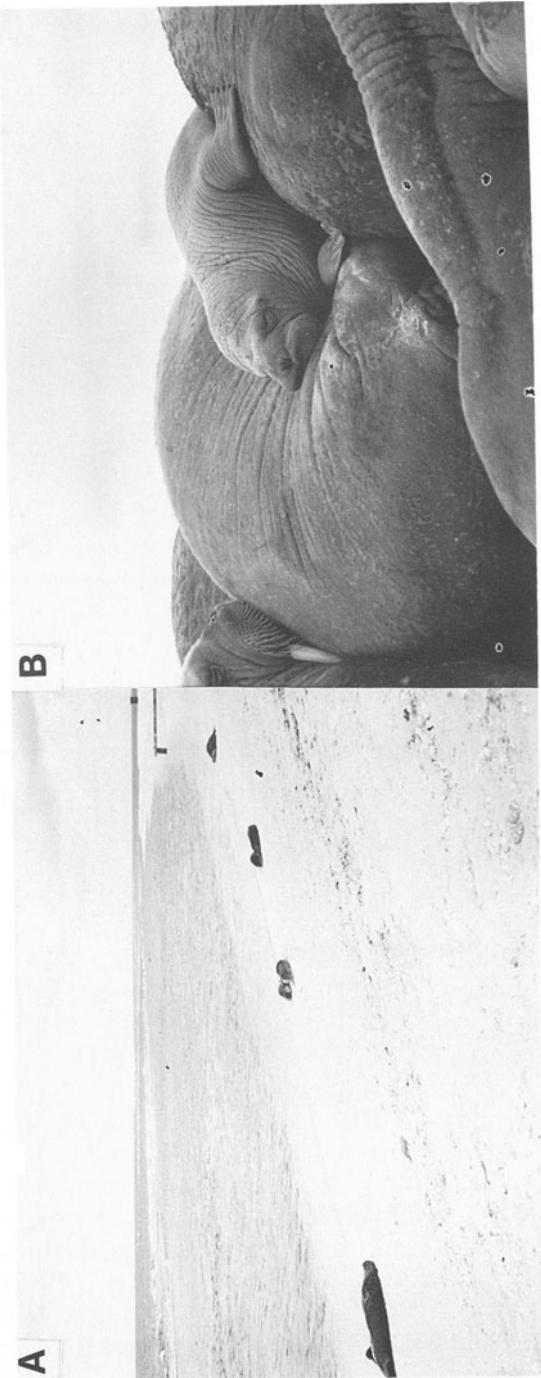


Figure 4.38 Examples of social dispersion with important implications for short- and long-range communication. A - Dispersion of female-pup pairs of Hawaiian monk seal (*Monachus schauinslandi*). B - Close contact of calf Pacific walrus (*Odobenus rosmarus divergens*) with mother and other herd members.

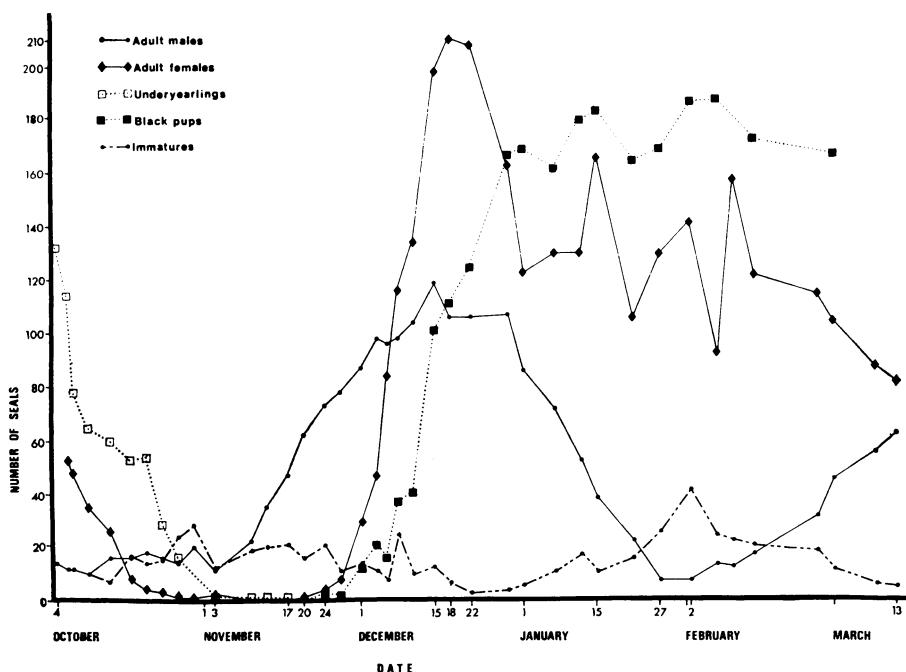


Figure 4.39 Changes in the numbers and proportions of different age and sex classes of the subantarctic fur seal (*Arctocephalus tropicalis*), over part of the annual cycle at Amsterdam Island. From Fig. 4 of Roux and Hes (1984).

such as the subantarctic fur seal (Roux and Hes, 1984; Figure 4.39). On a finer level, individuals of different ages and social experience show systematic differences in arrival times for breeding in the northern fur seal (Bigg, 1986). Harbour seals on Sable Island, Nova Scotia, show little or no segregation by age, sex or breeding condition, whereas segregation among and within haul-out sites is marked at other localities (Knudtson, 1974, 1977; Calambokidis *et al.*, 1978; Sullivan, 1979, 1980; Davis and Renouf, 1987; Allen *et al.*, 1988; Godsell, 1988; Thompson, 1989). Wintering female Steller sea lions segregate themselves from sexually mature subadult males on the same hauling grounds, presumably to avoid harassment and high levels of social interaction (Harestad, 1973; Harestad and Fisher, 1975; see also Sullivan, 1980). During the breeding season, non-breeding female Weddell seals are segregated in large groups away from pupping colonies (Stirling, 1969), and moulting southern elephant seals are segregated by sex and age: 'females show a definite preference for inland moulting grounds ... or for broken ground which is well sheltered. The young males show a preference for coastal areas ... or for irregular ground near the sea. The older males ... are almost entirely confined to the beaches' (Laws, 1956: 43). In other species,

some segregation occurs between breeding and non-breeding females, and even among females of different ages (McLaren, 1967). Finally, strong competition among female Galapagos fur seals for cool resting sites results in females with older offspring moving to other areas (e.g. habitats that are too dangerous for newborn pups; Trillmich, 1984; see also Gentry, 1973; Mattlin, 1978).

One important approach to documenting social and ecological influences on communication is in constructing a communication matrix, which reveals the frequencies and kinds of interactions among different age/sex classes (e.g. Harestad, 1973; Harestad and Fisher, 1975; Sullivan, 1979, 1982). Another approach is to quantify the amount of time spent in communicative activities. Time/activity budget estimates are available for a number of species; I discuss them in the following section.

4.5.2 Behavioural time budgets

Basic to the social dynamics of pinnipeds is how their time is apportioned among different activities. Time-budget studies can be applied at different levels, from an overall population level down to a specific portion of the life cycle. Sampling protocols are outlined in Altmann (1974), Lehner (1979), and Martin and Bateson (1986) (see also Burt *et al.* 1988). Basic requirements are that behavioural units be clearly defined and that samples be independent of one another. For studies on communication, the behavioural units chosen should reflect the facts that pinnipeds typically perform several activities simultaneously, and that many unspecialized 'non-social' activities may provide important information to other individuals. 'Alert' behaviour by hauled-out harbour seals is an example. Such behaviour is an important anti-predator behaviour and is closely attended to by herd members (Sullivan, 1979, 1982; Krieber and Barrette, 1984; Terhune, 1985; da Silva and Terhune, 1988; but see Renouf and Lawson, 1986b).

Independence of samples in time-budget accounts is rarely addressed by researchers, who may sample at intervals so close together in time that consecutive samples are not independent of one another. A sample interval for estimating time budgets needs to be based upon when independence is reached. Such a criterion should be established for different functional groupings of behaviour and should be assessed for robustness across different settings that are relevant to the study (e.g. night versus day samples; young versus old pups) (Walters, 1980; Figure 4.40). I am unaware of any time/activity study on pinnipeds that has addressed this basic statistical requirement.

Available time budgets of pinnipeds are mainly based on direct terrestrial observations. Some coarse estimates of behaviour at sea

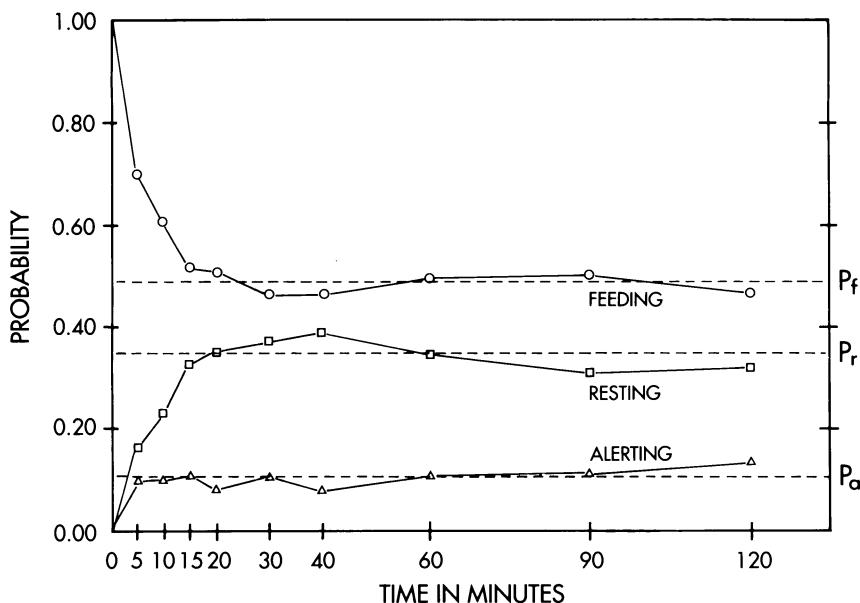


Figure 4.40 Relationship of the independence of consecutive time samples to the sampling interval. The probability that an individual was feeding, resting, or alerting at a time t_i given that it was feeding at time t_0 is plotted as autocorrelation (for feeding) and cross-correlation (for resting and alerting) functions. The dashed lines represent the unconditional probabilities (p_f , p_r , p_a) for the same behavioural categories. Independence of samples was achieved at about a 5 min interval for alerting, and at 15–20 min for feeding and resting. The data are for a bird species (long-toed lapwing, *Vanellus crassirostris*), but the principle is generally applicable. From Fig. 9 of Walters (1980).

are becoming available through instrumentation (Gentry and Kooyman, 1986b; Le Boeuf *et al.*, 1988; Feldkamp *et al.*, 1989), but little direct estimation of pinniped time budgets at sea has been done. Direct time-budget estimates of surface behaviour can be made for some species, especially coastal and gregarious ones (e.g. harbour seal, walrus). For good accounts of visible surface behaviour in other groups, see Packard and Ribic (1982) and Würsig *et al.* (1985). Despite the obvious difficulties of obtaining meaningful observations on pinniped behaviour at or below the water surface, much important communication occurs there (e.g. Sullivan, 1979, 1981; Miller and Boness, 1983; Gailey-Phipps, 1984).

The amount of time spent in communication has been estimated for many species of pinnipeds. Estimates are extremely difficult to compare because they are based on different parts of the annual cycle, different classes of communication, and different criteria, and often are described in vague, broad or interpretive terms. Most estimates rest on conspicuous displays or social interactions, and

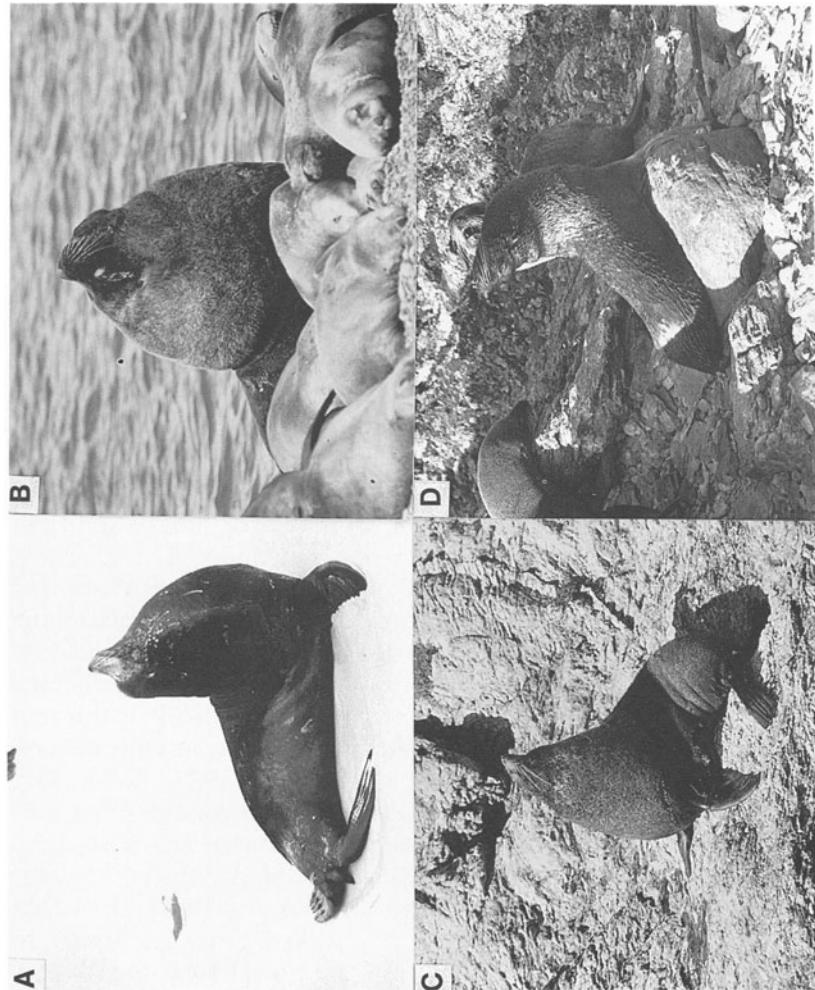


Figure 4.41 Upright postural signalling in otariids. A - Adult male California sea lion [*Zalophus californianus californianus*]. B - Subadult male southern sea lion (*Otaria byronia*). C - Adult male New Zealand fur seal (*Arctocephalus forsteri*). D - Adult female *A. forsteri*, following threat with another female.

exclude unritualized signalling (e.g. mutual staring; flippering by walruses; Figure 4.3C) and subtle displays such as certain upright postural displays of otariids (Figure 4.41). The latter category includes upright resting behaviour, distinctive 'neck-arching' when the head is thrown back (Figure 4.41D; see also Figure 4.32a of Schusterman, 1968), and upright alertness. Breeding male New Zealand fur seals spent about 13.5% of their time upright, compared with only 4.9% for adult females and 2.8% for pups (Crawley *et al.*, 1977).

Important factors that influence the amount of time that pinnipeds spend communicating are: stage of breeding cycle, diel rhythms, social class, and environmental variation on brief or long time scales. These are interdependent, and influence both the opportunities for communication as well as its form or sensory channels used. To increase the scope of the following discussion, I include examples that are not strictly time-budget estimates but are related to them (e.g. rates of interaction).

The social environment and communication are strongly influenced by major temporal and spatial ecological variation. The El Niño-Southern Oscillation (ENSO) is an irregular phenomenon that occurs over a period of years and that results in increased sea-surface temperatures, increased salinity, and decreased food (zooplankton, fish) available to pinnipeds (Trillmich and Limberger, 1985; Ono *et al.* 1987; Glynn, 1988). The 1982-83 ENSO was the most extreme in recorded history and resulted in major reproductive failure and high mortality in marine birds and mammals (e.g. Majluf Chiok, 1987). One effect of this was to drastically alter the age structure of affected pinniped populations in subsequent breeding seasons, since some cohorts were seriously depleted. In turn this altered each species' social matrix and communication patterns. Time budgets of affected species also reflected the trophic stress. Before the ENSO, California sea lion pups spent more time active and more time in communication involved in nursing and play (Ono *et al.* 1987; Table 4.6). Females spent more time at sea feeding in 1983-84, so spent less time ashore with their pups, nursing them and interacting with them in other ways. This reduced the growth rate of pups, who spent more time attempting to nurse from foreign females and thus interacting agonistically with them: only 6.4% of marked pups attempted to nurse from foreign females in 1982, compared with 54% and 42% in 1983 and 1984, respectively (Ono *et al.* 1987).

Some data on time/activity budgets for pinnipeds in different localities are available (e.g. Merrick, 1988). Boness (1984) compared time budgets of male grey seals breeding in the western (Sable Island, Nova Scotia) and eastern Atlantic (Monach Isles, Scotland; data of J. Harwood) (see also Anderson and Harwood, 1985). On Sable Island, males remained on the extensive sand beaches continuously, whereas

Table 4.6 Influence of the El Niño-southern Oscillation (ENSO) on time budgets of pups of the California sea lion (*Zalophus californianus*). Table entries are percentages of time^a

Behaviour	1982 Pre-ENSO	1983 ENSO	1984 Post-ENSO
Rest	39	41	37
Suckle	19	14	12
Active ^b	32	25	22
Aggression	0.2	0.4	0.3
Swim	6.0	5.6	5.9
Play	9.1	5.2	3.0

^a Data from Table 2 of Ono *et al.* (1987).

^b 'Active' includes aggression, swim, and play, plus other behaviours that are not listed (e.g. walking, other social interactions), so subtotals do not sum to the figures shown for 'Active'.

on the Monarchs they spent about 60% of their time in the water off the beach. The terrestrial time budgets of males at the two sites also differed: locomotion for social reasons occurred about twice as often on Sable Island, and males there spent thrice the amount of time in aggressive interactions and half the amount in sexual interactions. The difference in locomotion is related to the males' non-social movements between land and sea at the Monarchs, and the differences in level of sexual interactions reflect the higher female:male ratio there (Boness, 1984).

In an interesting study on a smaller spatial scale, Christensen and Le Boeuf (1978) reported differences among beaches in the incidence of aggressive behaviour between breeding female northern elephant seals (see also McCann, 1982). Similarly, Kovacs (1987) documented substantial variation in time budgets of female and pup grey seals on the Isle of May (England). Females that pupped on the beach spent less than 50% of their time with pups, on average, compared with 75% for inland females (see also Hewer, 1960, 1974). Many kinds of communication were influenced thereby; for example, simple visual 'checking' of pups by their mothers (which declined with pup age) occupied about 1.2% of females' time on the beach, but 6.6% inland, for females with young pups.

4.5.3 Behavioural rhythms

Changes in pinniped communicative behaviour over the annual cycle are virtually unstudied. Gailey-Phipps (1984) studied a captive pair of spotted seals through direct observation and automated data acquisition. She documented striking seasonal changes in the amount of time spent in interactive behaviour (Figure 4.42A) and in the rates of

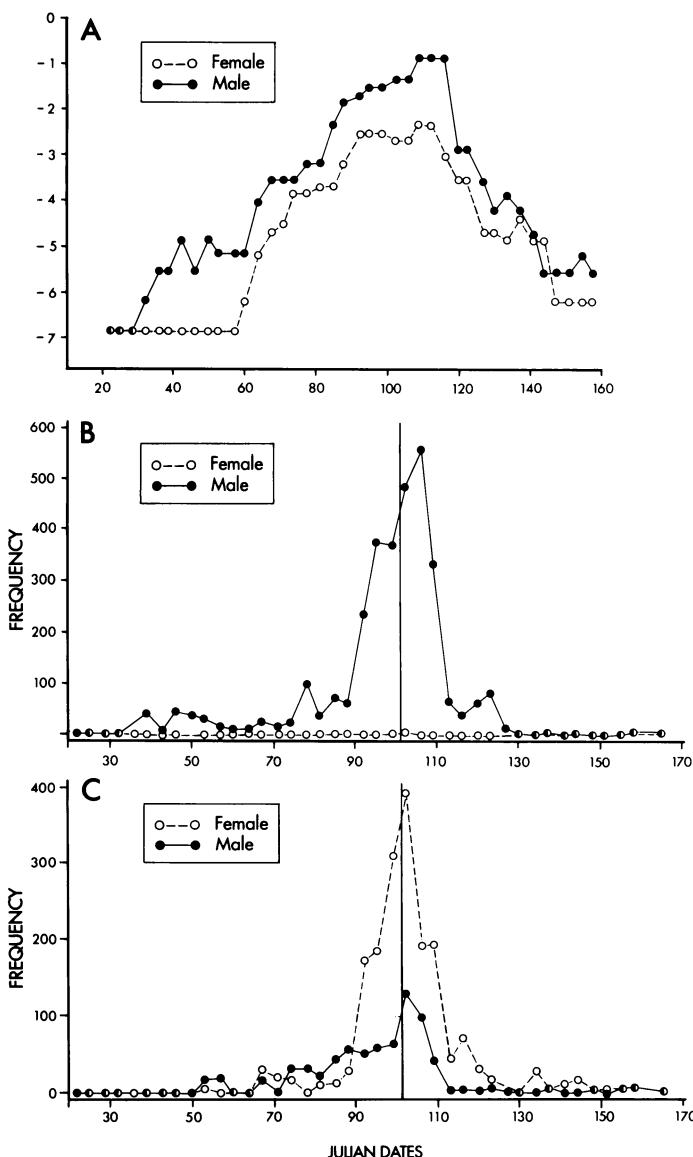


Figure 4.42 Seasonal changes in the incidence of communication in captive spotted seals (*Phoca largha*). Vertical line at day 101 signifies female sexual receptivity. A - Seasonal distribution of the percentage of time spent in 'interactive and sexual' behaviour (logit transformation of percentages is plotted on the vertical axis). B - Frequency of growls per day. The growl is presumed to function as advertisement by breeding males, and is uttered as a loud frequently repeated call, forming 70–100% of the male's repertoire each spring. C - Frequency of barks per day. The bark is presumed to be the most aggressive vocalization of the species, and most are given by unreceptive females towards males. From Figs 40, 9, and 16 of Gailey-Phipps (1984).

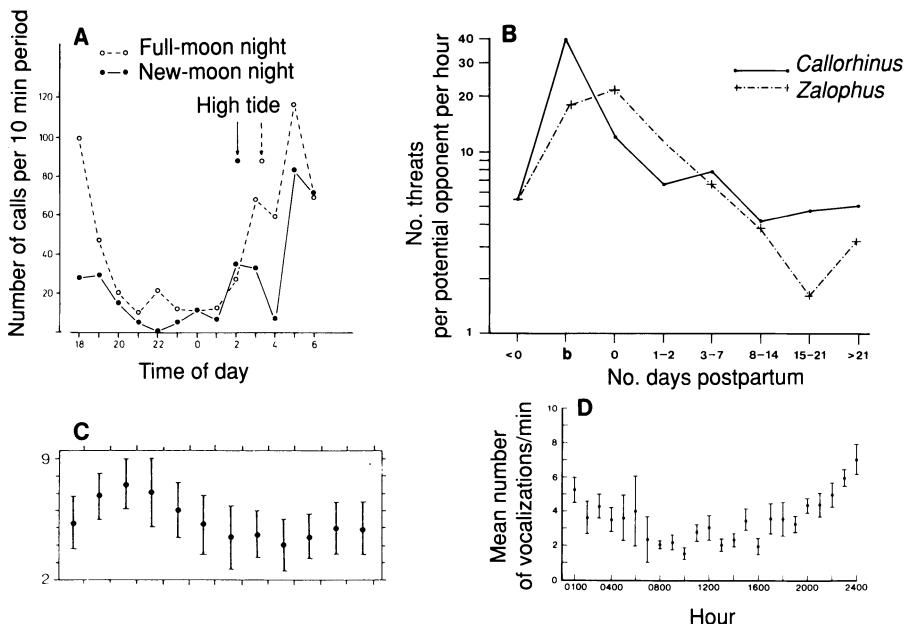


Figure 4.43 Relationship of communicative activity to periodic phenomena. A - Calling activity by Galapagos fur seal (*Arctocephalus galapagoensis*) in relation to time of day, during one night with a full moon and one with a new moon. The incoming tide (arrows) led to increases in calling in each night. B - Incidence of threat behaviour by female northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*) in relation to the day they pupped (b = 2 h period around birth; 0 = remainder of the same day). The curves were corrected for the number of potential opponents (the number of females whose snouts were within one body length of the focal female's snout) present when observations were made. C, D - Rates of underwater vocalization in relation to time of day for male bearded seal (*Erignathus barbatus*) (no. of calls per min \pm S.D.) (C) and crabeater seal (*Lobodon carcinophagus*) (mean \pm 1.96 S.E.) (D) during the breeding season. A is from Fig. 9 of Trillmich and Mohren (1981); B is from Figs. 3 and 11 of Francis (1987); C is from Fig. 6a of Cleator *et al.* (1989; = Fig. 1-12a of Cleator (1987)); and D is from Fig. 2b of Thomas and DeMaster (1982).

occurrence of displays in relation to breeding (Figure 4.42B,C). The percentage of time spent in 'interactive and sexual' behaviour ranged from about 0 to 30%, and varied with date and gender (Figure 4.42A). In her study on captive walrus, Gehnrich (1984) found that a 20-year-old male spent about 25% of his time displaying, both during and outside the breeding season, whereas a 14-year-old averaged 40% during and 21% outside the breeding season (figures estimated from her Figure 4.11; these and other figures for captives (e.g. Schusterman, 1968) are much higher than for wild pinnipeds).

The lunar cycle influences behaviour of the Galapagos fur seal,

with peaks in the numbers of animals ashore being highest around the full moon and lowest around the new moon (Trillmich and Mohren, 1981). The greater number of animals during a full moon naturally leads to more communication ashore, but the level is roughly proportional to the number of animals ashore so does not appear to be influenced by moonlight *per se* (Figure 4.43A). On a shorter time scale pinnipeds also exhibit marked changes in communicative behaviour in relation to breeding. Females tend to be highly aggressive around the time of birth, for example (Peterson, 1965; Stirling, 1971b; Le Boeuf *et al.*, 1972; Christensen and Le Boeuf, 1978; McCann, 1981, 1982; Davis and Renouf, 1987; Francis, 1987; Figure 4.43B).

Diel patterns in pinniped activity have been reported for many species (see Sullivan, 1980; Erickson *et al.*, 1989). Walruses show no diel trends in broadly defined activities during terrestrial haul-out (Salter, 1979), and single breeding male grey seals, each observed for two weeks, likewise exhibited no diel variation in behaviour (Anderson, 1978). In contrast, Chwedenczuk and Fryszt (1983) noted highest levels of vocal activity at night in a captive group of grey seals. Galapagos fur seal pups are generally more active during the day than at night (Arnold and Trillmich, 1985), but are most socially active at dawn and dusk, when it is cool; only wet pups interact much during the day (Limberger *et al.*, 1986). Breeding male northern elephant seals exhibit low vocal activity in the early afternoon, with high activity at other times (Shipley and Strecker, 1986); social interactions between weaned pups occur mainly in the early morning and late afternoon (Rasa, 1971). Male bearded seals are most vocally active in their underwater displays in the early morning (2400–0600), with a secondary peak in the late afternoon or evening (Cleator, 1987; Cleator *et al.*, 1989; Figure 4.43C), whereas crabeater seals have highest vocal activity around 2000–2400 (Thomas and DeMaster, 1982; Figure 4.43D). Diel rhythms in haul-out behaviour must strongly influence kinds and levels of communication (e.g. Müller-Schwarze, 1965; Tedman and Bryden, 1979; Thomas and DeMaster, 1983; Allen *et al.*, 1988; Yochem *et al.*, 1987). Claims of diel rhythms based on small samples should be examined critically, as is obvious from the findings of Green and Burton (1988a) in their analysis of an extensive sample: underwater vocal activity of Weddell seals showed strong diel variation but this differed from month to month and no single pattern prevailed.

The time spent in displays and other communication differs greatly across major social classes (e.g. territorial males versus parturient females), as must the nature of communication, though the latter has received little study. 'Idle' males of the subantarctic fur seal (those not on the breeding colony) on Gough Island spent 0.67% of their

Table 4.7 Percentage of time spent in social interactions by different population classes of Steller sea lion (*Eumetopias jubatus*) and California sea lion (*Zalophus californianus*) on wintering haul-out areas in British Columbia^a

	<i>Haul-out area</i>			
	<i>A</i>	<i>H</i>	<i>I</i>	
<i>Eumetopias</i>				
Large males	8.4 (14)	19 (5)	-	(0)
Medium males	16 (30)	33 (17)	-	(0)
Small males	23 (28)	30 (9)	-	(0)
Females	8.1 (24)	- (0)	-	(0)
Dependent young	12 (4)	- (0)	-	(0)
<i>Zalophus</i>				
Medium males	- (0)	3.2 (50)	1.8 (63)	
Small males	- (0)	4.9 (19)	2.4 (37)	

^a Data are from Tables 2, 17 and 22 of Brenton (1977). Table entries show percentage of time spent in social interactions and (in parentheses) percentage representations of each class on the different haul-out areas.

time in overt social interactions, non-breeding males at the colony spent 4.9%, and breeding males spent 5.6% (Bester, 1977) (in contrast, wintering male New Zealand fur seals spent 8.5% of their time in social interactions; Johnstone and Davis, 1987). At a finer level, young breeding females of the southern elephant seal spent 2.3% of their time vocalizing, whereas older females spent 3.4% (McCann, 1981). Steller sea lions wintering in British Columbia spent more time communicating than did sympatric California sea lions, and activity levels were greatest for small young males in both species (Brenton, 1977; Table 4.7). Similarly, the incidence of social play in harbour seals declines with age (Renouf and Lawson, 1986a, 1987). Dependent pups of this species interact less with their mothers as they age, and interact agonistically more with other seals (Eliason, 1986). The nature of interaction between mother and pup Steller sea lions must also change with pup age, since both female absences at sea and suckling bouts become longer, though overall the percentage of time spent by pups suckling decreases (Higgins *et al.*, 1988).

Time/activity budgets are relatively easy to document. Because of their relevance to many important ecological, developmental, and social processes, many more studies of them are called for. They underscore how important and widespread are ecological and social variation, which raises many questions about adaptation and phylogeny of communication patterns.

4.6 EVOLUTIONARY PATTERNS

The pan-selectionist view that all organismal attributes are closely adapted to the environment has been replaced by a more robust view: phenotypic attributes reflect complex processes including developmental and genetical inertia, mechanical constraints, conflicting selective pressures, adaptation to fluctuating and to unpredictable environments, phylogenetic propinquity, multiple or average adaptive solutions, and random processes (for a refreshing overview, see Wallace, 1989). In isolation, these and many other important evolutionary factors have been long appreciated, but only recently have they been applied routinely to temper adaptive inference. As an example, consider the evolution of polygyny in pinnipeds in light of phylogeny. Several analyses of pinniped polygyny have considered each species as an independent observation, but this is untenable: polygyny in the two species of elephant seal, for example, clearly represents only a single evolutionary event, so in this instance the genus - not the species - is the appropriate unit for analysis. Similar comments apply to 'reversed' sexual dimorphism in Monachinae, in which females average larger in size than males; if the Monachinae constitute a monophyletic group (but see Wyss, 1988a), this attribute presumably represents a single derived state, so the entire sub-family, rather than its component species, should be used in comparisons with other taxa. These examples illustrate the general point that derived attributes need to be used in comparative evolutionary studies. Depending upon the level of attributes chosen, species, genera, or higher categories may be used in the analysis. This reasoning is basic to both adaptive and phylogenetic inference.

First steps in phylogenetic analysis are the choice of a group of taxa among which relationships are to be investigated, and the choice of out-groups that provide a baseline relative to which character states can be judged as derived or ancestral (Eldredge and Cracraft, 1980; for ethological examples see Bolles, 1988; Gautier, 1988; McLennan *et al.*, 1988; Carpenter, 1989). Recent applications of cladistic analysis to pinniped evolution have revived the hypothesis that pinnipeds are monophyletic, and have challenged traditional views of higher-order relationships (Wyss, 1987, 1988a, 1988b, 1989; Flynn, 1988; but see Barnes, 1989). Most low-level relationships, such as among sea lions, have not been questioned. In the case of sea lions, it would be appropriate to choose the less recently derived fur seals as an out-group; in considering affinities among *Arctocephalus* species, it would be appropriate to choose *Callorhinus* as an out-group, since it diverged from the main otariid lineage long ago. Within the group of interest, we can then use information about the distribution of character states that are shared with the out-group, or that are

unique, and establish hypotheses about phylogenetic relationships.

As an example consider the trumpeted roar, or full threat call, a loud long-distance vocalization of otariids, used predominantly by territorial males. The trumpeted roar is absent in Phocidae and Odobenidae. It occurs in *Callorhinus*, and all *Arctocephalus* species except *A. pusillus*, but is absent in *Phocarctos*, *Zalophus*, *Neophoca*, and *Eumetopias* (though males in the latter species employ a roar that may be a derivative; Paulian, 1964; Peterson, 1965, 1968; Peterson and Bartholomew, 1969; Stirling, 1971a, 1972; Stirling and Warneke, 1971; Cooper, 1972; Lisitsyna, 1973, 1979; Marlow, 1975; Trillmich and Majluf, 1981). The trumpeted roar must have been present in the ancestor to the extant Otariidae, so its absence in some otariids is likely derived relative to Phocidae and Odobenidae. By identifying derived states for other characters, an overall picture of their distribution in the group can be established and a strong hypothesis about phylogenetic relationships can be proposed. In this example, it is likely that the evolutionary loss of the trumpeted roar occurred independently in several species, and this would become apparent by the incongruence of its distribution with the distributions of other attributes.

The trumpeted roar could be considered in much greater detail than just 'presence' or 'absence'. Its temporal and spectral properties could be quantified, and its contextual characteristics could be documented. All these attributes could then be used to establish relationships among, say, *Arctocephalus* species (excluding *A. pusillus*). Another widespread acoustic display in Otariidae is barking (also termed whimpering or whickering by different authors; Kenyon, 1960; Paulian, 1964; Peterson, 1965, 1968; Peterson and Bartholomew, 1967, 1969; Rand, 1967; Bonner, 1968; Peterson *et al.*, 1968; Stirling, 1971a; Stirling and Warneke, 1971; Cooper, 1972; Lisitsyna, 1973; Marlow, 1975; Miller, 1975a). Barking appears to be particularly important to communication by breeding males. It is highly directional (see Figure 4.11) and is accompanied by protraction of the mystacial vibrissae with each bark and vertical nodding of the head (marked during interactions; Figure 4.44). Breeding males use the sound almost incessantly as they move around their territory, move towards a social encounter or away from a completed boundary display, as they herd or investigate females, during copulation, and in response to general mild disturbances or stimuli. Barking varies in intensity, repetition rate, and frequency with an individual's level of activity and arousal, so it is a good example of tonic communication by which listeners can judge a caller's general activity level, location, and orientation (Schleidt, 1973). Otariid species vary greatly in the physical properties of barking and in the mode of sound production. The California sea lion, northern fur seal, southern sea lion, and

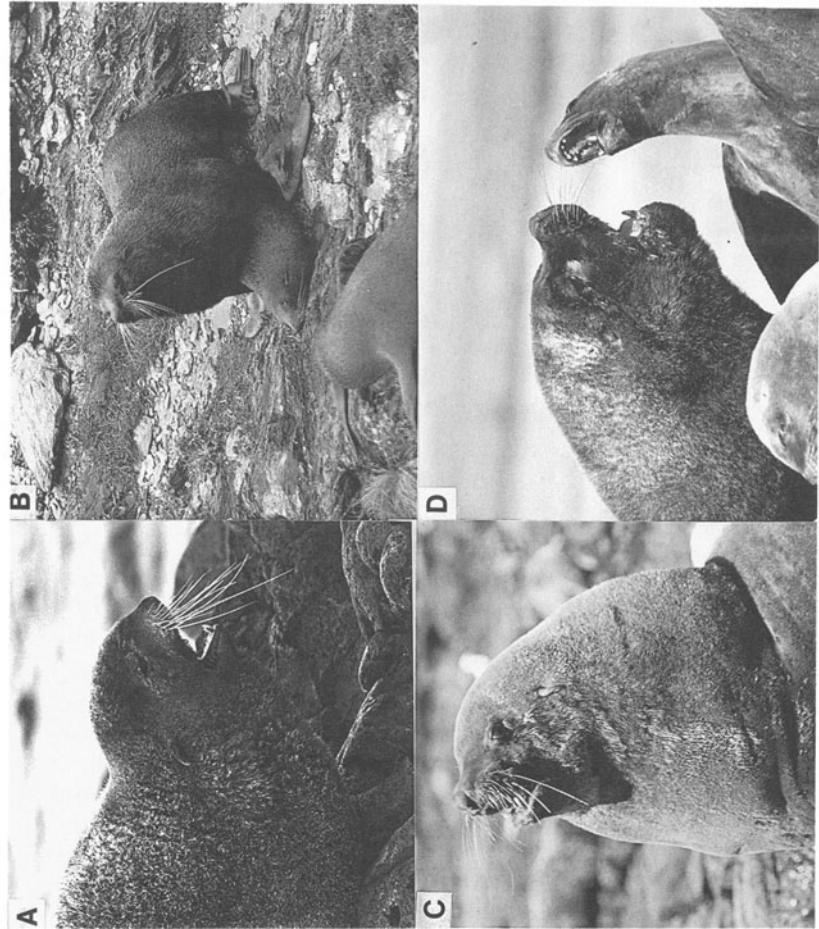


Figure 4.44 Barking in adult males of some species of Otariidae. A - Northern fur seal (*Callorhinus ursinus*). B - New Zealand fur seal (*Arctocephalus forsteri*) during copulation. C - Australian fur seal (*Arctocephalus pusillus doriferus*). D - Southern sea lion (*Otaria byronia*) interacting with female.

Australian/African fur seal utter barks through the open mouth, whereas in the New Zealand fur seal, Antarctic fur seal and subantarctic fur seal the nostrils are also (or solely?) involved in sound production (Miller, 1971, 1975a). In the Australian sea lion, the sound is produced 'by vibrating the posterior part of the tongue against the soft palate at a rate of about 3 per sec' (Marlow, 1975: 186). An acoustic component to the display may be lacking in the Steller sea lion, but motor components are clearly present: 'Bulls were frequently seen muzzle to muzzle or nose to nose with females in their harems . . . the vibrissae were moved forward . . . and the male moved his nose rapidly over the facial area of the female, sometimes nodding as he did so and keeping his mouth partly open. He also had short, rapid inspirations at such times . . .' (Orr and Poulter, 1967: 201–202; see also Sandegren, 1975, 1976b). A detailed physical analysis of the acoustic properties and motor components of this display might shed light on affinities within the Otariidae. The basic structure of the display may be phylogenetically ancient, since repeated simple sounds that function in tonic communication are widespread in mammals (Gould, 1983). Among relatives of pinnipeds, a strikingly similar display to barking occurs in the polar bear (*Ursus maritimus*; Wemmer *et al.*, 1976).

While some kinds of displays will be useful in resolving affinities among pinnipeds, phylogenies that have been hypothesized on other grounds (mainly morphological) hold great potential for investigating patterns and rates of behavioural evolution. For example, my inference that the trumpeted roar and bark were present in the ancestor to extant Otariidae suggests that they originated in the Middle Miocene, at a time when extant Otariidae shared a common ancestor (Repenning *et al.*, 1979; Barnes, 1989; the oldest known pinniped has been aged at 23 million years (Berta *et al.*, 1989)). The same age estimate applies to the boundary display, certain static upright displays (see Figure 4.41), and to the loud vocalizations used by female and pup otariids to locate one another (Peterson and Bartholomew, 1969; Stirling and Warneke, 1971; Stirling, 1972; Lisitsyna, 1980, 1988; Trillmich, 1981; Roux and Jouventin, 1984; Shaughnessy and Fletcher, 1984). Other motor patterns are much more ancient (e.g. neck-biting by males in copulatory behaviour; Miller, 1974; Eisenberg, 1981). Gould (1983) discusses some reasons for evolutionary conservatism in mammalian acoustic displays, and Emmons (1978) notes that related species may share the same display types but use them in different proportions (see also Moynihan, 1970; Gautier and Gautier, 1977). Displays may be evolutionarily conservative because they are complex, integrated neuromuscular patterns (Baerends, 1975); general-purpose displays may be particularly resistant to rapid or dramatic evolutionary change (Moynihan, 1973).

Differences in the extent to which certain kinds of behaviour are expressed may suggest obvious evolutionary trends, thereby facilitating adaptive and phylogenetic interpretations. In Otariidae, peripherally located or subadult males harass females, herd pups and treat them sexually (often very roughly), and several may simultaneously run through a breeding area (Bartholomew, 1953; Rand, 1967; Miller, 1971; Marlow, 1975; Krushinskaya and Lisitsyna, 1983). Such phenomena are developed to an extreme in the southern sea lion, in which coordinated group raids by males onto a breeding area and pup abduction by young males are recurrent and socially significant events (Campagna, Le Boeuf and Capozzo, 1988a, 1988b). The evolution of these phenomena in that species could be elucidated by study of the social stimuli, circumstances, consequences, and communication surrounding them in other species. At a finer level are differences in signals and signalling behaviour between closely related species and among populations of single species. A few such differences have been noted (e.g. Stirling and Warneke, 1971; Le Boeuf and Petrinovich, 1974; Thomas and Stirling, 1983; Stirling *et al.*, 1987; Thomas *et al.*, 1988), but much more work is needed to shed light on evolutionary rates and patterns.

Microevolutionary changes of the sort just mentioned will contribute to our understanding of the adaptiveness of pinniped communication, both in respect to the effects of short-distance signals on recipient behaviour and to the attributes of long-distance signals. General comparative data are particularly applicable to the latter. Many acoustic displays of pinnipeds conform to well established principles of adaptive 'design' for long-distance transmission: they are loud (e.g. trumpeted roar of Otariidae; clap threat of elephant seals; bark of the California sea lion; underwater phonations of the bearded seal, Ross seal, and walrus), lengthy, repetitive or with predictable temporal sequence (all of preceding except trumpeted roar; underwater vocalizations of the harp, crabeater, and leopard seals), and narrow in bandwidth (trumped roar; bearded seal 'song'; underwater vocalizations of the harp, crabeater, Ross and leopard seals) (Bartholomew and Collias, 1962; Ray *et al.*, 1969; Ray, 1970, 1981; Stirling and Siniiff, 1979; Watkins and Schevill, 1979; Stirling *et al.*, 1983; Watkins and Ray, 1985; Terhune and Ronald, 1986; Cleator, 1987; Stirling *et al.*, 1987; Cleator *et al.*, 1989; plus references on trumpeted roar cited earlier in text; Figure 4.9, 4.11, 4.13, 4.17, 4.19). Wiley and Richards (1982) and Brown and Waser (1988) provide useful summaries that are applicable to airborne acoustic signals. To infer adaptiveness of short-range signals is much more difficult, because they are adapted through effects on receivers' nervous systems and behaviour, which are exceedingly complex and difficult to assess. Compound visual and acoustic signals may evolve in colonial species

as adaptations to high ambient noise levels, for visible signals can indicate which local individual is signalling.

4.7 CONCLUDING COMMENTS

Organismic and comparative biology, 'especially those parts that study the manifestations of biological diversity . . . is being drained and there are few sources of replenishment' (Ehrenfeld, 1989: 1) - this despite widespread acknowledgement that the documentation and description of biological diversity are among the most vital tasks facing biologists today (Wilson, 1988; Devall, 1989). Comparative ethology is one of the most important components of this work, since species are becoming extinct at an increasing rate, and opportunities for studying them in natural circumstances are dwindling. Pinniped biologists should therefore incorporate rigorous and comprehensive behavioural descriptions in their research programmes where it is possible.

Detailed descriptions of behaviour, including signal structure and signalling behaviour, are needed for almost all species of pinnipeds, but are most urgently needed for endangered species like the Mediterranean monk seal (*Monachus monachus*) and for unique isolated populations such as the ringed seal (*Phoca hispida saimensis*) that inhabits Lake Saimaa in eastern Finland (Helle *et al.*, 1984; Hyvärinen, 1989). Gaps in our knowledge should also be filled for species whose communication systems are essentially undescribed (e.g. crabeater seal); in some cases this is so even though a species' social system and breeding biology are reasonably well known (e.g. grey seal). We also need studies on populations that are disjunct (e.g. walruses; Fay, 1985; and Australian/African fur seals; Repenning *et al.*, 1971) or ecologically distinctive (e.g. ice-breeding harbour seals; Hoover, 1983). Acoustic communication is the best known form of pinniped communication, in keeping with its prominence for mammals generally (Eisenberg, 1981). However, visual signalling is also extremely important in pinniped societies and remains remarkably under-studied. Chemical communication is important in all species of pinnipeds, and merits detailed anatomical and experimental research (Lowell and Flanigan, 1980). Tactual communication would be technically very easy to study, but is only slightly better known than is chemical signalling - mainly from anecdotal or general descriptions (an exception is Wilson and Kleiman, 1974). Overall, important basic tasks are physical description of signals, description of signalling behaviour, and documentation and quantification of: repertoire characteristics and repertoire sizes; the relative importance of display and non-display signalling; the extent

and nature of structural grading; the communication matrix; and the relative frequencies of use of signal classes, broken down by different age and sex groups (e.g. see Moynihan, 1970; Marler, 1976; Gautier and Gautier, 1977; Marler and Tenaza, 1977; Emmons, 1978).

Individual pinnipeds can become highly specialized in feeding preferences, feeding behaviour, and haul-out rhythms, and such profound individual differences should be quantified and included in any assessment of a population's or species' ecology (Fay, 1982; Danks, 1983; Gentry and Kooyman, 1986b; Łomnicki, 1987; Yochem *et al.*, 1987; Newton, 1988; Thompson, 1989). Similarly, individuality and learning must play key roles in structuring the social dynamics and communication systems of pinnipeds (Shipley *et al.*, 1981; Trillmich, 1981). To document and evaluate those roles is an important task for future ethological research on pinnipeds.

Ethologists tend to build a fragmented picture by focusing piecemeal on specific processes or social characteristics (Eisenberg, 1981). This is dictated by the need to study restricted classes of interactions in order to generate meaningful generalizations (Eisenberg, 1981). It is important to bear in mind, however, that most classes share characteristics with other classes and are often developmentally linked, so restricted observations on communication and social roles should be placed within a broad framework for interpretation. In some cases observations can only be made on captives, but resulting data can be extremely valuable in providing detailed baseline data against which sparser, more fragmented naturalistic observations can be viewed (e.g. Chuzhakina and Gudkov, 1979; Gailey-Phipps, 1984; Gehnrich, 1984; Wilson *et al.*, 1985; Kastelein and Wiepkema, 1988). Also, general trends and behavioural propensities are apparent from captive studies that also apply to the natural situation (e.g. see the comparative data in Table 4.3 of Schusterman (1968), on time/activity budgets of captives).

Exemplary published descriptions of mammal behaviour include analyses from specific viewpoints (e.g. Rose, 1977; Wineski, 1983; Yaniv and Golani, 1987), general ethograms (e.g. Wemmer *et al.*, 1987), ethograms with a quantitative emphasis (e.g. Rasa, 1977), and analyses of specific motor patterns (e.g. English, 1976). Regardless of a study's purpose, scope, or methods of analysis, the best and most useful descriptions remain as those provided by close observers (e.g. Bartholomew, 1952; Laws, 1956; Koford, 1957; Kenyon and Rice, 1959; Sandegren, 1976a; Golani *et al.*, 1979). Familiarity and intimate knowledge of a species' biology and behaviour, and the ability to describe that behaviour lucidly and fully, are the basic ingredients for excellent descriptions of any sort.

Pinniped biologists should improve and increase their training and activities in describing basic natural history and behaviour. However,

it is also important that archives be established for resulting data and images. Several natural-sound archives already exist, such as those at Cornell University and Ohio State University (Boswall and Couzens, 1982; Budney 1989). The only major initiative for archiving images appears to be that for ornithological material at the Academy of Natural Sciences in Philadelphia (Myers *et al.*, 1984, 1986; Anon., 1986; Nichols *et al.*, 1986). Established programmes in marine mammalogy - such as at the Marine Mammal Laboratory in Seattle (National Oceanic and Atmospheric Administration, Northwest Fisheries Center), or the National Museum of Natural History in Washington (Smithsonian Institution) - should shoulder such a responsibility for pinnipeds or possibly all marine mammals. Without such a repository, unique information and images will continue to be scattered and lost, with the consequent permanent impoverishment of our knowledge and appreciation of the world's pinnipeds.

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5

Physiology of behaviour in pinnipeds

Douglas Wartzok

5.1 INTRODUCTION

Behaviour is an evolutionarily labile species trait that responds to environmental opportunity within the constraints imposed by evolutionarily more conservative traits such as anatomy and physiology. Because of their different degrees of adaptation to a marine environment, pinnipeds provide an interesting group in which to look at these relationships between physiological constraints and environmental opportunities. Although behaviour is shaped by the interaction between environment and physiology, it in turn influences physiology and restricts the environments to which the animals are exposed. This chapter looks at the interplay between anatomy, physiology, environment and behaviour in producing the social and individual behaviours observed in a broad range of pinnipeds. Because pinniped behaviour and environmental parameters are more easily observed than physiological mechanisms are delineated, the contribution of physiology must often be inferred by comparison with animals from other orders.

5.2 THE PHYSIOLOGY OF REPRODUCTIVE BEHAVIOUR

Reproductive behaviour often falls into the category of a genetic 'closed programme' (Mayr, 1974) and remains more tightly controlled by physiology than other behaviours. Nevertheless, phocids, for example, with basically similar reproductive physiology can have social systems ranging from the serially monogamous crabeater, *Lobodon carcinophagus*, and hooded, *Cystophora cristata*, seals breeding in the pack ice to the moderately polygynous Weddell seal,

Leptonychotes weddelli, breeding in the fast ice to the highly polygynous elephant seal, *Mirounga* sp., breeding on island beaches (Stirling, 1983). Physiology and the environment both influence the development of these different social systems primarily by affecting the relative distribution and availability of males and females (Chapters 1 and 2).

5.2.1 Seasonal changes in behaviour

Seasonal changes in a number of behavioural patterns of both males and females are presumably driven by changing patterns of circulating hormones. Because of the difficulty of obtaining routine blood samples from most pinniped species, correlations between endocrinology and behaviour are primarily inferential. One basic behavioural response seen in males of a number of species, presumably in response to increased titres of testosterone, is that males become less tolerant of each other at the onset of the breeding season. This leads to an increase in the dispersion of males. In contrast, putative hormonal changes in the females, at least prior to parturition, do not similarly alter their basically gregarious behaviour. This means that in many species the females retain an underdispersed distribution (e.g. grey seal, *Halichoerus grypus*; Boness and James, 1979). In the South African fur seal, *Arctocephalus pusillus pusillus*, this female gregariousness plays an important role in reorganizing the herd after stampedes (Rand, 1967). The pattern of overdispersed males and underdispersed females, when combined with limited appropriate habitat, provides an opportunity for polygyny to develop, because a dominant male can monopolize access to a number of females. This is seen most clearly in cross-species comparisons, but even within a species, such as the grey seal, the response to environmental opportunity is displayed in a breeding structure that becomes more polygynous in areas where access to the harem is through a narrow gully that is relatively easily defended (Anderson and Harwood, 1985). Physiological and anatomical factors which allow better mobility of otariids relative to phocids on land or ice suggest that the polygynous behavioural response to female concentration should occur at lower female densities in otariids than in phocids.

Presumptive hormonal changes in males associated with breeding can be recognized in other ways than just the increased aggression and intolerance for each other. In a number of species the frequency of occurrence of vocalizations correlates with seasonal reproductive behaviour. Males are much less vocal outside of the breeding season than they are during the breeding season. This is true for harp seals, *Phoca groenlandica*, (Terhune and Ronald, 1976), spotted seals, *Phoca largha*, (Beier and Wartzok, 1979), ringed seals, *Phoca hispida*,

(Stirling, 1973), bearded seals, *Erignathus barbatus*, (Burns, 1981; Stirling *et al.*, 1983) and walrus, *Odobenus rosmarus* (Ray and Watkins, 1975). The use of vocalizations to infer underlying hormonal changes is strengthened by comparison with studies of birds, where manipulations are much easier. For example, exogenous testosterone administration causes male chaffinches to sing full song in mid-winter (Nottebohm, 1970), whereas castration greatly reduces song in zebra finches (Arnold, 1975).

5.2.2 Female gregariousness and synchrony of pupping and oestrus

There is an evolutionary feedback between polygynous behaviour and female gregariousness and synchrony of pupping and oestrus, (Chapter 1). The evolutionary advantages to gregarious behaviour in a polygynous breeding system were noted by McLaren (1967). He pointed out that even though a female might have a better chance of rearing an offspring away from the areas of highest male competition, she would likely produce male offspring that would not be successful breeders. The evolutionary disadvantages to being impregnated by a marginal male are an important contributor to female gregarious behaviour. Established males are less likely to be challenged by transient males near the centre of the established male's area of influence. Because these challenges are disruptive and potentially life threatening to females, and particularly to their young pups, it is to the females' advantage to be located as close as possible to the dominant male. In addition, the female will be more likely to be mated by a dominant male if she is near him when she comes into oestrus. The achievement of these objectives is enhanced through a tolerance for gregarious behaviour.

The temporal counterpart of the marginal male effect leads to a different physiological adaptation on the part of the females and that is synchrony of pupping and oestrus. In a number of species of pinnipeds the dominant, tenured males will have exhausted their body reserves shortly after the peak of the breeding season. When the more dominant males abandon their territories, they are replaced by subordinate males. Those females whose breeding cycle is synchronized with that of the majority of females will have a better chance of copulating with the dominant males. This temporal marginal male effect has been hypothesized to explain the relatively short breeding season in New Zealand fur seals, *Arctocephalus forsteri*, even though the environment is more equitable and would otherwise allow an increase in the duration of the breeding season (Miller, 1975a). Similar arguments also have been made for the synchrony of pupping in southern elephant seals, *M. leonina*.

(McCann, 1982). Female northern elephant seals, *M. angustirostris*, that are still nursing their pups when the alpha male begins to reduce his vigilance, are more likely to become separated from their pup through the disruptions occurring when peripheral bulls begin invading the sphere of influence of the dominant male (Le Boeuf *et al.*, 1972).

As noted above, there are a number of factors favouring synchrony of mating. Within the general pattern of synchrony though, there are advantages to producing a pup somewhat before the peak of the pupping season. In northern elephant seals the older, prime females are the ones most likely to produce pups earlier (Reiter *et al.*, 1981) whereas in southern elephant seals it is the primiparous cows that are most likely to pup before the peak of the season (McCann, 1982). In each case, similar advantages accrue to the pup born earlier: the rookeries are less crowded, pup mortality is lower, and, for the northern elephant seal, the pups have a greater opportunity of stealing milk from mothers still nursing later-born pups.

5.2.3 Male adaptations for maintenance of tenure

Anatomy can be used to make some predictions about social behaviour. Ralls (1977) reviewed the reliability of sexual dimorphism as a predictor of breeding systems and found that extreme sexual dimorphism was a good predictor of extreme polygyny whereas little sexual dimorphism was not a good predictor of monogamy. Hooded seals are sexually dimorphic with epigamic characteristics in the male that would imply some degree of polygyny (Miller and Boness, 1979). In spite of a low density of females in their pack ice habitat which would appear to limit one male to defending one female, hooded seal males appear to achieve a degree of polygyny both serially by moving from one female to another, and, on occasion, by controlling a cluster of females (Boness *et al.*, 1988). Galapagos fur seals, *Arctocephalus galapagoensis*, do not have the degree of sexual dimorphism usually associated with a breeding system as polygynous as theirs, although the males show high mortality (30%/year) associated with a polygynous breeding system (Trillmich, 1984).

The importance of one anatomical trait, large body size, in reproductive success was a cornerstone of Bartholomew's (1970) classic model for the evolution of pinniped polygyny. Large body size has a direct advantage in competitive interactions and an indirect advantage through a lowered weight-specific metabolic rate and through the presence of large stores of metabolizable fat, which allow the larger male to remain resident on territory for long periods of time. Metabolism of fat produces more than twice as much energy as metabolism of protein or carbohydrate. Furthermore, the fat is rich in

long-chain fatty acids (C_{14} to C_{22} ; e.g. elephant seals, Bryden and Stokes 1969) the metabolism of which yields approximately 1.1 g of water for each gram of fat metabolized (Schmidt-Nielsen and Schmidt-Nielsen, 1952). In contrast, metabolism of protein yields urea which must be secreted in the urine with net loss of water (Hochachka and Somero, 1973).

Elephant seals fit Bartholomew's (1970) model particularly well. A successful male elephant seal can sire 100 pups in a season and up to 250 in a lifetime (Le Boeuf, 1974). The most successful males are the ones whose body size allows them to establish tenure early and maintain it for the longest time in an area frequented by females. Large body size also appears to be the major factor contributing to reproductive success in southern elephant seals (McCann, 1981).

Elephant seals have additional anatomical and physiological adaptations associated with respiration that allow them to prolong the time they can stay hauled out. The nasal structure in elephant seals is reminiscent of that found in some desert rodents for which conservation of water is also of prime importance (Collins *et al.*, 1971). Countercurrent blood flow in the nose sets up a temperature gradient which allows recycling of moisture in the nasal passages. The temperature gradient that can be established depends on ambient temperature. At an ambient temperature of 13.7°C, the expired air temperature is reduced from body temperature to 20.9°C. All air in the lungs is 100% saturated at normal body temperature. This moisture would normally be lost on exhalation but because of the temperature gradient and the extensively turbinated nasal passages with greatly increased surface area (720 cm² in weaned pups and 3140 cm² in an adult male) much of the moisture in the exhaled air condenses on the surfaces within the nasal passage. This moisture can be used on the next inhalation to humidify the air on its way to the lungs. It is estimated that this recycling reduces respiratory water loss by 71.5% when the ambient temperature is 13.7°C. Reduction in water loss is inversely related to ambient temperature (Huntley *et al.*, 1984). Grey seals also reduce their water loss in the same manner (Folkow and Blix, 1987) so that at an ambient temperature of -20°C respiratory water loss is reduced by 80%. Another physiological adaptation that reduces the moisture loss for the seals is their apneustic breathing pattern (Ortiz *et al.*, 1978).

Grey seals show a similar interplay between body size, tenure and reproductive success. Boness and James (1979) found that only 2% of male grey seals younger than 8 years were able to establish tenure whereas one-third of 15 males known to be between 11 and 14 years old had acquired tenure. The increased success with age is probably not due exclusively to increasing size with age but also reflects the increased social experience of the older animals. Not surprisingly,

they also found that the reproductive success of the male grey seal increased as his tenure increased. Relative body size was not as important among tenured grey seal males as it is in other species. On Sable Island males that had achieved tenure were treated as equals regardless of their previous fighting record or the quality of the territory they held (Boness and James, 1979). In contrast, on North Rona, Anderson and Fedak (1985) found that some males were consistent winners and other males routinely lost encounters although there was not a strictly linear dominance hierarchy.

Large body size allows successful male Antarctic fur seals, *Arctocephalus gazella*, to withstand average losses of 1.57 kg/day (Payne, 1979). This weight loss continues over a shorter time than that of elephant seals, but the animals start with a much smaller body mass (170 kg (Payne, 1979) compared to 2300 kg (Deutsch *et al.*, in press)). The reduced time that male Antarctic fur seals are required to maintain a territory is a consequence of the fact that females are very tightly synchronized in their reproductive cycles. Over 90% of the births occur during a 21-day period (Payne, 1977). The rigorous but predictable environment, which severely limits the time when pup rearing conditions are suitable, is a major factor influencing the development of this synchrony.

New Zealand fur seals weighing 200 kg (Crawley and Wilson, 1976) can remain on their territories for up to 63 days before abandoning or losing the territory (Miller, 1975a). South African fur seal bulls weighing 363 kg (Rand, 1956) stay ashore continuously for about 40 days (Rand, 1967). Mean tenure for the South American sea lion, *Otaria flavescens*, of 24 days is only 38% as long as the maximum for New Zealand fur seals, but this is apparently sufficient for reproductive success since 94% of the males that maintain a territory for at least five days copulated. As in other otariids, the male South American sea lions that held territories the longest achieved the most copulations, but the variance between territory holders was lower than in other species (Campagna and Le Boeuf, 1988a), possibly because of the switch from territorial defence to female defence as the number of females increased. Other factors contributing to the reduced variance may be the repeated disruption of breeding colonies by bands of raiding marginal males (Campagna *et al.*, 1988a) and the time a tenured male must spend herding females to keep them from leaving his territory (Campagna and Le Boeuf, 1988a).

Galapagos fur seals do not show as much sexual dimorphism as other territorial breeding pinnipeds. The usual evolutionary pressures toward large size associated with their polygynous breeding structure have been countered by environmental factors requiring physiological adjustments to the demands of thermoregulation and mobility. They

live in an environment where they need to dissipate heat in order to avoid thermal stress. Surface temperatures can reach 60°C (Trillmich, 1986a) compared to black bulb air temperatures of 32°C at Guadalupe Island, Mexico, the southern end of the breeding range of northern elephant seals (White and Odell, 1971). The small body size of Galapagos fur seals facilitates heat dissipation and thermoregulation through a greater surface to volume ratio. Also the smaller size reduces the energetic costs of climbing about in their rocky territories. These factors have led to the Galapagos fur seal being the smallest of the fur seals and showing the least sexual dimorphism of any otariid (Trillmich, 1984). A consequence of this relatively smaller body size is that they have modified the usual strategy of exclusive maintenance of a territory for as long as possible.

Some male Galapagos fur seals combine a strategy of interspersing relatively long-term breeding site tenure with a period of refreshment in the sea. Established bulls remain ashore for up to 51 days (median of 27 days) defending their territory, during which time they lose up to 25% of their original weight. One reason they are able to maintain tenure for this long is that they drink sea water (Trillmich, 1984). The physiological adaptations allowing sea water consumption need to be investigated. Studies in harbour seals (Depocas and Hart, 1971; Tarasoff and Toews, 1972) and northern elephant seals (Ortiz *et al.*, 1978) indicate that these phocids ingest sea water only incidental to feeding and that they would suffer a net loss of body water, if sea water were drunk.

When the male fur seals have exhausted their physiological reserves, they abandon their territories for a month or so at sea. They only leave for the sea when they have depleted their physiological reserves to such an extent that, if they cannot replenish them quickly, they may not survive. This was clearly shown during the 1982–1983 El Niño event. El Niño events occur in the eastern tropical Pacific approximately every 4 years. During an El Niño event, the normal east-west trade winds subside, sea level rises, upwelling of cold waters diminishes, and sea surface temperatures rise (Wyrtki, 1982). These oceanographic changes result in reduced primary and secondary productivity and diminished food resources for birds and mammals (Barber and Chavez, 1983). The 1982–1983 El Niño event was the strongest recorded in this century (Cane, 1983; Rasmusson and Wallace, 1983), during which time dominant bulls experienced an almost 100% mortality (Trillmich and Limberger, 1985). When the dominant bulls leave the territory, younger males can acquire territory, and this enlarges the effective gene pool of the population, since the females mate with whichever male happens to be dominant at the time they come into oestrus. Approximately one-

third of the territorial males return for a second, shorter tenure of territory maintenance (Trillmich, 1984).

Galapagos sea lions, *Zalophus californianus wollebaeki*, also do not achieve uninterrupted site tenure throughout the breeding season. In low-density colonies, the breeding season of the sea lions extends for up to 10 months. It is physiologically impossible for a male to fast for this length of time regardless of the body stores he might have had at the start of the breeding season. Hence these territorial males abandon their territories on a daily basis, usually during the mid part of the day when the females are also at sea feeding. The males return in the late afternoon in advance of the return of the females (Trillmich and Trillmich, 1984). In higher-density colonies, the sea lion males follow a pattern similar to that of the Galapagos fur seal males. They remain on their territory continuously for a period of time, then abandon it to other males while they go to sea to feed and replenish the body stores, and then return to reclaim the territory. During the times of territory maintenance, the sea lions can reduce energy expended by patrolling their shoreline territory from the water. This reduces locomotion costs as well as thermal stress. These physiological constraints are reflected behaviourally in limiting successfully maintained territories to a linear pattern, one territory deep, along the beach (Trillmich and Trillmich, 1984).

Krieber and Barrette (1984) have proposed that in harbour seals, *Phoca vitulina*, the relationship between body size, thermoregulation, and tenure is different from that in other species. Tenure time is shorter and of less consequence in this promiscuous rather than polygynous species (Stirling, 1983). Therefore, the potential negative consequences of losing an agonistic encounter become more important. Krieber and Barrette (1984) suggest that because the loser is often forced into cold water, smaller animals suffer a greater thermodynamic cost than larger animals. The combination of smaller reproductive gains from a successful fight and reduced losses for a larger animal has led to the behavioural convention of accepting time of arrival as the indicator of established tenure. An established, smaller male is not likely to be displaced by a larger, more recently arrived male.

A contrasting interplay between physiology and payoffs for animals of different sizes is seen in Weddell seals. Here the territorial exclusivity of large males is compromised directly and repeatedly by the physiological requirements of smaller males. Male territories are maintained in the area of, and often centred on, a breathing hole. If the breathing hole is at a distance from alternative breathing holes, the physiological need of a smaller animal to breathe changes the usual motivational balance against challenging a resident male (Kooyman, 1968).

In South Australian fur seals, territory maintenance is so tenacious that it results in an expansion of the effective gene pool. The territorial males will not leave their territories, even under the most severe storm conditions. When the shoreline territories of the dominant males are awash in heavy seas, the females retreat landward and into the territories of subordinate males. Hence environmental factors determining the frequency of heavy seas during the breeding season can have a very direct influence on the size of the effective gene pool (Stirling, 1971).

5.2.4 Testes size and social structure

The reproductive social structure of a number of mammalian species has been shown to correlate with the relative size of the testes and penis of the males (Harcourt *et al.*, 1981; Hogg, 1984; Kenagy and Tromblak, 1986; Parker, 1984). In those species in which there is promiscuous mating, the testes, and in some cases the penis, are relatively larger with respect to body mass than in either monogamous or single-male-dominated species. In the promiscuous mating species paternity may well depend on sperm competition, hence there is an advantage to being able to produce large numbers of sperm and to deliver them close to unfertilized eggs. In species with monogamous or single-male-dominated breeding structures, there is less likelihood of sperm competition. Brownell and Ralls (1986) have used this model to help determine breeding structure in different cetaceans but such a comparative study has not been conducted among pinnipeds.

In the single-male-dominated groups in primates and other orders, the number of females coming into oestrus at any one time is low, so sperm production need not be high. In polygynous pinnipeds, however, even though sperm competition is probably not an important factor, the fact that many females (over 100 in the territories of some northern fur seals; Bartholomew and Hoel, 1953) come into oestrus over a period of a few days suggests that these males should have relatively larger testes compared to serially monogamous species, such as crabeater seals. Because of the large number of females that need to be serviced within a short period of time, the territorial male pinniped needs relatively large testes. Hence the difference in relative size of testes between pinnipeds with territorial-based breeding systems and those with dominance based breeding systems should not be as great as in other groups of mammals.

The anatomical and physiological adaptations allowing for production of large amounts of sperm over a short time have not been investigated in pinnipeds. Blix *et al.* (1983) have shown that production of sperm in phocids is facilitated by cooling the para-abdominal

testicles with cool blood flowing from the hind flippers through an extra-testicular plexus. This should be particularly important for the northern and southern elephant seals, which maintain tenure and mate with many females, sometimes under very warm conditions. Otariids that have a scrotum are able to keep their testicles at least 6°C below body temperature (northern fur seals; Bartholomew and Wilke, 1956). Dominant otariid males in highly polygynous species are able to produce sufficient sperm to maintain high levels of conception in females. Over 90% of mature northern fur seal females have been found to be pregnant (Bartholomew and Hoel, 1953). Since the females rarely accept more than one copulation, this indicates adequate sperm in each ejaculate.

5.2.5 Detection of oestrus

Males of different species vary considerably in the extent to which they use behavioural and physiological cues to determine oestrus in females. In some species, such as elephant seals (Le Boeuf, 1972) and crabeater seals (Siniiff *et al.*, 1979), the males apparently assess receptivity by the response of the female to repeated mounting attempts. In other species, such as northern fur seal (Bartholomew, 1953) and South African fur seal (Rand, 1955), the males use olfaction and sniff the hindquarters. Male South Australian fur seals, *Arctocephalus fosteri*, rely on a variety of signals. Stirling (1971) observed male interactions with marked females for which pupping dates were known and hence state of oestrus could be estimated. He found that males apparently could detect females likely to be in oestrus without smelling their hindquarters. The possibility that the female oestrus odour was so strong that it could be detected without smelling the hindquarters was discounted because the males could 'recognize' individual females as they came ashore when any scent cues were probably minimal. The males' blocking and barking activity directed toward particular females declined as the time passed when the females were likely to be in oestrus.

In Steller sea lions, *Eumetopias jubatus*, the female performs an elaborate courtship display that sometimes includes climbing on the male, biting him, then rushing away and making intention movements toward entering the water or a neighbouring territory. This behaviour stimulates sexual and territorial responses from the male (Sandegren, 1976). The California sea lion, *Zalophus californianus*, female also solicits copulation with characteristic submissive postures and body contact with the male leading to male olfactory investigation of the female's genital area and copulation (Peterson and Bartholomew, 1967).

Some learning is involved in the interpretation of the more subtle

signals indicating peak receptivity in females. Dominant, experienced southern elephant seal males mate with females at the time they are most receptive whereas younger males have a peak in their copulatory attempts about a week before maximum receptivity. McCann (1981) has suggested that the younger males are stimulated to copulatory attempts by the odour of the females but that the more experienced males are monitoring a number of factors, odour being only one of them, to determine the female's receptivity. The experienced bulls also display a behaviour termed 'heading' (McCann, 1981), in which the male places his head on the female and sniffs or bites her back prior to attempting copulation. There is also a potential, uninvestigated role for female choice whereby the females are more receptive when approached by a dominant male.

The physiological and behavioural indicators of receptivity are apparently not definitive in grey seals (Anderson *et al.*, 1975). Two-thirds of the females in one study were mounted at least three times before they were receptive (Boness and James, 1979). Male crabeater seals maintain attendance on a single female and her pup on a floe and apparently do not use physiological indicators to determine female receptivity. The male makes repeated approaches to the female, whose usual response is to bite the male on the head and upper neck. Only after a number of unsuccessful, and painful, approaches does the male finally find the female receptive (Siniff *et al.*, 1979). Because the male is apparently serially monogamous, there is an advantage to mate with the female as soon as possible in her reproductive cycle. This evolutionary pressure may counter the expected development of the male's ability to determine more accurately the oestrus state of the female. Marginal male South American sea lions also attempt to copulate with females without ascertainment of their reproductive status. When these marginal males have forced a female out of the breeding area of a territorial male, they can keep the female by herding her for only a day or so and hence they have to attempt copulations during this time regardless of the reproductive state of the female (Campagna *et al.*, 1988a).

5.2.6 Copulation acceptance by females

In general, female pinnipeds show little mate choice. When they come into oestrus they mate with either the only available male (e.g. crabeater seals; Siniff *et al.*, 1979) or the male that controls the territory in which the female is located (e.g. Galapagos fur seals; Trillmich, 1984). The physiological bases determining whether a female will accept multiple copulations have not been determined. However, there is a clear evolutionary explanation for different

behaviour patterns in females of species with different social structures (Le Boeuf, 1972).

The territory-based social structure of polygynous otariids allows the male freedom to complete copulations with females who come into oestrus in his territory. In northern fur seals, the mean number of copulations by females is 1.2 (Peterson, 1968), with most females becoming refractory toward further copulation attempts after the first copulation. Female Galapagos fur seals come into oestrus and copulate about a week post-partum. Only three female Galapagos fur seals were observed to copulate twice during a breeding season; all the rest copulated only once (Trillmich, 1984). Similar behaviour has been recorded in Steller sea lions where in one extensive study (Sandegren, 1970) no female was observed to copulate more than once and in another (Gentry, 1970) only 15% copulated twice and none more than twice.

In the dominance-based social structure of the elephant seals, there is a greater probability that matings will be interrupted prior to completion because of male-male competition. Also sperm counts for the dominant males are likely to be low because of high female:male sex ratios. The frequency of copulation for dominant males can be very high; as many as 13 copulations within 6 h with only 5-30 min intervals between copulations (Le Boeuf, 1972). Finally, the dominant males remain hauled out and active even when the temperature is high. Not having an effective avenue for heat dissipation, their testes could become too warm for effective spermatogenesis. The subordinate males at the periphery of the breeding area, and often in the adjacent water, would be much less likely to have experienced conditions that could lead to sperm depletion in the dominant males.

Female northern elephant seals compensate for this reduced probability of fertilization by the dominant males by increasing their receptivity to subordinate males shortly before they leave the breeding area. Cox and Le Boeuf (1977) have described how this mating with subordinate males is facilitated by a change in the females' behaviour over the course of the breeding season. At the time of their reproductive cycle when matings have the highest probability of producing fertilizations, the females protest all mounts. If there is a more dominant male nearby he will displace the male attempting a copulation. This increases the probability that the female will be mated with the most dominant nearby male. Later in the female's reproductive cycle she decreases her protests of mountings which allows subordinate males to complete copulation and increases the chance that the female will be fertilized by some male. The ultimate evolutionary advantages of this behaviour are clear and have been described by Cox and Le Boeuf (1977). They did not

speculate on the proximate hormonal and other physiological mechanisms that lead to this change in behaviour. It might be as simple as discomfort associated with the initial intromission post-partum but since post-partum copulation is common in many pinnipeds, the difference between elephant seal females and those of other species is not adequately accounted for by this explanation. It is clear, however, that the behaviour cannot be decoupled from the overall hormonal changes in the reproductive cycle. Females in small harems, where there is no chance of a more dominant male being nearby to displace the copulating male, protest mounts early in their period of oestrus just as vigorously as do females in situations where such behaviour is likely to result in copulation with a more dominant male (Cox and Le Boeuf, 1977).

Although the protesting is an invariant component of mounts early in the cycle, there is some discrimination on the part of the female in that the protests are more vigorous when she is mounted by an immature male (Cox and Le Boeuf, 1977). Grey seal females appear to achieve a similar assurance of mating with dominant males by responding aggressively to copulation attempts, varying their reactions depending on the status of the male. Transient males are the most likely to elicit an aggressive response from the female. This results in the mounts of the transient males being challenged by tenured males more often than mounts by other tenured males (Boness *et al.*, 1982).

5.2.7 Sexual maturity

Perhaps the most direct link between the environment, physiology and behaviour is the effect of population density and food resources on age at sexual maturity and subsequent reproductive behaviour of female pinnipeds. The effect of population density was seen in harp seals where, with decreasing population density due to the harvest, the mean age at sexual maturity declined from 6.2 years in 1952 to 4.5 years in 1979, while the fertility rates in the population increased from 85 to 94% (Bowen *et al.*, 1981). Southern elephant seal females in the exploited population at South Georgia gave birth when 3 years old, whereas those in the unexploited, dense population at Macquarie Island had their first pup at an average age of 6 (Carrick *et al.*, 1962). Similarly, the mean age of first reproduction in northern fur seals declined following the commercial harvest of females (York, 1979).

The effect of increased food resources can be seen in crabeater seals, which gained access to additional krill as the great whales were harvested. Earlier reports of a decrease in age at sexual maturity of crabeaters with the increase in whaling (Laws, 1977) have been shown to be flawed, because the technique of back calculation from

tooth samples was biased to the extent that animals that mature at different rates also may die at different rates and hence be present in different proportions in any sample (Bengston and Laws, 1985). Comparisons across species have shown that females in the species with the faster growth rates reach sexual maturity sooner but also die sooner than females in species with slower growth rates (Laws, 1959). Counts of ovarian corpora show the predicted decrease and later increase in age of sexual maturity following presumed changes in krill availability to the seals (Bengston and Laws, 1985).

It has been demonstrated that the onset of puberty in southern elephant seals is related to the attainment of a certain body size rather than a certain age (Laws, 1956b; Bryden, 1968a). This appears also to be the case in rats (Kennedy and Mitra, 1963) and some other mammals (Sadlier, 1969) including humans (Frisch, 1980).

5.3 MATERNAL BEHAVIOUR

Hormonal physiology is obviously critical to reproductive behaviour. In the absence of direct measurements of circulating hormones and their correlations with the reproductive cycle, changes in hormones are inferred from changes in female behaviour. These changes are most evident at two points in the reproductive cycle: immediately post-partum and during oestrus. Another important hormonal change occurs a number of months after copulation, leading to the delayed implantation of the blastocyst.

5.3.1 Behaviour changes at parturition

The female of a number of species (e.g. South African fur seals; Rand, 1967; northern elephant seals; Christenson and Le Boeuf, 1977; Ribic, 1988) displays a post-partum change from a gregarious behaviour to defence of the territory immediately surrounding herself and her pup. The South African fur seal, which has a temperament described as 'phlegmatic' (Rand, 1967) prior to the birth of her pup, becomes aggressive subsequent to the birth of the pup. The marked increase in maternal aggressiveness after birth clearly has an advantage for the pup. In northern elephant seals, there is a negative correlation between the number of times a pup is bitten by other females and the aggressiveness of its mother (Christensen and Le Boeuf, 1977). One of the primary causes of pup mortality in northern elephant seals is from being bitten by other females. Females that lose in inter-female aggressive encounters often become separated from their pups (Le Boeuf *et al.*, 1972). If the mother and pup are not soon reunited, the pup is unlikely to survive. Females that have lost their pups initiate

and win fewer aggressive encounters. For female elephant seals, dominance, measured by which seal remains in the area after an encounter, is a better indicator of female weaning success than is aggression (Ribic, 1988). A grey seal female is more likely to react aggressively toward another female approaching her from the side on which her pup is located than she is toward a female approaching from the opposite side (Boness *et al.*, 1982).

5.3.2 Maternal investment

Pinnipeds are convenient animals in which to study maternal investment, because the female usually has complete control over both the duration of nursing sessions and the time of weaning. In a majority of cases, the pup experiences an abrupt weaning when the female either leaves the pup (phocids) or no longer returns to the pup for nursing (otariids), (see Chapter 3). South African fur seals, at the birth of a new pup, usually forcibly wean their previous offspring, if the youngster is not already independent. Lactation can range from 8 to 18 months in these fur seals, but there is a peak of weaning when the youngsters are 9–11 months old. Young that nurse for longer than one year probably are associated with a female that has lost her new pup (David and Rand, 1986). Weaning is flexible in both South American fur seals, *Arctocephalus australis*, and Galapagos fur seals in which it can take place when offspring are 1–3 years old, depending on available food resources (Trillmich *et al.*, 1986; Trillmich, 1986a). In Antarctic and northern fur seals weaning is initiated by the pup (Doidge *et al.*, 1986; Gentry and Holt, 1986). The females remain on shore, available for nursing, after the pups have left the rookery. Weaning in crabeater seals appears to be initiated when the male dominates the female sufficiently to drive her from the pup and form a male-female pair (Siniff *et al.*, 1979). However, this is probably dependent on the hormonal state of the female because, prior to the change in her receptivity, she has demonstrated that she is capable of driving the male away.

The tremendous difference in lifetime reproductive success of successful as compared to unsuccessful males in highly polygynous species has led to a number of physiological and behavioural traits favourable to producing large, vigorous weaners. Several studies have demonstrated the advantages accruing to an elephant seal pup that is born early in the breeding season and close to the centre of the breeding area (Reiter *et al.*, 1978, 1981). The dominant males in the central area discourage younger males from infiltrating and attempting copulations. These attempted copulations by younger males lead to much disruption and mother-pup separation which is the major cause of pup mortality, accounting for 60–70% of pup deaths (Le

Boeuf and Briggs, 1977). An indication of how detrimental activities of younger males are to the survival of the pup is shown in the studies of Bryden (1968b) on two southern elephant seal populations. Pup survival was better at the Falkland Islands, where the density of elephant seal males had been reduced through harvesting, than it was at Macquarie Island where the seals were unharvested.

Elephant seal pups born early in the breeding season experience less crowding and fewer strains on the mother-pup bond. Also pups born earlier are weaned earlier and hence have a greater supply of nursing females from which to attempt to steal milk. Although the most significant gains in reproductive success devolve to the male pup that can get a head start, female pups also benefit from early weaning. A higher proportion of female pups born early in the season survive to reproduce and they give birth at an earlier age than their cohorts born later in the season (Reiter *et al.*, 1981).

An elephant seal mother in her physiological prime provides a number of advantages to a pup. Compared to other females, the prime females are more likely to be near the centre of the breeding area, to pup early in the breeding season, and to wean large pups. Because prime females are able to dominate aggressive encounters, their pups are less likely to be bitten by other females (Reiter *et al.*, 1981). Prime females also feed their pups milk that is higher in protein content than the milk provided by other females (Riedman and Ortiz, 1979).

Older Antarctic fur seal females give birth earlier in the season than younger ones. This is particularly important in this species, because the short rearing season leads to all pups being weaned at approximately the same time, regardless of date of birth. Hence the pups born early have the decided advantage of a longer nursing period than do those born later (Doidge *et al.*, 1986). In addition, the later a pup is weaned, the closer it is to the time of seasonally decreasing food availability, so the late-born pups suffer double jeopardy by being weaned at a lower weight and at a time when food resources are diminishing (Doidge and Croxall, 1989).

The exact combination between physiology and learning that leads mature females to give birth earlier in the breeding season is unclear. Some learning most likely is involved since there is evidence for improved maternal performance with experience. The mature female also has physiological advantages. Giving birth the previous year does not deplete her reserves as much as it does those of a younger female. Northern elephant seal females can lose up to 270 kg during the 4 weeks of nursing (Reiter *et al.*, 1981), a weight loss that is more affordable by mature females than it is by primiparous females. Most of the young females that give birth at 3 years skip pupping at 4 years, presumably because they have

expended so much of their physiological resources the previous year (Huber, 1987). Although the depletion experienced by mature females is relatively less, only those in their physiological prime can give birth one year and have adequate resources to give birth early in the next year.

5.3.3 Sex ratio

Life history theory predicts that if offspring of one sex require less maternal investment than offspring of the other sex, the sex ratio should be biased toward the cheaper sex (Fisher, 1930). Further elaborations on this theory have suggested that females should preferentially produce more offspring of the sex in which maternal investment is greatest, males, when they are in the best physical condition (Trivers and Willard, 1973) and that their reproductive effort should increase as they age and their reproductive value decreases (Pianka and Parker, 1975). One can hypothesize ways in which female physiology could alter the environment of the reproductive tract, such that sperm carrying X or Y chromosomes would have different survivorships, hence altering the probabilities of producing males or females. However, the ability to manipulate the sex ratio at birth or weaning does not appear to have evolved in either pinnipeds or other mammals, and indeed where biases in sex ratio do occur in polygynous mammals, males are usually the more common sex (Clutton-Brock and Albon, 1981).

Northern elephant seals would seem to be an ideal species in which to investigate life history theories. Females' reproductive success increases with age, the larger, older females are most successful in weaning pups, and the fecundity of the females does not decline with age (Reiter *et al.*, 1981). Although the sex ratio is slightly biased toward males at birth (1.05), it is not significantly different from unity at weaning. Also northern elephant seals show no variation with age or physiological condition of the female in the sex ratio of offspring with the exception of 6-year-old females that produced significantly more males (Le Boeuf *et al.*, 1989a). The combination of greater energetic investment in males, and yet no evidence of a biased sex ratio towards females, initially appears to contradict Fisher's (1930) theory that the female should produce more of the sex in which her investment is less. However, the correct measure of maternal investment is not energetic investment, but rather the effect on the mother's subsequent reproductive performance. Since there is no evidence that the sex of the pup has any effect on future reproductive performance of the mother (Le Boeuf *et al.*, 1989a), the observed sex ratio of unity is in accord with the theory.

Costa *et al.* (1988) used maternal mass as an indicator of maternal condition in Antarctic fur seals and found no clear indication that larger females produce males. There was no significant difference in the mass of females that produced sons and those that produced daughters. Maternal mass was a better predictor of the mass of female pups than it was of the mass of male pups. Furthermore, the pup mass relative to maternal mass decreased in larger, and presumably older, females, implying a reduced rather than increased maternal reproductive effort with declining reproductive value. In contrast Boyd and McCann (1989) found that male mass was directly related to two metrics of female condition: maternal mass and the ratio of mass to length. Larger females gave birth to larger pups earlier in the season. This relationship was clearest for male pups. Boyd and McCann's (1989) interpretation was that male pups grow faster, both pre- and post-natally, at a rate limited by the maternal resources, whereas female pups may not tax maternal resources maximally. Hence differences in foraging ability of females will be reflected in the size of male pups produced whereas these differences in foraging abilities will not correlate with the size of female pups produced.

5.3.4 Sex differences in pup growth rates

In accord with expectations consequent upon the four times greater variance in reproductive success of northern elephant seal males compared to females (Le Boeuf and Reiter, 1988), the average weight of male pups at weaning is significantly greater than that of female pups. The nursing period for male pups averages one full day longer than it does for female pups (Reiter *et al.*, 1978, 1981). Whether this differential result is produced by the behaviour of the pup toward the nursing female or by that of the female toward the pup is not clear. It is advantageous for the pup to be as large as possible, because it will fast for 2–2.5 months while learning to swim and forage (Reiter *et al.*, 1981).

Male fur seal pups of several species are also born heavier, grow faster and are weaned at a greater weight than female pups (Croxall and Gentry, 1987). In northern fur seals, male pups are significantly heavier than females at birth, consume 61% more energy than female pups, and are weaned at a heavier weight. The mothers of male pups do not spend more time at sea nor do they spend more time suckling than do mothers of female pups. The additional energy for male pups comes from the mother's resources rather than from additional foraging during lactation. Mothers of male pups often come ashore with more weight than do mothers of female pups. Mothers of male pups lose weight faster during lactation than do the mothers of female

pups. Male pups appear to have a greater sucking efficiency, and they also have reduced metabolic rate compared to female pups, which improves the efficiency with which they can convert milk intake into body mass (Costa and Gentry, 1986).

In grey seals where the comparative variance in reproductive success of males and females is less than that in elephant seals and some fur seals, there is less evidence of sex differences in growth rates. Grey seals at North Rona showed a surprising reversal in relative weight gains for the sexes with the females gaining 1.4 kg/day and the males gaining 1.3 kg/day (Boyd and Campbell, 1971). Pups of different-sized females generally grow at the same rate, and the growth rate is not dependent on whether the pup was born early or late in the breeding season (Fedak and Anderson, 1982). Compared to mothers of female pups, mothers of male pups maintain closer proximity with the pup and are more aggressive toward other females, thus enhancing survival of the pup (Kovacs, 1987).

The behavioural and physiological mechanisms whereby the female determines or is influenced by the sex of the pup as well as the feedback loops which reinforce this differential maternal behaviour have not been elucidated. However, Trillmich (1986c) has indirectly argued that females can recognize the sex of their offspring. He finds the equal sex ratio, differential sex investment seen in otariids to be more in accord with Maynard Smith's (1980) model of sexual investment than it is with Fisher's (1930). One of the axioms of Maynard Smith's (1980) model is that the female is able to recognize the sex of her offspring.

In the sexually monomorphic harp seal, there is no difference between the sexes in birth weight, growth rate or weaning weight (Stewart, 1986), and the sex ratio of the nursing pups is unity (Stewart and Lavigne, 1984). As with grey seals (Fedak and Anderson, 1982), females of all ages invest approximately the same amount of energy to successfully wean their pup. The harp seal pup grows at the same rate regardless of the size of the mother. This means that younger, smaller females invest more of their total resources in reproduction than do older, larger females. At the time when she weans her pup, the young nursing female has sufficient stores to last for only 3.8 more days of fasting in comparison to an older female that has sufficient stores to fast for another 23 days (Stewart, 1986). Clearly the younger females are much more vulnerable to vagaries of weather and food resources than older females.

The advantages to males that start life at maximum weight are great enough that pups as well as mothers have several physiological adaptations to facilitate achievement of this goal. In northern elephant seals, the male pups moult at an older age than the female pups. Thus, for a longer period of their lives, they maintain a neonate

pelage which may allow them to gain access more easily to areas with nursing females. Similarly the male pups' canine teeth erupt at a later stage than those of the female pups, which allows the males to have a greater chance of remaining undetected when they are stealing milk. Because vocalizations are important in mother-pup recognition, the milk stealers do not vocalize when they are stealing milk. Finally, the male pups are more willing to accept physical abuse from the adult females than are female pups and are less discouraged by the trauma they experience when they are attempting to steal milk (Reiter *et al.*, 1978). Those pups that are able to steal milk successfully can maintain or gain weight while other weaners are losing weight at the rate of 0.5% of their body weight per day (Ortiz *et al.*, 1978). Milk stealing is much less likely to be successful in southern elephant seals, since all females, including those with pups and those that have lost their pups, are much less tolerant of alien pups than are northern elephant seal females. Southern elephant seal male pups do not show the delayed eruption of canine teeth; teeth erupt at the same time in both males and females (McCann, 1982).

5.3.5 Milk composition

Otariids show a trend toward increasing the fat content of the milk as the time between shore visits by the mother increases. Phocids show a trend toward increasing fat percentage in the milk as the time between birth and weaning decreases (see Oftedal *et al.*, 1987 for a review; see Chapter 6). Galapagos fur seals, which alternate short (ca. 1-day) on-shore visits with correspondingly short foraging trips, have milk with a low fat (23%) and protein (4%) content (Trillmich, 1984). California sea lions, which have longer (ca. 2.5-day) foraging trips, produce a 35% fat and 13% protein milk (Pilson and Kelly, 1962). Northern fur seals with foraging trips averaging 6.9 days (Gentry and Holt, 1986) produce a richer milk containing 42% fat and 14% protein (Costa and Gentry, 1986). Lactating northern fur seals do not have metabolic rates significantly greater than non-lactating females (Costa and Gentry, 1986), which implies that there is little heat increment associated with moving lipids from the female's fat stores to the milk. Similar results have been found in Antarctic fur seals (Costa and Trillmich, 1988).

The fat content of harp seal milk rises from 25% at the onset to 40% at weaning, yet growth rate of the pup is constant at 2.5 kg/day. This implies that the pup maintains constant energy intake, either through a reduction in efficiency of transferring milk energy to body mass or, more likely, through a reduction in the frequency of nursing (Lavigne *et al.*, 1982b). The enhanced thyroxine (T_4) levels in

nursing female harp seals (Engelhardt and Ferguson, 1980) should facilitate the breakdown of blubber lipids and their direct transfer to milk fat, which has a fatty acid composition virtually the same as that of blubber (Jangaard and Ke, 1968). This would help account for the very efficient transfer of energy from female stores to pup mass. Stewart and Lavigne (1984) have calculated that the cost of milk production is 1.04 to 1.2 times the energy content in the milk, based on a milk-to-pup mass conversion efficiency of 80–90%.

Hooded seal milk has the highest fat percentage (61%; Oftedal *et al.*, 1988) of any seal milk, consistent with the animal's short, 4-day, nursing period (Bowen *et al.*, 1985). Hooded seal milk is as concentrated at the start of lactation (56%; Oftedal *et al.*, 1988) as elephant seal milk is at the end (55%; Riedman and Ortiz, 1979). Fat content of northern elephant seal milk rises from about 12% shortly after parturition to well over 50% two weeks later. During the same time, the water content falls from 75% to about 35%. The protein content remains constant for any given female throughout lactation but varies between females from 5 to 12%, with some evidence that older females are feeding their pups a milk richer in protein. The fatty acid composition remains fairly constant, in spite of the changes in total fat content of the milk. Most of the fatty acids have carbon chains with lengths between 14 and 22, with the 16:0, 18:1 and 20:1 species making up more than 70% by weight. More than 75% of the fatty acids are unsaturated and have one or more double bonds (Riedman and Ortiz, 1979). Northern fur seals also have over 70% unsaturated fatty acids, with a significant percentage of chains 20–22 carbons in length (Ashworth *et al.*, 1966).

5.3.6 Nursing patterns

Nursing patterns of female pinnipeds show a number of interactions between physiology and behaviour. Phocid females usually stay with the pup and fast during the entire nursing period which lasts from 4 to 50 days. Otariid females alternate nursing bouts with trips to sea for feeding over nursing periods that can last as long as 36 months. Otariid pups spend more time nursing per day when the female is in attendance than do phocid pups (see Oftedal *et al.*, 1987 for a review; see Chapter 3 and 6).

Fur seal maternal behaviour has recently been reviewed by Gentry *et al.* (1986b). They summarize an extensive body of data by contrasting the pup-rearing strategies employed by species at the subpolar and tropical or subtropical extremes. The subpolar species, northern fur seals and Antarctic fur seals, face a rigorous but predictable environment, whereas the tropical and subtropical species, Galapagos fur seals, Galapagos sea lions, and the South American fur

seal in Peru, inhabit a more equitable but less predictable environment. The subpolar species have a well-defined, short nursing season with females alternating between several days on shore nursing and several days at sea feeding. For the tropical and subtropical species, however, the nursing season is less well defined and up to 36 months in length. The females' feeding trips to sea are usually on the order of a day or less in duration, and the time they spend on shore between feeding trips is similarly reduced. Pups of the tropical and subtropical species are weaned with smaller fat stores than are the pups of the subpolar species. This smaller fat store is probably compensated for by the fact that the tropical and subtropical pups are older at weaning and already have learned some foraging techniques. Pups of the subpolar species need the large fat stores to tide them over while they are learning to forage effectively.

One invariant characteristic of the fur seals is that the pup is weaned when it has achieved approximately 40% of the weight of an adult female. In the high latitudes this weight threshold is reached more quickly, both because the food resources available to the nursing females are more predictable and because the females provide the pups with a richer milk. For some species the relatively short, 4-month, nursing period is a necessity, because environmental conditions preclude a longer nursing period. Antarctic fur seals and northern fur seals have the shortest pup rearing periods of all otariids (Doidge *et al.*, 1986). Females at lower latitudes raise pups in an environment that is less predictable with respect to food resources. This variability in food resources leads to variable lengths of time required for the pup to achieve a weaning weight of 40% of the weight of an adult female. Neither the environment, which is suitable for pup rearing year round, nor the behaviour of the animals, which does not include exclusively pelagic periods, limits pup rearing to a few months out of the year, as is the case for species breeding at high latitudes. Galapagos fur seals can continue nursing for up to 3 years (Gentry *et al.*, 1986b).

Another relative constant in the behaviour of female otariids is the proportion of time spent in transit on any feeding trip, regardless of the duration. This proportion ranges from 12 to 29% and indicates that the amount of time spent feeding increases with longer transit times (Gentry *et al.*, 1986b). Northern fur seals and Antarctic fur seals were in transit for 25–28 hours before beginning feeding dives on trips of a total duration of 128–165 h (Kooyman *et al.*, 1986; Gentry *et al.*, 1986a). California sea lions spent about 8.5 h in transit on trips of 52 h duration (Feldkamp *et al.*, 1989) and Galapagos sea lions spent 2 h in transit on trips of 16 h duration (Kooyman and Trillmich, 1986b).

Except for the northern fur seal (Gentry *et al.*, 1986a), most otariid

females on foraging trips during lactation spend less than 5% of their time resting while at sea (Gentry *et al.*, 1986b; Feldkamp *et al.*, 1989). In some cases, the nutritional demands of the pups and their limited fasting ability require the prompt return of the female. Pups left for too long an interval between feedings either suffer reduced growth (Ono *et al.*, 1987) or are tempted to steal milk from other females, which can result in injury to the pup (Doidge *et al.*, 1984). When foraging conditions deteriorate, as they did for Antarctic fur seal females during 1984, those females that already are active 95% of the time at sea have little latitude to increase the proportion of time active and can only increase the total time at sea. In 1984, females stayed at sea twice as long to meet their foraging needs and as a result pup mortality doubled to 32%, of which 68% died of starvation (Costa *et al.*, 1989).

Most high-latitude female pinnipeds pup every year. They nurse for a short, defined period then mate and go to sea for extended periods of feeding. They are able to devote much of the year to building up fat stores, hence spreading the costs of nursing over most of the year. Females of tropical species have a continuing investment in the pup which may inhibit reproduction in the next year. A combination of physiological and environmental factors appears to determine whether or not a female Galapagos fur seal produces a pup two years in succession. Seventy per cent of the females without an attendant yearling give birth to a new pup, whereas only the healthiest 15% of the females with attendant yearlings produce a new pup (Trillmich, 1984). Since pup mortality is only 20% during the first year, this means that most females only produce a pup every other year. The combination of the female's condition and the presence of a nursing pup could shift the hormonal balance to preclude successful implantation of the blastocyst. In kangaroos, for example, stimulation of the nipple by a nursing joey is sufficient to arrest the development of the next embryo (Sharman, 1963). In grey seals, females that were able to replenish their body stores most quickly were also the ones in which implantation occurred the earliest (Boyd, 1984). Because Galapagos fur seal and sea lion females are on shore throughout the year, they would be good subjects in which to investigate the hormonal factors associated with delayed implantation and the effect of nursing on hormonal profiles. Other measures of female condition and available resources could also help elucidate the role of female health on hormones and successful reproduction.

Even the healthiest 15% of female Galapagos fur seals are unlikely to raise the new pup successfully. If the older sibling is a yearling, the new pup almost always dies before reaching one month of age. If the older sibling is a 2-year-old, the pup has only a 50% chance of survival. Death is usually by starvation, but in 5% of the cases the

younger pup is killed by its older sibling (Trillmich, 1984). In the particularly adverse conditions of an El Niño event, even the curtailing of pup production is not sufficient for the females to have resources available to nurse a dependent offspring successfully. In the 1982–1983 El Niño event all of the dependent young starved to death (Trillmich and Limberger, 1985).

5.3.7 Pup growth

Seals follow the general mammalian allometric scaling of increasing neonatal mass relative to maternal mass as maternal mass decreases. The exceptions are the ringed, Baikal, *Phoca sibirica*, and Caspian, *P. caspica*, seals that produce relatively smaller pups than expected. The ringed and Baikal seals give birth in lairs constructed in the snow above the ice surface. These lairs provide thermal protection for the pups as well as some protection from predators. This more favourable environment allows these species to have a longer lactation period and a growth rate of the pups more similar to that of species pupping on land than to the faster rate of species pupping on pack ice (Kovacs and Lavigne, 1986). The ringed seal has a lactation period of about 42 days (McLaren, 1958) and the Baikal seal has a period of about 58 days (Frost and Lowry, 1981). For a detailed consideration of the physiological dynamics of pup growth, see Costa (Chapter 6).

5.3.8 Nursing set points

There appear to be physiological set points that determine when nursing fur seals leave for a feeding trip at sea and when they return to nurse their pups again. These set points have been investigated most thoroughly by Gentry and Holt (1986), who performed field manipulations on northern fur seals, whereby female and pup reunion was delayed when the female returned to land or the pup was fed prior to the female's return. Both of these manipulations resulted in extended on-shore time for the female. When the pup was fed prior to the female's return, presumably its demands on maternal stores were reduced and the energy balance of the female took longer to reach the set point stimulating a return to sea. Similarly, when the reunion of the pup and female was delayed after the female's arrival on land, her time ashore was extended. For each hour the reunion was delayed, the female remained on land for an additional hour. The experimental condition was manipulated so that these females spent three to four times as long on shore as did control females. This clearly indicated that the duration of maternal-pup contact and not total time on shore dictated when the female left for foraging.

Other evidence that the female northern fur seal leaves shore in response to falling nutritional reserves is found in the steady decline in lipid content of the milk during any shore visit. The high lipid content is restored when the female returns from a foraging trip to start another nursing session (Costa and Gentry, 1986). Conversely, in phocid seals, the lipid content of milk increases during lactation as a means of conserving water. The fur seal does not appear to be water-limited but is lipid-limited.

As Antarctic fur seal pups age, they wander further from their last feeding site which means that the returning female spends more time locating the pup before nursing can commence. This natural delay in re-establishment of contact results in an increase in on-shore time, similar to that found in the experimentally manipulated situation. Also, after weaning their pups, the females mean shore visit is twice as long as it was when they were nursing (Doidge *et al.*, 1986). Since Antarctic fur seal pups wean themselves (Doidge *et al.*, 1986), the increased time females are on shore after weaning may indicate a continuing contribution by nursing set points to the females' activity cycles. Galapagos fur seals reduce the time they spend on shore as the nursing demands of the pups increase, particularly when they are nursing yearlings, which increases the rate of energy flow from females to offspring (Trillmich, 1986a).

The clearest evidence of feeding satiation controlling when the female returns to land is seen in natural experiments in which food resources are depleted. The 1983 El Niño event in the Galapagos and South America was one case, and the 1984 depletion of krill at South Georgia was another. In both instances, the female Galapagos (Trillmich and Limberger, 1985), South American (Trillmich *et al.*, 1986) and Antarctic (Costa *et al.*, 1989) fur seals increased the duration of their trips to sea and apparently fed until satiated, even though this greatly increased the mortality of their pups due to starvation. The Antarctic fur seals returned with the same increase in mass after foraging trips of variable duration, further supporting the idea that the female returns from feeding only after satiation.

The female northern fur seal also always returns to shore with the same gain in mass, no matter how long she remains or how much energy she expends while at sea. Energy expenditure was determined directly by ^{18}O measurement (Costa and Gentry, 1986) or surmised to be increased, because of increased drag, in those females that wore time-depth recorders (Gentry *et al.*, 1986a). A reasonable explanation for the constant gain in mass under different levels of energy expenditure is that females feed until satiated and then return to land (Gentry *et al.*, 1986b). The behaviour of Galapagos fur seal females under two different conditions supports this conclusion. When the availability of food declines, the duration of foraging trips increases.

When the availability of food is constant but the demands of the offspring increase, the duration of the foraging trips remains constant, but the frequency of trips increases (Trillmich, 1986a).

These set points for both feeding satiation leading to the female's return to land and nursing depletion leading to the female's return to sea result in nursing females having much more regular and predictable patterns of shore visits than do females not suckling a pup. The nursing females make more foraging trips, pay about twice as many visits to land and spend more days on shore than do non-suckling females (Gentry and Holt, 1986).

5.3.9 Mother-pup recognition

Females and pups utilize a variety of cues - spatial, visual, acoustic and olfactory - to recognize each other prior to nursing. In most cases, the final arbiter in the recognition process appears to be the nursing female. Seals that breed in the pack ice can rely almost exclusively on spatial cues, because there is usually only one pup within their defined space. Crabeater and ribbon seals have little need to identify the nursing pup, because they rarely leave the floe on which their pup is located. Male crabeater seals actively prevent females from leaving the ice floe (Siniff *et al.*, 1979). A spotted seal female will allow nursing by the pup occupying the floe on which she left her pup. This is an adequate paradigm for identifying her offspring except when the pup has been switched by investigators (Burns *et al.*, 1972) in which case the female nurses the alien youngster.

In the unstable pack ice habitat of the harp seal, spatial cues are less reliable, and the females use a combination of acoustic, visual, olfactory and tactile cues in recognizing their pups (Ronald and Dougan, 1982). No one sense appears to be relied on exclusively, and the females appear to be using a multi-modal gestalt to identify their pups (Terhune *et al.*, 1979). In over 900 hours of observation, no harp seal female was ever observed nursing more than one pup, and no pup was ever observed nursing from more than one female (Stewart, 1987). Harbour seal females and pups maintain close contact throughout the nursing period. The pup appears to imprint on the mother soon after birth and follow her closely (Renouf, 1984). This pup recognition of the mother is unusual in pinnipeds. Since the pup can follow the mother at a distance both on land and in the water, vision must play a major role in the pup's recognition of the mother. On the other hand, audition plays a major role in the mother's recognition of the pup. The pup produces a unique call up until weaning. Renouf (1985) demonstrated that an adult female could distinguish between recorded vocalizations of different pups. When

in the water, the pup vocalizes with its head just out of the water so the sound is transmitted both through air and through water. Although the vocalizations have different characteristics in air and water, both the airborne and waterborne vocalizations are unique for each pup. An intriguing, untested hypothesis is that a female can determine the distance to her pup by comparing time delays between receipt of its waterborne and airborne vocalization (Renouf, 1989; Perry and Renouf, 1988).

Seals that breed in dense aggregations show the most developed mother-pup recognition systems (see Chapter 3). There is evidence that in some species, older females are better in establishing the mother-pup bond than are younger females. In northern elephant seal colonies, young females have more trouble identifying their pups than do older females (Reiter *et al.*, 1981). In southern elephant seals, experienced females begin to smell the pup more quickly after parturition than do primiparous females. Experienced females also appear to learn the pup's odour and vocalizations more quickly than do inexperienced females (McCann, 1982). Females are more discriminating than pups and usually will reject an alien pup. Some females will allow other young to nurse, however, and some will adopt an alien pup and nurse it exclusively until it is weaned (Le Boeuf *et al.*, 1972). No female will adopt an injured pup.

There are advantages for a female northern elephant seal if she adopts a healthy pup after she has lost her own. Apparently females that have given birth to a pup need the stimulation of nursing to trigger their oestrus. None of the eight females that nursed occasionally or not at all after giving birth were observed copulating, whereas 16 of 24 females that nursed a pup to weaning were observed copulating (Le Boeuf *et al.*, 1972). It is difficult to postulate an evolutionary basis for the development of this nursing prior to oestrus sequence, if indeed such a requirement does exist. On the other hand, such a link does not have to have an evolutionary explanation: it can arise through more proximate physiological mechanisms. Whatever the neuroendocrine bases are for the observed differences in behaviour, they are fairly complex. Such a situation does not appear to hold in the southern elephant seal since females that have lost their pups are just as likely to bite an alien pup as are females nursing their pups (McCann, 1982).

5.4 Motor development and play

Most pinnipeds are born with advanced locomotor development. The capabilities of northern fur seals at birth for locomotion and vocalization have been estimated to be equivalent to those of domestic dogs

at 3 weeks of age (Bartholomew, 1959). This locomotor ability soon after birth is important for both pinnipeds born in dense aggregations and those born on unstable ice. In polygynous species the pup needs to avoid contact with adults other than its mother. The males, intent on sexual and agonistic encounters, can damage pups that are in their path, and females other than the mother are likely to bite the pup. Northern fur seal pups have a predisposition to climb upward rather than downward on the rocky hillsides of their rookeries. This predisposition takes them away from the most active areas of the rookery, as well as from the danger of being washed out to sea. Being washed out to sea is a significant cause of mortality of pups of a number of species. It is the greatest cause of pup loss at some grey seal rookeries where pups cannot move inland (Baker, 1984; Anderson *et al.*, 1979). Depending on weather conditions, up to 28.5% of northern elephant seal pup mortality can be attributed to drowning when the pups are washed out to sea (Le Boeuf and Briggs, 1977).

Most pinnipeds learn to swim independently, without instruction or support from their mothers. Northern fur seal pups apparently can swim from birth, but they show no interest in entering the water during their first few weeks of life (Bartholomew, 1959). Gentry (personal communication quoted in Farentinos, 1971) observed a Steller sea lion pup with umbilicus and placenta still attached swimming in tidal waters adjacent to a rookery. Galapagos sea lion pups enter the water when they are only a week old, whereas Galapagos fur seals wait until they are 3–4 weeks old (Trillmich, 1986b). Harbour seals that are born on tidal beaches and rocky shorelines can swim with their mothers on the first flood tide after birth (Bonner, 1984) or even within minutes of birth, if flushed into the water by a disturbance (Lawson and Renouf, 1985).

Bearded seals are born on unstable pack ice and can swim as soon as they are born (Burns, 1981). In contrast, Weddell seal pups, that are similar in size to bearded seal pups, are born on the stable fast ice and do not enter the water until they are about 10 days old (Elsner *et al.*, 1977).

Elephant seal pups usually don't enter the water for several weeks after they have been weaned. They have an extensive blubber coat, which is used as an energy resource, while they learn to swim and forage. On their initial swimming attempts, they remain under water for only a few seconds. After 2–3 weeks of swimming, they can remain submerged for several minutes when they are active and for up to 7 min when they are sleeping. By the time they have been swimming for 5 weeks, they are able to remain asleep under water for up to 15 minutes (Reiter *et al.*, 1978). Pups born late in the season enter the water sooner after weaning than do pups born early in the season. This results in a shorter interval (3 weeks) during which pups

leave the breeding area than the interval (8 weeks) during which weaning occurs (Reiter *et al.*, 1978).

The extent to which motor skills of young pinnipeds are refined through play shows some support for one aspect of Fagen's (1981) functional model of play behaviour. This model predicts that in sexually dimorphic species in which the variance in reproductive success is greater in males than in females, males should spend more time in play than females. Male Galapagos fur seal pups spend more time in play than do female pups. As the pups age, the males devote increasing amounts of their time to activity, whereas females show the opposite trend (Arnold and Trillmich, 1985). These sexual differences in play behaviour are not as striking in the Galapagos fur seal as they are in the Steller sea lion, where aggressive components of play are seen more often in male than female pups (Gentry, 1974). As Arnold and Trillmich (1985) have pointed out, this difference is in accord with the reduced sexual dimorphism of the Galapagos fur seal, compared with that of the Steller sea lion and most other otariids.

Pups in highly polygynous species are surrounded by sexual and agonistic activity from birth. This might contribute somewhat to the precocious sexual behaviour that forms a major component of their play. Prolonged sessions of copulatory activity with behaviours that appeared to be virtually identical to those of adults have been observed between pairs of northern fur seal pups as young as one month of age (Bartholomew, 1959). Play constitutes the majority of interactions between different subadult age classes in South African fur seals. Play sessions usually include copulatory behaviour patterns by subadults of all ages, including pups, one of which was observed to have an erection when it mounted a yearling (Rand, 1967).

In the promiscuous harbour seal, females play more than males and there is a surprising amount of play by adults. For all ages, solitary play is more frequent than social play but only weaners showed no social play behaviour. Adult social play occurred only during the mating period. The predominance of sexual play seen in polygynous species was not observed in the harbour seals (Renouf and Lawson, 1987).

Play is infrequent in grey seal pups prior to weaning, although it is unclear which of a number of possible explanations account for this fact. The nursing period is short, and neonatal motor development may not be sufficient during this period for extensive play. Since play often leads to changes in the location of the pups, it can delay the reunion of the mother and the pup (as is the case in Antarctic fur seals; Doidge *et al.*, 1986) and increase the chance of permanent mother-pup separation. Any delay in reunion may be critical in a species with a short nursing season. Finally, because the pup is

building up the maximum blubber layer in the minimum amount of time, play might dissipate energy that could otherwise be stored as blubber. What little play grey seal pups engage in is not social play but self- or object-oriented play (Kovacs, 1987).

Male elephant seal pups exhibit behaviour patterns similar to those used by adult males in fighting, whereas the female pups are more likely to show behaviour patterns that are used by adult females in agonistic encounters (Reiter *et al.*, 1978). Adolescent elephant seal males can produce all of the elements of adult male threat vocalizations. Even though their proboscis is not as fully developed, the difference in the juvenile and adult male threat vocalization is not so much in the acoustic content of any of the components as it is in producing these components in the adult sequence (Shipley *et al.*, 1986). Learning the adult sequence develops after attaining the ability to produce the individual components. A similar learning pattern occurs in the development of walrus vocalizations (F. H. Fay, pers. comm.).

The process by which males learn and develop their copulatory behaviour is often at the expense of younger animals. Northern elephant seal weaners that fail to join weaner pods run the risk of being mounted by peripheral males. The head or neck bite that accompanies the mounting attempt can be fatal to the weaner (Reiter *et al.*, 1978). About 50% of the weaners at the Año Nuevo mainland site have fresh tooth punctures or scars indicative of bites by males (Le Boeuf and Mesnick, in press). Subadult South American sea lion males will separate a pup from its mother and practise herding the pup. The techniques learned in herding and controlling the movements of the pup will be used by the male, when he becomes an adult, to control the movements of the females with which he will eventually mate (Campagna *et al.*, 1988a). This behaviour results in the death of over 1% of the pups born each year (Campagna *et al.*, 1988b). Vocalizing South American sea lion pups stimulate aggressive responses by subadult males. The subadult males will charge a vocalizing pup from as far away as 50 m and, upon reaching the pup, bite it and shake it until it is dead (Vaz-Ferreira and Achaval, 1979).

Male south Australian fur seals attempting to mount cows in terrain dominated by boulders have much difficulty, because of the various positions of the females with respect to the boulders. Although successful mounting is more difficult in the boulders than it is in flatter terrain, there is some evidence that males learn with experience and become more efficient at mounting females among the boulders (Stirling, 1971).

5.5 IMMUNE SYSTEM

One physiological characteristic of pinnipeds that needs more investigation, particularly in the polygynous species that breed on land, is the immune system. The breeding grounds are sites where many animals with open wounds are packed close together on a substrate soiled by excrement. For example, approximately 70% of adult male South American sea lions were wounded over the course of the breeding season (Campagna and Le Boeuf, 1988a). The presence of wounds on the necks of male common seals, *Phoca vitulina vitulina*, has been used as an indicator to establish that the mating season occurs after nursing and before moult, as in other *P. vitulina*, rather than after moult as had previously been thought to be the case (Thompson, 1988). Male South African fur seals rarely groom their fur when they are hauled out and it soon becomes soiled with excreta (Rand, 1967). Wounds through this soiled fur should provide significant challenges to the immune system. It is surprising that more of the wounds do not become infected, particularly considering that many of them are punctures. Possibly the apparent lack of susceptibility to infections is more a reflection of the lack of necropsies than it is an indication of immunity to infection. Baker and McCann (1989) conducted detailed post-mortem examinations of 102 male Antarctic fur seals dying at Bird Island during three breeding seasons. Eighty-six per cent of the animals had fighting injuries, and, in many cases, bacterial infection of the wounds was the primary cause of death. Sometimes extensive cellulitis was associated with quite minor wounds.

Clear evidence of the opportunities for infection because of soiled habitat comes from studies of the peritonitis/navel-ill complex affecting grey seal pups. The incidence of peritonitis correlated with the condition of the beach at three sites on the Isle of May. The onset of peritonitis also correlated with when the young came in contact with fouled areas on different beaches (Baker and Baker, 1988). Older pups were less likely to die of peritonitis after their umbilicus healed and the cord remnant are shed.

The immune system becomes more active as the pup matures. In 7-day-old pups, gamma globulin levels were depressed to similar levels in both diseased and healthy pups. Weaned pups had levels halfway between those of 7-day-old pups and adults (Baker, 1984). Depressed pup humoral immunity has also been reported in northern fur seals (Keyes *et al.*, 1981).

5.6 DIVING

Diving in pinnipeds is accompanied by a number of physiological changes which were originally called a diving reflex. This reflex was delineated primarily in captive, restrained and forcibly dived animals. Under these conditions, the animal exhibited a profound bradycardia, during which the heart rate dropped to 10% or less of its pre-dive rate, although stroke volume was maintained. The bradycardia was accompanied by a simultaneous constriction of peripheral blood vessels. The concomitant increase in peripheral resistance compensated for the reduced cardiac output and maintained normal blood pressure in those organs where blood continued to flow, primarily the heart, lungs and brain. Muscles operated under anaerobic metabolism and contributed a large pulse of lactic acid to the blood when circulation was restored at the conclusion of a dive. Metabolic rate appeared to be depressed during the dive (Irving, 1938, 1939; Irving *et al.*, 1941, 1942; Scholander, 1940; Scholander *et al.*, 1942a, 1942b; see Harrison and Kooyman, 1968 for a review).

It has now become clear that this interlocking suite of changes in heart rate, peripheral vasoconstriction, blood redistribution and metabolism is better termed a diving response than a diving reflex. The animal has a good deal of control over the response; it is not exclusively a reflex action to facial wetting (Dykes, 1974b) or cessation of respiratory movements (Dykes, 1974a) although these certainly play a role, as does input from arterial chemoreceptors and baroreceptors (see Elsner and Gooden, 1983 for a review). Rather, the extent of the diving response is dependent on the type of dive the animal is making, with greater physiological responses invoked when the anticipated dive will be longer (Kooyman and Campbell, 1972). Even the shortest dive, however, is much different from an equivalent amount of exercise at the surface. Circulation shows substantial alteration during short dives as well as during sleep apnea on land (Guppy *et al.*, 1986; Castellini, 1988). Also, bradycardia is relaxed at certain points during feeding and exploratory dives (Guppy *et al.*, 1986; Wartzok *et al.*, 1987) allowing a redistribution of heat, oxygen and metabolic substrates and products.

Further evidence of behavioural, in contrast to reflexive, responses to physiological processes in diving was shown in the changes in diving behaviour of harbour seals exposed to altered inspired gas composition. When the partial pressure of oxygen in the inspired air was decreased, and that of carbon dioxide was increased, the seals responded with a change in the proportion of time on the surface relative to the total time between dives, rather than with the more typical mammalian reflexive response of a change in ventilation frequency. The seals did not alter their breathing rate and increased

tidal volume only slightly (Craig and Pasche, 1980). Young seals have the usual mammalian reflexive response to decreases in inspired oxygen concentration (Mortola and Lanthier, 1989). Apparently the older seals learn to substitute behavioural control of diving patterns for reflexive control of ventilation.

The physiological bases of diving behaviour in phocids has been studied most extensively in the Weddell seal (Kooyman, 1981). The aerobic diving limit of adult Weddell seals is on the order of 20–25 min. This value can be obtained either by calculating oxygen stores or by measuring lactate in the blood following dives of different durations. Dives of greater duration utilize anaerobic metabolic pathways. This physiological limit is reflected in the behaviour of the seals whose dives rarely (3–8%) exceed the 25 min aerobic dive limit (Kooyman *et al.*, 1983). Younger animals, that have been shown to have a lower aerobic capacity, dive for shorter times to shallower depths, usually less than 200 m. Foraging demands push young seals close to, and often over, the aerobic dive limit, and result in an increase in lactate in their blood after voluntary dives (Kooyman *et al.*, 1983). Weddell seals occasionally will continue diving with elevated lactate levels when in the midst of a foraging bout. This voluntary tolerance of increased lactate, and use of surface time to replenish oxygen stores rather than process metabolites, allows the seals to continue foraging. The seals restore metabolic homeostasis when resting at the surface at the completion of a dive bout (Castellini *et al.*, 1988).

California sea lions exceed their calculated aerobic diving limit on only 4% of their dives and rarely approach the limit on the majority of their dives. The typical depth of dives, less than 80 m, is also much less than the maximum depth of over 275 m. Distribution of food resources appears to be the primary determinant of diving patterns in these animals rather than physiological constraints (Feldkamp *et al.*, 1989). Walruses are also probably capable of diving to depths greater than their customary maximum depth of 100 m, but there is little advantage to their doing so. Their benthic food resources are primarily located where bottom depths are less than 100 m (Fay and Burns, 1988). California sea lions are active at all hours of the day and night although there is some increase in dive frequency at dusk and dawn (Feldkamp *et al.*, 1989). This is in contrast to most otariids that specialize in foraging either during the day, e.g. Galapagos sea lions, or at night, e.g. Galapagos fur seals (Kooyman and Trillmich, 1986a, 1986b).

Although the Weddell seal is indeed a 'consummate diver' (Kooyman, 1981), it possesses few unique biochemical adaptations for anaerobic metabolism (see Kooyman *et al.*, 1981 for a review). Greater oxygen stores in blood and muscle make the major contribution to its

enhanced diving abilities. There is some evidence of augmented anaerobic metabolic capacity in the liver, kidney and possibly the heart, but the primary biochemical adaptation appears to be an increased tolerance to the end products of anaerobic metabolism, for example, through increased buffering capacity for lactic acid in muscles (Castellini *et al.*, 1981).

The behavioural trait of exhaling prior to diving seen in almost all (99 out of 100 observed) Weddell seals, and presumably other long, deep diving seals, has the beneficial physiological consequence of minimizing the absorption of nitrogen from the lungs into the blood, under the increased pressures encountered during a dive. The only Weddell seals which consistently fail to exhale before a dive are the pups whose dives are short and shallow and provide little opportunity for high-tension nitrogen absorption (Kooyman, 1968). Seals have a flexible thoracic cavity and rigid cartilage in the bronchial tree (Kooyman *et al.*, 1970) so that by 50 m depth, external water pressure has collapsed the chest sufficiently to force most of the gas from the lungs into the non-absorbing bronchial tree (Kooyman, 1972). On most deep dives, the descent is rapid which minimizes the time between the surface and 50 m during which the blood could obtain higher nitrogen tensions (Kooyman, 1968).

Weddell seals and elephant seals dive the deepest and longest of any of the pinnipeds whose diving profiles have been recorded. Weddell seals can dive for up to 73 min (Kooyman *et al.*, 1980) and to depths of at least 600 m, the maximum depth in McMurdo Sound (Kooyman, 1966). Based on Weddell seal stomach contents and the depths at which different size classes of the principal prey, *Pleuragramma antarcticum*, are found, Plotz (1986) suggested that in the 1000 m deep Weddell Sea the seals were diving to 850 m and possibly deeper.

Elephant seals have been shown to be the deepest divers among pinnipeds (Le Boeuf *et al.*, 1988, 1989b). Dives to 930 m have been recorded and dives to 1250 m, beyond the range of the recording instruments, have been extrapolated. More interesting than just the maximum depths are the dive patterns. Time-depth recorders were attached to females prior to their leaving the rookery, after weaning their pups, and were recovered when the females returned to land 2 1/2 months later to moult. The animals dove almost continuously throughout this entire period with modal dive durations per female of 17.1-22.5 min to modal depths per female of 500-700 m with mean surface intervals of less than 3.5 min. Le Boeuf *et al.* (1988) provided three possible explanations for this continuous deep diving behaviour. First, of course, is that they are able to exploit prey that are available to few competitors, since few other animals can dive this deeply. In fact, the ability to feed on unexploited resources may

have contributed to the spectacular increase in northern elephant seal populations after near extinction in the last century. Second, spending a major portion of their time at great depths puts them beyond the range of their major predator, the white shark, *Carcharodon carcharias* (Le Boeuf *et al.*, 1982). Finally, the reduction in metabolic rate expected from the diving response (Elsner and Gooden, 1983; Hochachka and Guppy, 1987) and the possible reduction in metabolic rate because of potential reduction of body temperature in the cold, deep water (Hill *et al.*, 1987) should lead to a significant reduction in maintenance metabolism and allow the animals to direct more of their resources toward replenishing the 42% of their mass lost during nursing (Costa *et al.*, 1986).

There is evidence of behavioural control over oxygen utilization by northern elephant seal during deep dives. For dives up to 400 m, the time spent getting to depth increases linearly with the maximum depth of the dive. For dives of just over 400 m, there is an abrupt decrease in time to reach that depth. As the maximum depth increases from just over 400 m to greater than 1000 m, the time spent getting to depth again increases. Le Boeuf *et al.* (1988) speculate that for dives over 400 m, foraging time at depth is maximized by a faster descent, even though this increases metabolic rate and results in a shorter total dive time.

We do not yet know the full suite of physiological adaptations which allow elephant seals to make continuous dives to great depths. The seals apparently maintain steady-state conditions during these long, deep dives, which continue over an extended time. Great depths imply great pressures which, in other mammals, result in the fatal convulsions of the high-pressure nervous syndrome (Bennett *et al.*, 1974). Pressure-induced neural excitation can be reduced with anesthetics, including high-pressure nitrogen (Lever *et al.*, 1971). Thus, high tissue nitrogen tension, which is considered a danger for most diving mammals, could be used by elephant seals to help them avoid the high-pressure nervous syndrome (Kooyman, 1989; Le Boeuf *et al.*, 1989b). Elephant seals do not begin deep dives immediately after going to sea, rather they progressively increase the depths of their dives. This behaviour might indicate that they need to build up nitrogen tensions prior to deep diving (Le Boeuf *et al.*, 1989b).

5.7 METABOLISM

The amount of food seals require to meet the energy costs of free existence has a significant influence on pinniped behaviour, determining the time that has to be allocated to foraging and setting limits on the time available for other behaviours. In a number of

studies Lavigne and coworkers (Lavigne *et al.*, 1982a, 1986) have called into serious question the previously accepted dogma (e.g. Irving, 1972) that marine mammals inherently have standard metabolic rates well above the value predicted on the basis of the allometric scaling function of metabolic rate to body mass; i.e. the mouse-to-elephant curve (Kleiber, 1975). Many studies had erroneously concluded that metabolic rates were greater than expected in marine mammals because one or more of the criteria for defining standard metabolic rate were violated in its determination. The most often ignored criterion was that the experimental animals should be mature. Because many marine mammals are large and difficult to maintain in captivity, studies have often been done on immature animals. Immature animals of most species have higher than predicted mass-specific metabolic rates. Other problems included the animals not being post-absorptive, hence measured metabolic rates included a contribution by specific dynamic action associated with digestion, and animals not tested within their thermoneutral zone. When corrections are made for these deviations from standard conditions, pinnipeds appear to have metabolic rates about what would be expected based on their masses.

Feeding rates of growing pinnipeds are higher than predicted on the basis of their body size and compared with juveniles of terrestrial species. However, as Innes *et al.* (1987) note, pinniped juveniles are growing at much faster rates than terrestrial juveniles. When the rate of growth is considered, juvenile pinnipeds do not consume more food than predicted. Innes *et al.* (1987) assert that, contrary to popular belief, adult pinnipeds have lower maintenance requirements than adult, non-mustelid carnivores. Comparisons can only be made across mammalian orders when standard conditions are employed. However, when assessing the impact of pinnipeds on their food resources, real-world conditions are more interesting than standard conditions. In the former instance, pinnipeds' measured metabolic rates are substantially above predicted standard metabolic rate.

A number of otariids apparently spend most of their lives in water at temperatures outside of their thermoneutral zone, below their lower critical temperature. Hence it matters little that their metabolic rate in the thermoneutral zone may be that predicted by the mass-specific allometric equation. If the animals have to increase their metabolic rate in order to maintain thermostasis, then their energy requirements will be increased by that amount and they will have to devote proportionally more time to foraging.

Adult Antarctic fur seal females, when foraging for themselves and their pups, have a metabolic rate 5.6 (calculated by Doidge and Croxall, 1985; based on energetics data in Costa and Gentry, 1986) to 6.7 (Costa *et al.*, 1989) times the predicted basal metabolic rate; when foraging

only for themselves their metabolic rate is 3.0 times predicted (Doidge and Croxall, 1985); and when they are ashore providing milk for their pups their metabolic rate is 3.2 times predicted (calculated by Doidge and Croxall, 1985; based on energetics data in Costa and Gentry, 1986). Adult males have a metabolic rate 3.1 times predicted. Juveniles and weaners, that are foraging and growing, have a metabolic rate 5.6 times predicted (see Chapter 6). Doidge and Croxall (1985) derived an energy budget for Antarctic fur seals that required consumption of prey equivalent to 19–23% of their body weight each day. Antarctic fur seals meet these energy demands by feeding primarily on krill (69%) with fish (19%) and squid (12%) representing much smaller percentages of their diet. This feeding rate translates into over 1 million tons of krill taken in the summer alone (Doidge and Croxall, 1985).

Northern fur seals need to consume 14% of their body weight each day (Miller, 1978). The correct determination of the energy cost of free existence has major implications for estimating the impact of pinnipeds on their food resources and is particularly important in reference to those marine resources also under human exploitation (see Beddington *et al.*, 1985). For example, the California sea lion population consumes from 100,000–250,000 tons of Pacific hake annually (Bailey and Ainley, 1982).

5.8 ACTIVITY PATTERNS

In spite of the high mass-specific energy requirements discussed above, adult males of both northern and Antarctic fur seals spend over a month on their territories without going to sea for food (Peterson, 1968; McCann, 1980). Females also spend 9–10 days on shore, without feeding, at the same time they are giving birth to, and nursing, a newborn pup. Antarctic fur seal females give birth about 2 days after coming ashore, nurse the pup until 6 days post-partum, come into oestrus, copulate and return to sea to feed (Doidge *et al.*, 1986). This pattern is very similar to that of northern fur seals where parturition occurs about 2 days after coming ashore, copulation about 6 days post-partum and the return to sea and feeding within a day after mating (Bartholomew and Hoel, 1953).

The rapid increase in numbers of New Zealand fur seal females on the rookery has been interpreted as indicating that the females are spending the maximum time at sea, feeding actively until they come ashore to pup (Miller, 1975a). New Zealand fur seal females, similar to northern and Antarctic fur seal females, remain on shore for about 10 days. They give birth about 2 days after arriving on shore, come into oestrus about 8 days later, and leave for foraging within a day after

mating (Miller, 1975a). South American sea lions give birth about 3 days after coming ashore, mate about 6 days after parturition, and go to sea about 2 days after mating (Campagna and Le Boeuf, 1988a).

Most studies of activity budgets of pinnipeds on shore have shown that the majority of their time is spent resting. Factors contributing to this finding include the difficulty of locomotion on land, the problems of dissipating sufficient heat when out of water, and the need to conserve energy when hauled out for long periods during the mating season. New Zealand fur seal males spend less time interacting with other males during the breeding season than they do outside of the breeding season. Even agonistic behaviours occur more frequently outside of the breeding season than they do during the time the males are defending their territories (Johnstone and Davis, 1987). South Australian fur seals spend over 90% of their time either lying or sitting relatively motionless. Territorial males spend only 3% of their time in intersexual and intrasexual encounters (Stirling, 1971). At a non-breeding beach, male New Zealand sea lions, *Phocarctos hookeri*, spent 90% of their time lying down during the summer and 80% of their time lying down during the winter (Beenjtes, 1989).

Territorial male grey seals spend about 88% of their time resting. Non-resting time is spent in aggressive behaviour and sexual activity. These two activities are compensatory; as the season progresses and sexual activity increases, aggressive activity declines. Boness (1984) had hypothesized that body stores would be a limiting factor for males maintaining territory and that the males most active sexually would compensate by increasing the amount of time spent resting. He found that this was not the case but rather the males most active sexually were also the most active in general. An explanation for this result had to await Anderson and Fedak's (1985) study that considered size of the animals as well as activity. They showed that larger males, that maintained higher levels of activity both sexually and in general, lost proportionally more mass than smaller, less sexually active animals. Dominant male northern and southern elephant seals are more active than the subordinate animals (Le Boeuf, 1974; McCann, 1983). High-ranking northern elephant seal males lost 41% of their body mass during the breeding season, compared with a 34% loss of body mass in subadult and subordinate adult seals (Deutsch *et al.*, in press). Weddell seal males maintain aquatic territories and spend most of the breeding season in the water (Green and Burton, 1988), actively patrolling their territories (Wartzok *et al.*, 1990). An even higher correlation between activity and copulatory success would be predicted for these animals. The few males seen hauled out at this time of the year all have wounds (Green and Burton, 1988) and appear to be losers in sexual competition.

Northern fur seals maintain the same circadian activity pattern when they are on shore as they have at sea, although total activity is greater at sea. The seals are most active in diving at dusk and dawn, resting during the daylight hours. This pattern continues during the short period each year when the seals are on land for breeding. General activity and copulations peak at dawn and dusk (Gentry *et al.*, 1986a). Apparently the circadian rhythms of activity are sufficiently ingrained in the animals that the change of behaviour and habitat from foraging at sea to breeding on land is not sufficient to change the physiological rhythms.

Grey seals and northern elephant seals maintain a basically constant pattern of activity on the rookery day and night (Anderson, 1978; Shipley and Strecker, 1986). Northern elephant seal vocalizations increase at night, but the increases are not significant. In both species, visual threats are common at night, implying that the visual system adapted for prey detection at depth also functions quite well in guiding intraspecific encounters on land under moonlight or starlight illumination levels.

Harbour seals on land increase sleeping time as the number of animals hauled out increases. Increased group size decreases the amount of time any given individual devotes to visual scanning. As surveillance time decreases, sleeping time increases (Kriebel and Barrette, 1984). This benefit of group hauling out plateaus with group sizes of about ten (Terhune, 1985). When observations of harbour seals are restricted to breeding groups, the preceding conclusions regarding vigilance do not apply. In breeding groups, adult males increase their scanning as group size increases, whereas other age and sex classes show no changes in scanning rate. The males become more vigilant as mating season approaches, and pay more attention to females arriving from the sea than they do to disturbances arising from the land (Renouf and Lawson, 1986). Harbour seals do not appear to have socially stable groups that haul out at specific sites; rather individuals will be observed with different companions at different sites (Godsell, 1988).

5.9 THERMOREGULATION

Pinnipeds need to maintain thermal balance in environments with very different thermal characteristics. Water has twenty times the thermal conductivity of air so for most of the time for most pinniped species, the problem is to conserve heat in the water and to dissipate heat when out of the water. One of the arguments for the development of a mammalian homeothermic set point at around 37°C is that this temperature is higher than the temperature of most

environments the animals inhabit. Hence thermoregulatory mechanisms can be designed to deal primarily with heat flow in one direction, outward, and this can be regulated by varying insulation (Crompton *et al.*, 1978; Heinrich, 1977). Pinnipeds cannot emphasize only one side of the heat balance equation. Anatomical adaptations, such as an insulative layer of blubber and counter-current heat exchangers, function to conserve heat in the water; out of the water, these same adaptations inhibit heat dissipation.

Thermoregulatory requirements often influence the behaviour of pinnipeds during the breeding season. Territory-holding male California sea lions (Odell, 1974), Galapagos fur seals and sea lions (Trillmich and Trillmich, 1984), New Zealand fur seals (Gentry, 1973), Australian sea lions, *Neophoca cinerea* (Marlow, 1975), and even antarctic fur seals (McCann, 1980) occasionally must leave their territories to cool off in the sea. Prior to invoking the extreme measure of territory desertion, otariids adopt a variety of behaviours that allow them to dump heat. They dissipate heat through conduction to a cooler substrate, such as wet rocks or sand near the seaward side of their territories. They also dissipate heat through convection by exposing their flippers to the air, by urinating on their flippers, by flipping damp sand onto their backs, and by wetting themselves in any surface water available on their territories. They reduce their thermal loading by reducing energy expenditures and by seeking areas on their territories which afford maximum shade. Finally, they store as much heat as possible in their bodies, and become visibly uncomfortable before finally abandoning their territories (Bartholomew and Wilke, 1956, Peterson and Bartholomew, 1967; Rand, 1967; Whittow *et al.*, 1971, 1972; Odell, 1974; Beentjes, 1989).

When exposed to conditions that approach or exceed their upper critical temperature, phocids employ a range of behaviours similar to those used by otariids. They change position to align their bodies with the sun, reduce their activity, move to areas of dampness and, in elephant seals, also flip damp sand over their bodies. For both phocids and otariids, the final defence is an escape into the sea (White and Odell, 1971; Whittow, 1978).

The need to remain close to the water, in order to retreat to it when necessary for thermoregulatory requirements, has implications for several aspects of the social structure of South American sea lions. At the Punta Norte breeding site, territories are placed linearly along the high tide mark of the shoreline, only one territory deep. The beach at this site is a homogeneous pebble surface and there are no thermoregulatory advantages to the females occupying any particular area of the beach. Here the territorial social structure has given way to males attempting to maintain groups of females by herding them (Campagna and Le Boeuf, 1988a). At another South

American sea lion breeding site, Puerto Pirámide, the substrate is not homogeneous and females gather by choice at certain sites with access to water. Males that hold these sites do not have to herd females, but rather need only to defend the wet territories in order to assure access to females. Hence the thermoregulatory demands of the females, combined with the availability of territories with different degrees of wetness, dictate a change in breeding structure from female sequestering to territorial defence (Campagna and Le Boeuf, 1988b).

The significant advantage of having a territory that includes a pool of water is seen in other species as well. It is essential for South Australian fur seal males to have access to water on their territories, if they are to remain on them continuously (Stirling, 1971). New Zealand fur seal males that had access to water on their territories achieved 82% of the 109 observed copulations (Gentry, 1973), although Miller (1975b) reported that the availability of fresh water had no effect on the tenure of territorial males. The generally cooler environment of the Antarctic fur seal is reflected in a reduced, although still observable, difference in copulation success among males, based on access to water on their territories (McCann, 1980).

The severe thermoregulatory strain fur seals can be under when on land is most clearly illustrated in the case of pups that are too young to avail themselves of the usual escape route of cooling off in the sea. Pups have the advantage of a relatively larger surface-to-volume ratio, and yet this is not always sufficient to prevent overheating. Galapagos fur seal pups that are exposed to high incident solar radiation experience operative temperatures above body temperature for 6–9 h each day (Limberger *et al.*, 1986). After continued exposure, skin temperature exceeds body temperature and the seal must reduce its incident radiation load. They do this by seeking shelter in the shade of boulders and in lava tunnels. Appropriate locations where mothers and pups can find shade are limited, and this leads to resting site competition between females and a reduced density of seals in the colonies during the pupping season (Limberger *et al.*, 1986). The distribution of Galapagos fur seals may be dependent on appropriate substrate, which provides shaded crannies, so that this member of a genus with its major distribution in the cool temperate to subantarctic climates can survive in a tropical climate (Bartholomew, 1966).

Galapagos fur seal pups run the risk of being washed out to sea when they venture as close to the cool water and wet rocks as they can, in order to have a cool substrate to which they can dump excess heat (Trillmich, 1984). The pups reduce their production of metabolic heat by curtailing their activity during the day and engaging in social play primarily at night and in the cool morning and evening (Limberger *et al.*, 1986).

The fur seal's pelage acts both as an insulator for the retention of body heat which is long wave-length radiation, and, somewhat, as an insulator against skin surface absorption of incident radiation which includes much more short-wavelength radiation. The surface of the fur can be as much as 20°C above the skin surface (Limberger *et al.*, 1986). Similar studies in harp seals (Øritsland, 1970) have shown that dark fur can be much warmer than the underlying skin surface temperature because the incident radiation is absorbed at the fur surface. Light fur allows the incident radiation to penetrate and heat the skin directly. Harp seals are able to control their peripheral circulation such that they can transport heat from areas of warmed skin to the central body mass for warming or they can dump heat to the ice substrate to maintain homeothermy (Øritsland, 1968). The newborn harp seal pup's primary thermoregulatory challenge is to conserve heat, although on bright, sunny days it sometimes needs to dissipate heat to the substrate. Basking in the sun can raise its skin temperature to 41°C (Øritsland and Ronald, 1978). The white lanugo of the pups is an effective absorber of shorter-wavelength radiation; the pups appear black when photographed with 300–400 nm ultraviolet bandpass filters (Lavigne and Øritsland, 1974).

Galapagos fur seals do not have a heat sink available so they have to limit the amount of heat absorbed from solar radiation. The more sparsely haired Galapagos sea lion is able to dissipate heat through both conduction and convection more easily and can stay on sandy beaches without shade, if there is sufficient wind. When the animals need to conserve heat they can rest in contact with each other and when they need to dissipate heat they can move further apart and lie singly (Trillmich and Trillmich, 1984).

California sea lions respond to increasing temperatures and incident radiation with a sequence of behavioural changes ranging from dispersal from close aggregations, to waving their flippers to enhance convective cooling, to movement to wet substrate for conductive and evaporative cooling, to final retreat into the sea (Odell, 1974). The change from one thermoregulatory behaviour to the next occurs in response to short-term changes in incident radiation rather than to more gradual changes in air temperature. White and Odell (1971) hypothesized that the closeness with which the behaviour of California sea lions and northern elephant seals tracked changes in incident radiation indicated that the rate of skin heating was the stimulus for behavioural modification, rather than the more slowly responding deep body temperature.

Weather plays a significant role in the haul-out behaviour of most species of pinnipeds. The time harp seals remain hauled out correlates more closely with the hours of sunshine than it does with wind speed or temperature. Weather has more effect on the haul-out

behaviour of female harp seals when they are not nursing than it does when they are (Stewart, 1987). The number of Weddell seals hauled out is negatively correlated with the wind velocity (Smith, 1965) and is also influenced by cloud cover, although the general diurnal pattern of hauling out is maintained (Tedman and Bryden, 1979; Thomas and DeMaster, 1983).

Haul-out patterns of walruses have been shown to correlate with weather conditions in a way that suggests this behaviour is influenced by thermoregulatory considerations. Animals at a terrestrial haul-out site tended to haul out when the temperatures were rising and tended to leave the haul-out site when temperatures were falling. They also left the land when it was snowing. During times of light drizzle the numbers on land remained constant and only increased during times of no precipitation (Salter, 1979). Wartzok and Ray (1980) reported that the numbers of walrus hauled out in a 1000 km² area of Bering Sea ice increased from 437 animals on the first day sampled after a storm to 1200 the next day to 9479 the third day as the winds progressively decreased and the amount of insolation progressively increased.

The occurrence of most active behaviours decreases in frequency as temperature increases. Exceptions are flipping sand, rolling in the sand and grooming. The first two are clearly related to convective and conductive dissipation of heat. Beentjes (1989) suggested that grooming in New Zealand sea lions was a response to increasing irritation of the skin during periods of intense solar radiation. New Zealand fur seals also show increased grooming during the summer (Johnstone and Davis, 1987).

Young northern fur seals experience thermal stress when they are in the water. The pup increases its layer of blubber slowly after birth and by 10 days the subcutaneous fat is only 3-4 mm thick and internal fat deposits are similarly small (Blix *et al.*, 1979b). The lower critical temperature in water for juveniles as large as 35 kg is 18°C, a temperature well above what the seals regularly encounter in the north Pacific. Hence they must always have a high metabolic rate in waters they customarily inhabit (Miller, 1978). Fur seal pups have a source of non-shivering thermogenesis in their muscle fibres (Grav and Blix, 1979). In addition, they have to engage in physical activity in order to maintain body temperature in waters cooler than 12°C (Kooyman and Davis, unpublished data quoted in Gentry *et al.*, 1986b). It is perhaps surprising that these animals have not acquired sufficient insulation so that they can survive in their typical habitats without needing to increase their resting metabolic rate and use additional heat of exercise to maintain body temperature, although sea otters appear to be in a similar situation (Costa and Kooyman, 1984).

Harp seals on the other hand have a wide thermoneutral zone, ranging from 1.8 to 28.2°C (Gallivan and Ronald, 1979). Their blubber layer allows them to maintain thermoneutrality over this range by controlling heat loss with no need for changing metabolic rate. The development of a blubber layer is a first priority for a newborn harp seal. Initially, the newborn has to rely on shivering and non-shivering thermogenesis. Brown fat is a source of non-shivering thermogenesis in a number of mammalian species (Smith and Horwitz, 1969). The newborn harp seal has this thermogenic fat in a subcutaneous layer along the back and at several sites internally, such as around the venus plexus in the neck and on the pericardium, kidneys and abdominal walls (Blix *et al.*, 1975). The brown fat provides a reservoir for thermogenesis that is under physiological control. The mitochondrial coupling between oxygen uptake and oxidative phosphorylation becomes 'looser' when thermogenesis is required (Pedersen and Grav, 1972). In pups of less than one day old, the mitochondria in the brown fat are loosely coupled and the brown fat is a major source of non-shivering thermogenesis. The importance of non-shivering thermogenesis in the young pup was shown by a two-fold increase in deep body cooling rate when a 4-day-old pup was injected with the beta-blocker, propranolol, which blocked non-shivering thermogenesis. In contrast there was no change in cooling rate when the pup was injected with curare which blocked shivering (Grav and Blix, 1976). By the time the pup is 10 days old, most thermogenesis occurs in dorsal subcutaneous tissue that is histologically intermediate between brown and white fat (Blix *et al.*, 1979a).

Non-shivering thermogenesis is critical for survival at several points in the pup's life. The first is immediately after birth when the pup's lanugo is still wet and has a conductance 15 times that of dry fur (Blix *et al.*, 1979a). A combination of shivering and non-shivering thermogenesis maintains core temperature until the moisture in the fur has frozen and fallen out, and the fur has dried. Thermogenic fat continues to maintain body temperature as the pup builds up its blubber stores through nursing. After a few days, the subcutaneous thermogenic fat is converted into normal insulative blubber (Blix *et al.*, 1979a) but the internal thermogenic fat stores remain to provide heat at the time the pups are weaned and enter the water for the first time (Blix and Steen, 1979). Harp seal pups greatly increase their blubber stores through nursing. The sculp weight increases from 30% of a total neonatal body weight of 10.8 kg to 60% of a total weaning body weight of 34.4 kg. Three-quarters of the 2.5 kg/day mass increase is in the sculp with almost all being accounted for by blubber increase (Stewart and Lavigne, 1980). Hooded seal pups, that have only 4 days in which to build up their blubber layers through nursing

(Bowen *et al.*, 1985), are born with a 3-cm thick layer of blubber and have shed their lanugo in utero (Blix and Steen, 1979).

The importance of an insulative blubber layer is seen most clearly by noting the body reserves used to maintain harp seal pups during their post-weaning fast. Rather than drawing exclusively from the blubber layer, core lipids and protein provide about half of the energy requirements during the first 2 weeks of the fast (Worthy and Lavigne, 1983). Grey seals also lose mass from both blubber and core during the post-weaning fast, with 70% of the mass loss taking place in the blubber and 30% in the core for seals fasting on land. In contrast to harp seals, grey seals showed differences in the relative proportions of mass loss from core and blubber depending on whether or not the youngsters were in the water during the fast. Grey seals fasting in water lost more mass from blubber and less from core than did grey seals fasting on land (Worthy and Lavigne, 1987).

Elephant seal pups can fast after weaning for 2.5 months, until their blubber stores are almost exhausted. During this time, the pups can develop their foraging skills. The blubber provides the elephant seal pup with a safe start in life; less than 1% of pups weaned in good condition die during the next 2.5 months before they leave the rookery (Reiter *et al.*, 1978). Harp seal pups utilizing core protein and fat are required to learn foraging techniques much more rapidly in order not to deplete either their limited core energy stores or their essential blubber layer (Worthy and Lavigne, 1983). Ringed seals also need to preserve their blubber layer after weaning. They lay down blubber during nursing in such a way that the ratio of blubber thickness to body radius is nearly constant over the entire body, with the exception of the hind part where the blubber is relatively thicker. During the transition from nursing to foraging, they can use blubber from this relatively 'over-insulated' area to supplement internal lipid and body core energy stores (Ryg *et al.*, 1988).

Galapagos fur seals use their blubber stores as a reserve so they can maintain a constant level of activity and play, in spite of variations in the attendance-absence cycle of their mothers dictated by foraging success on variable food resources (Arnold and Trillmich, 1985).

Several lines of evidence suggest that the pineal gland is involved in thermoregulatory control in young seals. Neonatal seals have pineal glands which are both large and active. The gland is relatively and absolutely larger in Weddell seals than in elephant seals and this correlates with the more severe thermoregulatory demands placed on the Weddell seal pup (Bryden *et al.*, 1986). In Weddell seal pups that are exposed to continual light, the pineal gland does not exhibit the normal cyclical patterns of activity. As the animal ages the gland becomes more cyclically active and assumes its traditional role in photoperiodic control of gonadotrophic activity of the hypothalamo-

hypophyseal system (Reiter, 1973). Elden *et al.* (1971) attribute the comparatively large pineal gland in mature northern fur seals to the need of these animals for precise timing of a number of events in the reproductive cycles such as establishment of breeding colonies, parturition, oestrus, and implantation.

5.10 MOULT

Pinnipeds experience an annual moult in which they shed all of their fur and, in some species (e.g. elephant seals, Laws, 1956a), portions of their epidermis. The physiological changes associated with moulting appear to have more of an influence on the behaviour of phocids than they do on otariids. Some animals lose much of their hair before new hair grows back, whereas other animals have a gradual loss with regrowth occurring simultaneously, so the animal is never without a coat. Two captive adult spotted seals showed that different individuals of the same species could experience the different moulting sequences. Although the sequence of hair loss and regrowth was different, the pattern of hair loss was similar, beginning on the lips, around the eyes and on the distal edges of the flippers and then advancing onto the neck, shoulders and abdomen, and, finally, onto the flanks, sides and back (Ashwell-Erickson *et al.*, 1986).

The hormonal changes associated with moulting were investigated in the harp seal by Riviere *et al.* (1977). They found that the initiation of hair loss corresponded with a drop in plasma T_4 and an increase in plasma cortisol. Reciprocal changes in T_4 cortisol occurred with the appearance of new hair. John *et al.* (1987) monitored changes in both triiodothyronine (T_3) and T_4 , and found that both increased during the moult. T_3 fell during the post-moult phase whereas T_4 remained high. They suggested that a high T_3/T_4 ratio was the best indicator of the initiation of moult. Free fatty acids reached their highest plasma levels during the moult. This lipid mobilization provided a source of metabolizable energy for the seals while they are hauled out during the moult.

Ashwell-Erickson *et al.* (1986) measured metabolic rate during the moult and found that in spotted and harbour seals the resting metabolic rate declined an average of 18.6% below its pre-moult level. Lowered metabolic rate means a reduced need to feed and this corresponds with the observation that many species of pinnipeds increase the proportion of the time they spend hauled out during moult. When seals are hauled out, blood flow to the skin increases and warmer skin temperatures are conducive to hair growth (Feltz and Fay, 1966; Ling, 1974). Concurrent with the decrease in resting metabolic rate was the fall in total serum T_3 and T_4 and a rise in

serum cortisol. The concentration of serum cortisol was at a maximum at the time serum T_3 and T_4 were at their minima. T_3 and T_4 increased to their maxima at the time of most rapid growth and emergence of new hair. The combination of histological, metabolic and hormonal measurements undertaken by Ashwell-Erickson *et al.* (1986) allowed them to estimate that the total time, from first descent of hair bulbs on the face to the final emergence of new hair on the back, required 4–6 months. Thus although the external signs of moult are limited to a few weeks, the animals are physiologically involved in moult for one-third to one-half of the year.

Engelhardt and Ferguson (1980) monitored T_3 , T_4 , cortisol and aldosterone during the moult of the lanugo in harp and grey seals, which takes place when the pups are about 3 weeks old. In the pups, levels of T_3 and cortisol were the best indicators of the initiation of the moult. Both hormones peaked at the onset of the moult. In addition, plasma levels of T_3 and T_4 were higher in the pups than in the adults.

Grey seal females moult at the beginning of February whereas the males moult in the middle of March (Bonner, 1972). Harp seal males and females moult at the same time and the animals haul out in denser aggregations than those seen during pupping and mating (Sergeant, 1976 unpublished manuscript referenced in Ronald and Dougan, 1982). Common seal males change their haul-out behaviour during moult, but the females do not. The males haul out every day during moult, while the females continue to spend large amounts of time at sea. Apparently, recovery of body resources following lactation is more important for females than is the acceleration of moult that can occur when they haul out and allow peripheral tissues to warm (Thompson *et al.*, 1989).

The only moult-related behavioural response seen in South African fur seals is an increase in the amount of time spent ashore. The animals do not show the ill humour and listlessness associated with moult in some phocids. They have the gradual replacement type of moult and throughout the moult maintain a water-repellent coat (Rand, 1967).

5.11 ORIENTATION

Few studies have addressed the question of sensory input for the orientation and navigation capabilities of marine mammals. James and Dykes (1978) studied the orientation of harbour seals toward the beach on Sable Island and concluded that they moved as though they could detect a magnetic meridian, that they could differentiate

between the N and S poles of this meridian, that their orientation on that meridian could be calibrated by the sound of the surf, that visual landmarks were used and that olfaction was unimportant. Oliver (1978) conducted a laboratory study of grey seals swimming through different obstacle courses in the dark. He showed that although they might use sound for orientation passively, there was a negative correlation between sound emission and improved navigational ability.

Three captive California sea lions, placed in enclosed cages and flown to a release site 115 km from their home facility, returned to the home facility. When the release site was 240 km away, two of the four released animals returned to the home facility. The release sites were primarily to the west of the home facility (Ridgway and Robison, 1985). New Zealand sea lions return to the same non-breeding site after extended absences (Beentjes, 1989).

Males and females of a number of species of land-breeding pinnipeds return to the same site year after year to mate and pup. Grey seal females return to almost the precise location from one year to the next. The median distance between locations where the females gave birth from one season to the following season was 18 m with a range of 14–51 m (Boness and James, 1979). Elephant seal females also show site fidelity, although females who are unsuccessful in weaning a pup one season are more likely to move to an alternate breeding site the following season (Reiter *et al.*, 1981). Young grey seals radiate out in all directions from their birth sites; some born in England have been recovered as far away as Spain. However, they all return to the site of their birth when they reach breeding age. No grey seal marked as a pup in one area was recovered as a breeding animal in another area (Bonner, 1972).

Even Weddell seals that do not have specific land features to which to return, but breed in the fast ice, return to the same general area from one year to the next, after spending the winter in the pack ice (Smith, 1965). Over 95% of tagged seals have been resighted in the area in which they were tagged. Of 35 tagged females with pups in 1966, 31 (89%) were resighted in 1967 at either the same colony or the next adjacent one. Females without pups tagged at a given colony are less likely to return to that colony the next year. Only 56% of 23 females tagged without pups in 1966 gave birth in 1967 in the colony where they were tagged or the next adjacent colony (Stirling, 1969). As pointed out by Croxall and Hiby (1983), site fidelity can only be proven if the proportion of the population returning to a given site is greater than would be expected if the tagged animals were distributed on a random basis in a subsequent year. Using this criterion, they showed that the population breeding at Signy Island shows some degree of site fidelity among the adult females, but no

fidelity is shown between where a pup is born and where it returns as a breeding adult.

Both male and female northern fur seals return to their breeding sites on St Paul Island with remarkable site fidelity. Of 18 marked bulls, the 12 that returned the second year and the 8 that also returned the third year, all occupied the same territories from one season to the next. Of 7 marked females, the greatest distance between birth sites from one year to the next was 18 m (Peterson, 1968).

The orientation and navigation mechanism employed by these pelagic animals to return to their specific breeding sites with such fidelity has not been investigated. Kajimura (1985) suggested that the migration pathways of northern fur seals are genetically programmed in broad outlines, and the seals feed opportunistically on prey along these migration pathways. An alternative suggestion is that larger oceanographic structural patterns determine where prey species are likely to be and the fur seals learn the location of these food resources. By moving along learned foraging pathways, the seals follow reasonably consistent migratory paths (Perez and Bigg, 1986). In addition to the annual migration to breeding areas, seals need to be able to return to defined points in the sea where foraging is successful. If seals are able to return to known, profitable foraging grounds, they will use much less energy on foraging trips than if they have to find prey concentrations anew each time (Loughlin *et al.*, 1987). This is particularly important for lactating females, that need to consume 1.5–1.8 times as much food as non-lactating females (Costa and Gentry, 1986; Perez and Mooney, 1986).

Walruses returning to terrestrial hauling-out sites often press their mystacial pads against the substrate as soon as they haul out. This behaviour would provide both olfactory and tactile cues for site recognition (Salter, 1979).

Some extraordinary feats of under-ice navigation have been reported for Weddell seals (Kooyman, 1968, 1981; Elsner *et al.*, 1970). Individuals of this species have demonstrated that they are capable of finding their way back to a given breathing hole after excursions of up to 6 km under sea ice 2 m thick. Early observations of these seals returning to holes from approximately the same direction as they left (Kooyman, 1968) have been confirmed by real-time acoustic tracking (Wartzok *et al.*, 1990), in which initial dives from a novel breathing hole produce a pattern that looks like spokes of a wheel whereas later dives yield increasingly open-loop dive patterns.

The importance of vision can be inferred from Kooyman's (1975) observation that seals prefer to dive during the day (58% of dives) rather than during darkness. The types of dives were also different between day and night, with no dives of over 50 min occurring

during the darkness, whereas 5% of the daylight dives were longer than this. The night dives were also shallower in general and, specifically for exploratory dives of greater than 20 min, night dives were only one-third as deep as daylight dives. Three times as many animals were observed hauled out during the night as during the day. At the time of the year when the sun is up for 24 h, the seals shift their diurnal activity pattern and rest during the day and dive during the period that would have been night.

Further evidence of the importance of vision in hole finding behaviour comes from acoustic tracking studies which have shown that the distance from a novel hole at which the animal turns toward it, and swims directly to it, matches the calculated visual detection distance based on light attenuation in the water column and laboratory-determined spectral sensitivity of seals (Wartzok *et al.*, 1989).

In addition to vision, other senses likely to be employed in under-ice orientation include hearing and vibrissal sensitivity. The ability of a blindfolded seal to orient toward, and apparently determine the range to, an acoustic stimulus has been demonstrated in both ringed seals and Weddell seals (Elsner *et al.*, 1989; Wartzok *et al.*, 1987; 1990). One Weddell seal used the vocalizations of conspecifics to direct her swimming for 4 km under continuous ice cover when she left an 'isolated' hole and returned to a seal colony (Wartzok *et al.*, 1990).

Blindfolded ringed seals do not appear to use all the potential information available from the vibrissae in locating holes through the ice (Elsner *et al.*, 1989). The vibrissae are well-developed, having ten times the innervation normally found in other mammals (Hyvärinen, 1989). Montagna (1967) suggested that one function of the vibrissae might be to detect the speed at which the seal was swimming. This would be a valuable piece of information for an animal that was navigating by dead reckoning. However, Renouf and Gaborko (1982) reported that a captive harbour seal was able to maintain a learned speed just as well after its vibrissae had been removed as it was before. Hyvärinen (1989) suggested that the vibrissae could sense sounds as well as compressional waves. The role of the vibrissae as current sensors and the role of currents in under-ice orientation remain to be investigated. The importance of sensory systems to pinniped behaviour is discussed more completely in Chapter 7 by Renouf.

5.12 CONCLUSION

The evolutionary history of pinnipeds as amphibious mammals has resulted in elaborations of basic mammalian physiological characteristics. However, these modifications are not as important as environmental factors in determining pinniped behaviour. The

initially surprising, but ultimately satisfying conclusion of this review is that, in spite of the physiological idiosyncrasies of pinnipeds, the models combining social structure, individual behaviours and environment which were developed for terrestrial mammals are equally applicable to pinnipeds.

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6

Reproductive and foraging energetics of pinnipeds: Implications for life history patterns

Daniel P. Costa

6.1 INTRODUCTION

In his classic treatise on the evolution of pinniped breeding systems, Bartholomew (1970) identified terrestrial parturition and marine feeding as prerequisites for the evolution of polygyny. Such spatial and/or temporal separation of feeding from reproduction is a fundamental component of the reproductive biology of all pinnipeds, regardless of their breeding system. Adaptation to this constraint has resulted in reproductive patterns that incorporate varying periods of time spent fasting on the rookery and feeding at sea (Bonner, 1984; Kovacs and Lavigne, 1986). This chapter will examine the partitioning of energy during lactation and its acquisition while foraging. In this way the fundamental relationship between the foraging ecology and reproductive pattern of pinnipeds can be examined. Information about feeding is difficult to acquire, and conclusions are often of necessity inferred from records from relatively new instruments like time/depth recorders. Previous to the development of this technology, our understanding of foraging was based on measures such as the animal's partitioning of time on land and at sea, and simple indices of feeding such as stomach content and scat analyses. Because of these constraints, much of what follows is speculative and must sometimes be based on a small number of species. However, it is hoped that these ideas will serve as a catalyst for future research as new methods are developed to acquire data while the animals are out of view at sea.

6.2 REPRODUCTIVE BIOLOGY

The Otariidae, the eared seals (sea lions and fur seals), and the Phocidae, or ear-less seals ('true' seals) will be addressed in this chapter. In both groups, young are conceived during the previous reproductive season and the embryo undergoes a period of delayed implantation that usually lasts 2-3 months. Actual fetal development then occurs over a 9-month period. During this time the mother is free to feed at sea continuously in the case of phocids, or intermittently for many of the otariids, which have not yet weaned their pups.

The major difference between otariid and phocid reproductive biology occurs after parturition. In those species of phocids in which mothers remain on the rookery continuously from the birth of their pup until it is weaned (Figure 6.1), milk must be produced from body reserves stored prior to parturition. Although some phocids, most notably harbour (*Phoca vitulina*), ringed (*Phoca hispida*) and Weddell (*Leptonychotes weddelli*) seals, feed during lactation, most of the maternal investment is derived from body stores (Testa *et al.*, 1989). Weaning is abrupt and occurs after a minimum of 4 days of nursing (in the hooded seal, *Cystophora cristata*, Bowen *et al.*, 1985) to a maximum of approximately 6-7 weeks (in the Weddell seal, Kaufman *et al.*, 1975; Thomas and DeMaster, 1983) (Table 6.1; and Chapter 3). In some species, like northern elephant seals (*Mirounga angustirostris*), the pup remains on or near the rookery fasting after it is weaned, soon thereafter developing feeding and diving skills (Reiter *et al.*, 1978). In other species like harp (*Phoca groenlandica*), or hooded seals, the weaned pups undergo a prolonged migration (Lavigne and Kovacs, 1988).

In contrast to these phocids, otariid mothers remain with their pups only during the first week or so following parturition (Figure 6.2). After the initial perinatal period the female returns to sea to feed, intermittently returning to suckle her pup which remains on the rookery (Bonner, 1984). Depending on the species, the mother spends between 1 and 7 days feeding at sea, then returns to her pup, which has been fasting, and suckles it for 1-3 days (Gentry *et al.*, 1986a). This period of intermittent suckling on the rookery and feeding at sea lasts from a minimum of 4 months in the polar fur seals (Antarctic, *Arctocephalus gazella*, and northern, *Callorhinus ursinus*) to up to 3 years in the equatorial Galapagos fur seal (*A. galapagoensis*) (Gentry *et al.*, 1986a). The remaining otariids are temperate and, in these species, pups are usually weaned within a year of birth (Table 6.1; and Chapter 3), although a significant number suckle their pups for an additional year or two depending upon species, location and environmental factors. In all pinniped



Figure 6.1 Northern elephant seal rookery at Año Nuevo, CA. Photo by author.

Table 6.1 For each pinniped the maternal mass, length of lactation, mass of the pup at birth in kg and relative to maternal mass, growth rate, given as the time to initially double their mass, and weaning mass in kg and relative to maternal mass. The values given in parenthesis under maternal mass are the mass of the female at weaning. The values given in parenthesis under the relative weaning mass, are the relative weaning mass calculated with maternal mass at weaning where data are available.

Species	Maternal mass (kg)	Lactation duration (days)	Birth mass			Weaning mass		
			kg	% maternal	time (days)	kg	% maternal	
Galapagos fur seal ¹	27	720	3.7	14	72	15.0	56	
Sub-Antarctic fur seal ²	55	300-330	4.7	9	49	16.2	29	
Antarctic fur seal ^{1,3,4}	39	117	5.2	13	62	15.8	48	
Northern fur seal ¹	37	118	5.5	15	85	12.9	35	
South African fur seal ¹	57	330	5.8	10	72	23.0	41	
New Zealand fur seal ¹⁸	35	300-365	3.6	10	79	13.4	38	
California sea lion ^{5,6}	85	300-365	8.2	10	79	39.1	46	
Galapagos sea lion ¹	80	180-365	6.0	8	45	25.0	31	
Australian sea lion ⁷	82	532	7.3	9	66			
Southern sea lion ⁸	121	360	12.8	11				
Steller's sea lion ⁹	273	300-365	17.9	7	47			
Ringed seal ¹⁰	62	41-48	4.5	7	25	9-12	19	
Harbour seal ¹¹	85	24	10.8	13	18	25.4	30	
Harp seal ¹²	130	12	10.8	8	5	33.0	25	
Ribbon seal ¹¹	[92]						(36)	
Grey seal ¹³	141	21-28	10.5	7	9	27-30	20	
	174	18	15.4	9	9	40.3	23	
	(106)						(38)	

(contd over)

Table 6.1 contd

Species	Maternal mass (kg)	Lactation duration (days)	Birth mass		Mean time (days)	Weaning mass	
			kg	% maternal		kg	% maternal
Hooded seal ¹⁴	179 (150)	4	22.0	12	3	42.6	24 (28)
Crabeater seal ¹¹	220	17, 28 12-18	20.0 33.6	9 13	5 10	94.6 85.1	43 34
Bearded seal ¹¹	250	38	13.4	5	10	67.0	25 (39)
Hawaiian monk seal ¹¹	265 (170)						
Weddell seal ¹⁵	447 (242)	53	24.0	5	12	108.0	24 (45)
Northern elephant seal ¹⁶	513 (292)	28	38.4	7	10	134.0	26 (46)
Southern elephant seal ¹⁷	506 (334)	22	42.7	8	12	115.5	23 (35)

¹ Gentry *et al.*, 1986b; ² Kerley, 1985; ³ Dodge *et al.*, 1986; ⁴ Costa *et al.*, 1988; ⁵ Oftedal *et al.*, 1987; Higgins, unpubl.; ⁶ Oftedal *et al.*, 1987^b; ⁷ Higgins *et al.*, 1988;¹⁰ Frost and Lowry, 1981;¹¹ Kovacs and Lavigne, 1986;¹² Stewart and Lavigne, 1984;¹³ Fedak and Anderson, 1982;¹⁴ Bowen *et al.*, 1985;¹⁵ Tedman and Green, 1987; ¹⁶ Costa *et al.*, 1986;¹⁷ McCann *et al.*, 1989;¹⁸ Mattlin, 1978.



Figure 6.2 An Antarctic fur seal mother and pup at South Georgia Island, South Atlantic. Photo by author.

species, postnatal male parental investment is non-existent and twins are exceptionally rare.

Differences between the reproductive pattern of phocid and otariid seals in part relate to the amount of stored energy at parturition, in so far as most phocids studied are capable of storing what is required for the entire lactation interval, whereas otariids must feed during the lactation interval. The differences in the reproductive strategies of phocids and otariids are reflected in the amount of time spent nursing the pup versus the time spent feeding at sea, and are dependent on a number of variables, including maternal energy/nutrient investment, maternal mass, metabolism and energy stores, duration of the lactation interval, milk composition, trip duration and distance to the foraging rounds. Unfortunately, for many of these parameters quantitative data are limited and often incomplete. This chapter will synthesize the existing data to point out trends and relationships to stimulate interest and further research in this area. In this way these ideas can be tested or more appropriate ones generated as additional data become available.

6.3 MATERNAL INVESTMENT

How do the different lactation patterns of pinnipeds compare with respect to investment in offspring? Maternal energy/nutrient investment can be divided into prenatal and postnatal investment. Comparison of neonatal mass and maternal mass for 10 otariids (ranging from the 27 kg Galapagos fur seal to the 273 kg Steller's sea lion (*Eumetopias jubatus*), and 11 phocids (ranging from the 62 kg ringed seal to the 513 kg northern elephant seal) suggests that relative pup mass at parturition is a similar proportion of maternal mass for both groups (Figure 6.3; and Bowen Table 3.3 this volume). This is not totally unexpected since the timing and patterning of fetal development is essentially the same in both families (Bonner, 1984). However, as detailed earlier, the pattern and timing of postnatal investment is strikingly different, and it is here that we find significant differences in maternal investment.

One index of postnatal investment is weaning mass. There does not appear to be a difference in weaning mass as a percentage of maternal mass between phocids and otariids (Table 6.1 and Chapter 3). Weaning mass by itself masks fundamental differences in the reproductive patterns of these families, most notably differences in the duration of investment, changes in maternal mass and body composition of the pup at weaning. Differences in the duration of lactation lead to overestimates of phocid investment and underestimates of otariid investment. Furthermore, weaning mass does not

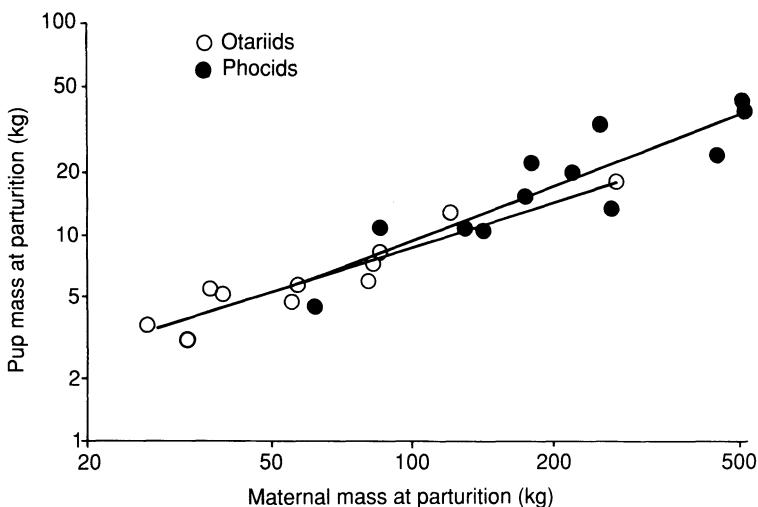


Figure 6.3 Pup mass at parturition plotted as a function of maternal mass for 12 phocids and 11 otariids; $r = 0.95$. Data are from Table 6.1

necessarily reflect maternal investment, since there may be differences in the behaviour or metabolic rate of pups that alter how efficiently they use maternally derived resources. Although phocids are weaned at an earlier age, they are not truly nutritionally independent at that time in so far as they rely on maternally derived energy, stored as blubber, for weeks or months after weaning. In contrast, otariid pups are weaned much later, and are not as reliant on stored reserves maternally derived prior to weaning. The longer lactation interval of otariids requires that more energy be supplied to the pup to support its maintenance metabolism. Perhaps for this reason, many otariid pups begin to feed prior to weaning and may therefore be nutritionally independent when weaning occurs. Nonetheless, it seems likely that otariid mothers must invest more total energy into their pups than phocid mothers in order to achieve an equivalent relative weaning mass.

A comparison between northern elephant seals and northern fur seals illustrates this point. Northern elephant seal pups are nursed over a 28 day lactation interval and are weaned at 26% of maternal mass. After weaning, pups remain on the beach fasting for 2.5 months (Reiter *et al.*, 1978) and then go to sea to feed after losing approximately 30% of their mass at weaning (Kretzmann, unpub. obs.). Therefore pups are not nutritionally independent until they are at least 3.5 months of age (Ortiz *et al.*, 1978) and by this time weigh 18% of maternal mass. Northern fur seal females suckle their pups over a 4-month period and wean them at 35% of maternal mass. At or near weaning, northern fur seal pups have begun to feed and thus

may be considered nutritionally independent at this time. Therefore, northern fur seal pups may be proportionately larger at nutritional independence than northern elephant seal pups.

An interesting aspect of this comparison is that even though suckling is ongoing for 118 days, northern fur seal females are on the rookery only 27% of the time for a total of between 31 and 35 days (Gentry and Holt, 1986). The time fur seal mothers are available to their pups is surprisingly similar to the 28 days northern elephant seal mothers nurse (Table 6.1). The similarity in time available for suckling but difference in relative weaning mass implies that maternal investment may be greater in northern fur seals. This follows because fur seal pups require more energy to support their greater maintenance metabolism, resulting from the longer lactation interval. In addition, fur seal females expend more energy making multiple trips from the rookery to the foraging grounds.

Another problem with comparisons of otariid and phocid weaning weights is that there are few species where mass at weaning is known for both mother and pup (i.e. data collected on matched mother-pup pairs). Conclusions based on comparisons of relative weaning mass made with unmatched data sets (i.e. pup weaning mass data collected separately from data on maternal mass) may be misleading because of the tremendous variation in maternal body size and pup size within a species. For example, at parturition southern elephant seal (*Mirounga leonina*) females range from 346 to 803 kg and Antarctic fur seal females range from 26 to 53 kg (Costa *et al.*, 1988; McCann *et al.*, 1989). This relationship is further confused by the very large mass lost by some phocid females during lactation. For example, at the end of lactation northern elephant seal females weigh 42% of their post-parturient mass, grey seals (*Halichoerus grypus*) 63% and Weddell seals 54% (Costa *et al.*, 1986; Fedak and Anderson, 1982; Tedman and Green, 1987). Such changes in mass over the lactation interval raise the question as to which maternal mass should be used to determine the relative mass of the pup at weaning. For the seven phocid species for which there are data, weaning mass is only 26% of maternal mass at parturition but 38% of maternal mass at weaning (Table 6.1).

For these reasons conclusions based on relative weaning mass of phocids and otariids are risky, considering the inadequacy of the available data and the potential errors associated in calculations of relative weaning mass. This is especially true if calculations are derived from data which include pups of small mothers as well as non-lactating, immediately postpartum or unrepresentatively large females. Finally, weaning mass can obscure differences in growth rate that are due to variations in the metabolic efficiency of different species or sexes. For example, pups with high mass-specific metabolic

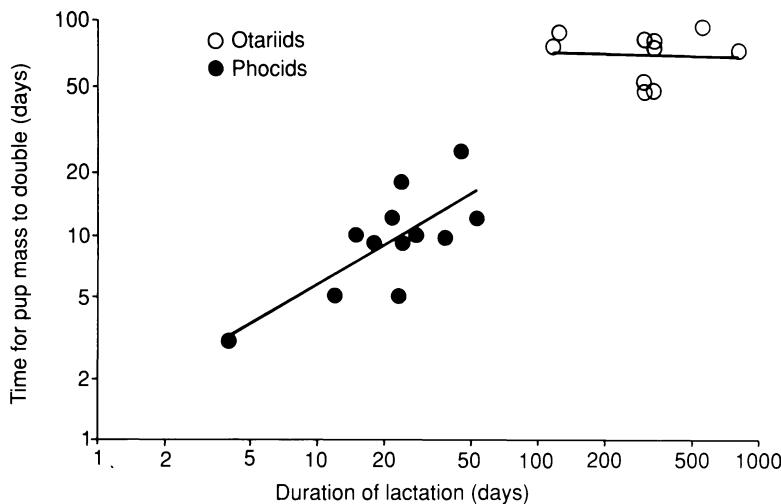


Figure 6.4 Growth rate expressed as the time required for pups to double their mass is plotted as a function of the length of the lactation interval. Data derived from Table 6.1.

rates have lower weaning masses for an equivalent amount of maternal investment, because a higher proportion of the maternal energy is required by this higher metabolism.

6.3.1 Pup growth rate

Given the problems associated with using relative weaning mass as a measure of maternal investment, a more informative comparison might be made by examining growth rate. Problems pertaining to imprecise data on maternal mass can be avoided by exploring the patterns associated with the length of time required for pups to double their mass. Data of this type are available for 22 species and indicate that phocids grow significantly faster than otariids (Mann Whitney U -test, $p < 0.001$, $U = 120$). On average phocids double their mass in the first 8 days, whereas otariids double their mass in the first 66 days (Table 6.1).

Doubling time is shorter in phocids than in otariids (Table 6.1), but is there an association between doubling time and lactation duration? Interestingly, there appears to be in phocids ($p < 0.05$, $r = 0.62$) whereas no such relationship exists for otariids ($p > 0.1$, $r = 0.008$) (Figure 6.4). Furthermore, a pattern exists between lactation duration and breeding habitat in phocids (Kovacs and Lavigne, 1986). The shortest lactation interval and fastest growth rates occur in pack ice breeding seals such as hooded and harp seals (Figure 6.5). The longest lactation intervals are found in fast ice breeding Weddell and ringed seals, with island-breeding seals intermediate. Pack ice is a very

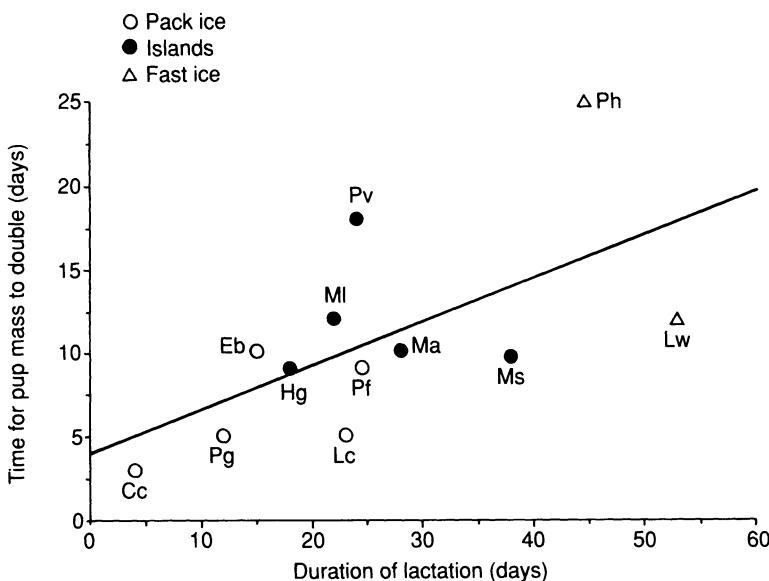


Figure 6.5 Growth rate of phocid pups, expressed as doubling time are plotted as a function of lactation duration and the type of breeding substrate. C.c., hooded seals (*Cystophora cristata*); P.g., harp seals (*Phoca groenlandica*), H.g., for grey seals (*Halichoerus grypus*); M.l., southern elephant seal (*Mirounga leonina*); M.a., northern elephant seals (*Mirounga angustirostris*); M.s., Hawaiian monk seals (*Monachus schauinslandii*); E.b., bearded seal (*Eignathus babatus*); P.f., ribbon seal (*Phoca fasciata*); P.v., harbour seal (*Phoca vitulina*); L.c., crabeater seals (*Lobodon carcinophagus*); P.h., ringed seal (*Phoca hispida*); L.w., Weddell seals (*Leptonychotes weddellii*). Where doubling time (days) = $3.94 - (\text{lactation duration (days)} \times 0.263)$ and $r = 0.61$.

unstable breeding substrate and can disappear at any time. Therefore the shortened lactation interval of pack ice seals would ensure that the pup is weaned prior to the break up of the pack (Bowen *et al.*, 1985; see Chapter 3). Island breeding seals that feed far offshore like elephant and grey seals may not be able to feed during the lactation period because the food resource is too distant. In this case there would be a significant advantage in concentrating the investment interval to reduce metabolic overhead (Fedak and Anderson, 1982; see Section 6.3.4). The shorter the lactation period the greater the proportion of stored maternal resources that can go into milk production and not maternal maintenance metabolism.

The longer lactation interval of Weddell and ringed seals which breed on stable fast ice and the island-breeding harbour seal require a different explanation. Fast ice breeders and harbour seals could augment their maternal reserves by feeding since prey are nearby (i.e. directly below or immediately offshore) (Testa *et al.*, 1989). A small amount of feeding could allow the investment duration to increase

slightly. If food is nearby, short feeding trips could be made during lactation and thereby decrease the pressure to concentrate the investment interval and reduce metabolic overhead. However, it is unlikely that such short-duration feeding trips could supply sufficient energy to support the rapid growth rates of phocid pups. It is likely that most of the energy and materials supplied to the pup are derived from maternal body reserves and that feeding during lactation is an augmentation of the maternal energy budget. Further research is needed to determine the importance of feeding during lactation in these species. For example, a recent study on Weddell seals indicates that some females feed during lactation whereas others do not (Testa *et al.*, 1989). Feeding while lactating has the advantage of providing the pup with the opportunity of learning foraging skills from the mother.

Comparisons of weaning mass and growth rate alone obscure important differences in pinniped maternal investment. For example, growth in phocid young primarily takes the form of adipose tissue with proportionately little growth in lean tissue while otariids put on lean mass during the lactation interval (Bryden, 1968; Worthy and Lavigne, 1983; Ortiz *et al.*, 1984; Oftedal *et al.*, 1987a). Furthermore, the longer dependency period of otariid pups requires greater utilization of energy by the pup for its maintenance. This diverts energy from growth and requires that otariid mothers provide more energy for an equivalent relative mass at weaning. Also a greater amount of energy is expended in transit to and from the foraging grounds by otariid females.

A more informative comparison of maternal investment relies on measurements of energy provided to the pup in the form of milk. Two methods have been used to estimate milk intake of pinniped young. The first method calculates milk intake necessary to meet the pup's estimated energy metabolism and measured growth over lactation. This method has been used to estimate milk consumption over the entire lactation interval for harp seals (Stewart and Lavigne, 1984), grey seals (Fedak and Anderson, 1982; Anderson and Fedak, 1987) and hooded seals (Bowen *et al.*, 1987). The other method measures milk intake of suckling pups by following the decline of either tritiated or deuterated water (Costa, 1987; Oftedal and Iverson, 1987). This method has been used in northern elephant seals (Ortiz *et al.*, 1984, Costa *et al.*, 1986), northern fur seals (Costa and Gentry, 1986), California sea lions (*Zalophus californianus*, Oftedal *et al.*, 1987a), Weddell seals (Tedman and Green, 1987), Steller's sea lions (Higgins *et al.*, 1988) and Antarctic fur seals (Costa and Croxall, 1988). This method uses the relationship between total water influx determined with labelled water and the oxidative water produced from the pup's maintenance metabolism. Milk consumption can

then be calculated since the water content of milk is known. This procedure requires that the pup obtain all of its exogenous water from its mother's milk. In all of the above investigations, other water sources were negligible. Furthermore, validation studies have found no significant difference between measured amounts of milk fed to 8 captive northern fur seal pups and that estimated from the isotope water dilution method (Costa, 1987). These data are discussed in relation to overall investment in offspring, maternal body size, mass and metabolism, foraging trip duration, and variation in milk composition in the following sections.

6.3.2 Total energy and nutrient investment

Of ultimate importance are the total energy and material invested in the pup. Phocids offer the best system to estimate total maternal investment, because the investment period is brief, the young are completely dependent upon maternal provisioning until they are weaned and the transition from dependence to independence is abrupt.

Total maternal investment has been reported for a variety of phocid seals, including harp (Stewart and Lavigne, 1984), grey (Fedak and Anderson, 1982; Anderson and Fedak, 1987) hooded (Bowen *et al.*, 1987), Weddell (Tedman and Green, 1987) and northern elephant seals (Ortiz *et al.*, 1984; Costa *et al.*, 1986), but only portions of the investment interval have been measured in otariids such as northern (Costa and Gentry, 1986) and Antarctic fur seals (Costa and Croxall, 1988), California (Oftedal *et al.*, 1987a), and Steller's (Higgins *et al.*, 1988) sea lions. However, a significant complication in measurements of total investment in pinnipeds is that during the course of lactation the rate of milk ingestion and the composition of the milk may change as the pups get older (Costa and Gentry 1986; Oftedal *et al.*, 1987b). Measurements of milk intake in otariids is difficult because the lactation interval is prolonged and in many cases weaning is gradual and pups may begin to feed on their own prior to weaning. Certainly more research is needed before conclusions regarding total maternal investment in otariids can be made. However, a preliminary approximation of the total energy and material invested by otariid females can be made by multiplying mean daily milk intake over the entire lactation interval by the length of the lactation period (Table 6.2).

Comparison of total energy investment into phocid or otariid young shows that, relative to their body mass, otariids invest more energy and protein in their offspring than phocids (Figures 6.6 and 6.7). It appears that the otariid strategy promotes lean growth early, whereas phocids defer lean growth until after weaning and nutritional

Table 6.2 The data on maternal mass, period of maternal investment, mean milk consumption of the pup per day of lactation used to calculate total maternal investment in terms of energy and protein are given for each species. Data on maternal mass, lactation duration and total energy and protein invested by mothers in the pup are given

	Maternal mass (kg)	Lactation duration (days)	Milk energy (MJ/d)	Total maternal investment in pup			
				Energy MJ	Energy MJ/kg	kg	Protein g/kg
Harp seal	135	12	67.3	810	6	3.2	2 (2)
Grey seal	174	18	70.8	1270	7	6.4	37 (3)
Hooded seal	179	4	203.0	680	4	1.4	1 (5)
N. elephant seal	504	28	96.3	2700	5	18.0	36 (4)
Weddell seal	447	45	73.7	3320	7	14.2	32 (6)
Antarctic fur seal	39	117	10.5	1240	31	7.6	192 (7)
Northern fur seal	37	125	8.6	830	22	5.9	159 (1)
California sea lion	85	300	10.2	3050	36	17.2	202 (8)
Steller's sea lion	273	330	21.0	6930	26	55.8	204 (9)

Numbers in parentheses are the sources for the data as follows: (1) Costa and Gentry, 1986; (2) Stewart and Lavigne, 1984; (3) Fedak and Anderson, 1982; (4) Costa *et al.*, 1986; (5) Bowen *et al.*, 1985, 1987; (6) Tedman and Green, 1987; (7) Costa and Croxall, 1988; (8) Oftedal *et al.*, 1987a; (9) Higgins *et al.*, 1988.

independence. It is important to consider that this comparison includes only the energy provided to the offspring and does not consider the cost of its acquisition and processing.

6.3.3 Effect of latitude on total investment in pinnipeds

Both otariids and phocids have adjusted to latitudinal differences in the length of the reproductive season. In each family the total amount of energy invested in the young is a surprisingly similar proportion of adult body mass, and appears relatively independent of latitude or the length of the breeding season. Even though the two subpolar otariids, the northern and Antarctic fur seal, have shorter reproductive seasons (4 months) than the temperate Steller's and California sea lions (10–12 months), total energy investment follows a consistent relationship with maternal body mass (Figure 6.6). A similar pattern exists for phocids. Even though the duration of lactation is considerably shorter in pack ice breeding species such as the hooded (4 days) and harp seal (12 days), the total energy delivered to the offspring is quite similar to that for the longer lactation intervals of the Arctic to sub-Arctic grey seal (18 days), temperate elephant seal (28 days), and Antarctic Weddell seal (45 days) (Table 6.2).

This ability to compensate for differences in the length of breeding

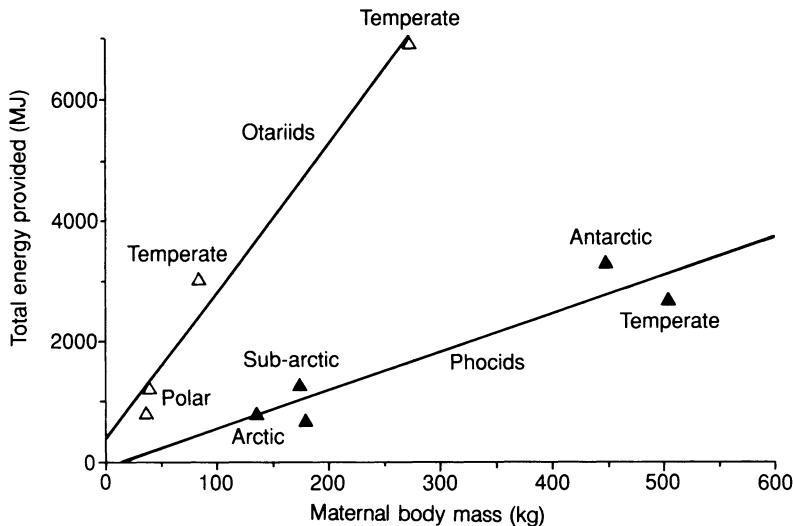


Figure 6.6 Total energy provided to pups is plotted as a function of maternal mass in otariids (open triangles) and phocids (solid triangles). The two regression lines are the least-squares linear fit for the otariid and phocid data. Latitudinal gradients are given for each group. High-latitude species have shorter lactation periods than low-latitude species. Data are from Table 6.3. The breeding latitude for the various species is given to illustrate that investment is independent of breeding latitude.

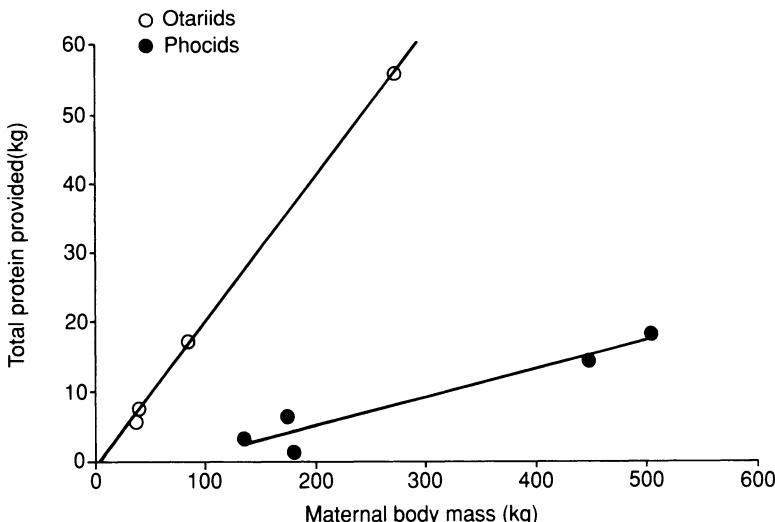


Figure 6.7 Total protein provided to pups is plotted as a function of maternal mass in otariids and phocids. The regression lines are least-squares linear fit for the phocid and otariid data, where for otariids protein intake (kg) = (maternal mass (kg) × 0.209) - 1.04, $r = 0.95$ and $p < 0.05$.

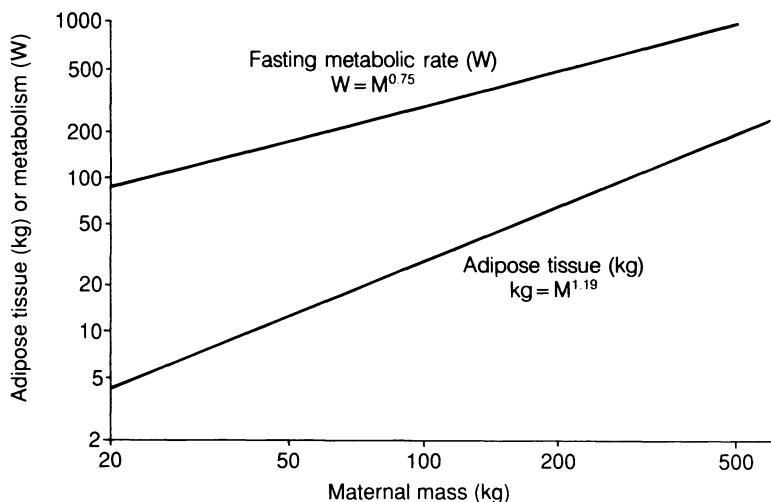


Figure 6.8 The theoretical relationship between fasting metabolic rate (W) and adipose tissue content (kg) is plotted as a function of maternal body mass (kg) for a typical phocid female. Fasting metabolic rate scales with body mass raised to the power 0.75, and adipose tissue scales with body mass raised to the power 1.19.

season without alteration in total energy investment is made possible by lactation. As will be developed later, lactation allows pinnipeds to concentrate the energy content of their milk independent of prey type or breeding pattern. It is interesting that the length of the breeding season appears to be genetically fixed. For example, small populations of Antarctic and northern fur seals breed in temperate habitats but wean their pups at 4 months of age, while sympatric otariids wean their pups close to 1 year of age (Gentry *et al.*, in manuscript; Kerley, 1985).

6.3.4 Body size and maternal resources

It is clear from the previous sections that there are distinct differences in the patterning of maternal energy expenditure and resources among the Pinnipedia. The following section will examine the physiological mechanisms that enable these different maternal investment patterns. Fedak and Anderson (1982) defined the amount of energy expended to maintain the female while she is onshore with her pup as metabolic overhead. The smaller this component the greater the proportion of body stores that can be devoted to the pup. If all other parameters are constant, metabolic overhead should increase with increasing body size, but at a lower rate of increase ($M^{0.75}$) than the amount of energy stored as adipose tissue ($M^{1.19}$) (Calder, 1984). Such a relationship for a hypothetical pinniped is seen

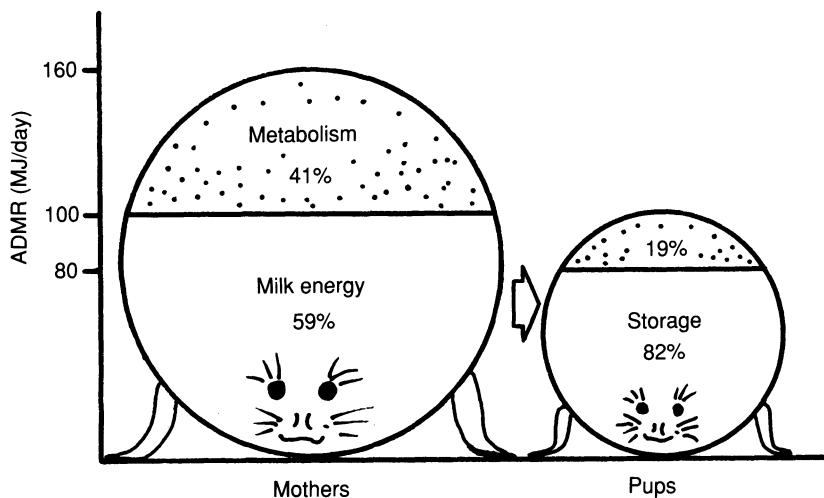


Figure 6.9 Total energy budget of a typical northern elephant seal mother is graphically divided between the energy expended on her maintenance metabolism and that contained in the milk fed to the pup. The pup's total energy budget is divided between energy storage and that utilized for maintenance metabolism. Figure drawn by A. C. Huntley from data in Costa *et al.*, 1986.

in Figure 6.8. From the above argument it would seem that the phocid maternal investment strategy would favour large body mass. A large female could store proportionately more adipose tissue than a small female and she would have a proportionately lower fasting metabolic rate. Large size would allow her to store the energy necessary to produce milk for her pup to achieve nutritional independence without having to feed to supplement her body stores, thereby reducing transit costs, predation risk, etc. A low fasting metabolic rate would ensure a low metabolic overhead, which would increase the proportion of maternal energy stores that can be transferred to the pup as milk. Such a pattern has been reported in northern elephant seals, where 59% of the female's total energy expenditure during lactation is in the form of milk provided to her pup (Figure 6.9; Costa *et al.*, 1986).

We might expect a greater premium on a lower fasting metabolic rate, greater maternal body mass and greater adipose stores in those phocids which fast during lactation. This would allow all of the material necessary to suckle the pup to come from maternal body reserves. Interestingly, female phocids (median mass 223 kg, range 55–513 kg, $n = 17$ species) are considerably larger than female otariids (median mass 57 kg, range 27–283 kg, $n = 15$ species). Therefore, based on size alone phocid females can store greater amounts of adipose tissue and have a lower mass-specific metabolism. Furthermore,

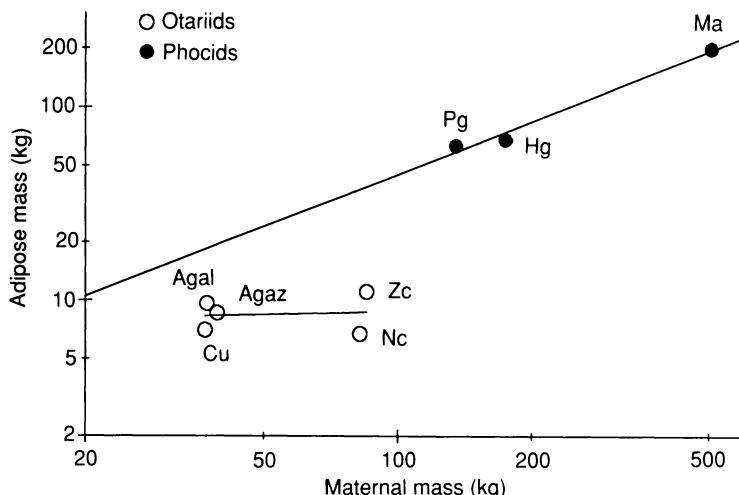


Figure 6.10 Adipose mass is plotted as a function of maternal body mass for three phocids and five otariids. Lines represent least-squares linear regression for each group. Data for grey seals (H.g.) from Fedak and Anderson (1982), harp seals (P.g.) from Stewart and Lavigne (1984), northern elephant seals (M.a.) from Costa *et al.* (1986), Antarctic (A. gaz.) and Galapagos (A. gal.) fur seals from Costa and Trillmich (1988), northern fur seals (C.u.) from Costa and Gentry (1986), California sea lions (Z.c.) from Costa *et al.* (1990) and Australian sea lions (N.c.) from Costa *et al.* (1989).

phocids have greater adipose stores per kilogram body mass than otariids (Figure 6.10). At parturition otariid females are composed of 8–26 % fat whereas phocid females are composed of 40–50% fat. Costa and Trillmich (1988) suggested that this is a major factor enabling phocids to fast during lactation and thus devote a larger proportion of maternal energy stores and nutrients to their pup.

6.3.5 Maternal metabolism

Given the larger lipid reserves, phocid mothers are able to store more energy than otariid mothers. In addition, the smaller size of otariid females predicts that not only do they carry smaller energy reserves, but that they should utilize their lipid reserves at a greater rate due to their higher mass-specific metabolic rate. Unfortunately data available to test this hypothesis are limited and are complicated since they were not acquired using comparable techniques. For example, metabolic rate measurements using labelled water methodologies are available for 4 otariids and only 1 phocid (Australian sea lions, *Neophoca cinerea*, northern, Antarctic and Galapagos fur seals and northern elephant seals; Costa *et al.*, 1989a, 1989b; Costa and Trillmich, 1988; Costa and Gentry, 1986; Costa *et al.*, 1986). Metabolic rates estimated from mass change are available for two

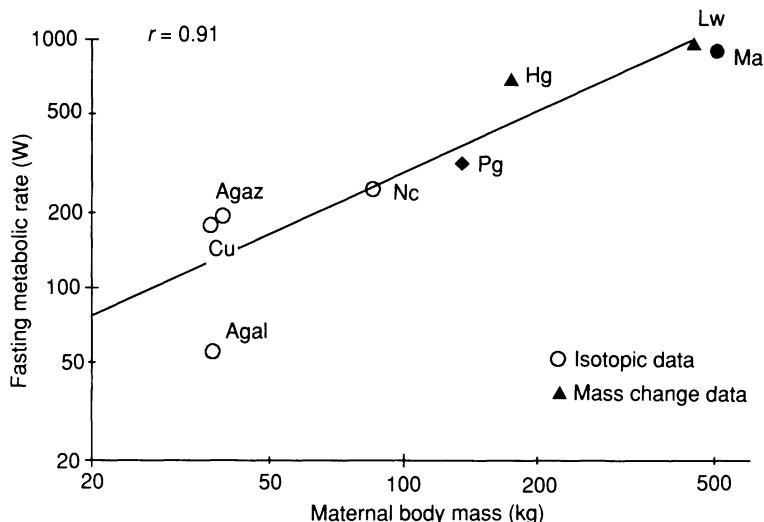


Figure 6.11 Fasting metabolic rate plotted as a function of maternal body mass for four phocids (solid symbols) and four otariids (open symbols). Data given as circles represent measurements made using labelled water methodologies taken from Costa and Gentry (1986), for northern fur seals (C.u.); from Costa and Trillmich (1988) for Antarctic (A. gaz.) and Galapagos fur seals (A. gal.), from Costa *et al.* (1986) for northern elephant seals (M.a.) and from Costa *et al.* (1989b), for Australian seal lion (N.c.). Measurements derived from mass change data are given as triangles for grey seals (H.g.) taken from Fedak and Anderson (1982) and for Weddell seals (L.w.) taken from Tedman and Green (1987). The diamond represents an estimated value for harp seals (P.g.) taken from Stewart and Lavigne (1984). Lines represent least-squares linear regression for the entire group with the exception of the Galapagos fur seal (A. gal.) and harp seals.

phocids (grey and Weddell seals; Fedak and Anderson, 1982, 1987; Tedman and Green, 1987).

Differences in ambient temperature profoundly influence onshore metabolic rate in fur seals. For example, Galapagos fur seal females in the warm equatorial environment exhibited fasting metabolic rates on land that were only 1.1 times the predicted basal metabolic rate (BMR) (Costa and Trillmich, 1988; see Chapter 5), whereas, northern and Antarctic fur seals, inhabiting the cold subpolar environment, exhibited metabolic rates 3.4 times the predicted basal rate (Costa and Trillmich, 1988; see Chapter 5). Northern elephant seals lactating in temperate northern California, on the other hand, exhibited metabolic rates that were 2.4 times predicted basal (Costa *et al.*, 1986). However, with the exception of the Galapagos fur seal, when taken together and plotted as a function of body mass there does not appear to be an intrinsic difference in maternal metabolism between phocids and otariids (Figure 6.11). As expected by metabolic scaling, mass specific metabolism is lower for larger pinnipeds than

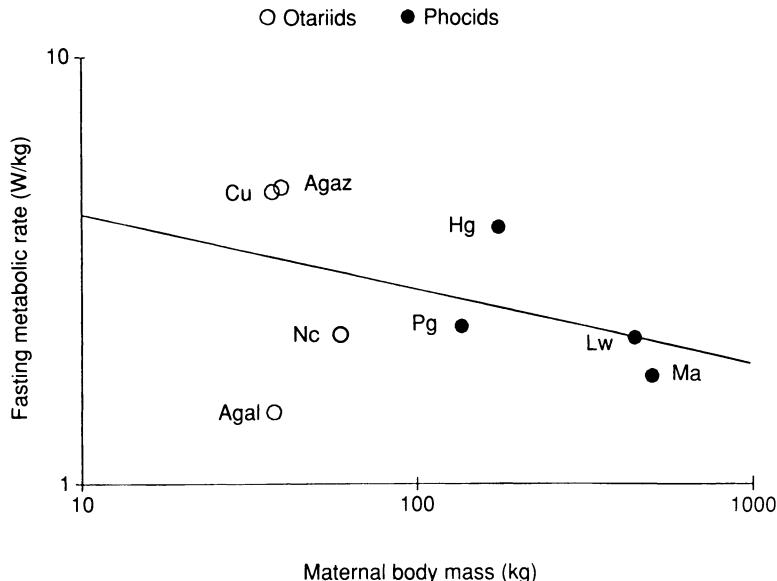


Figure 6.12 Data on fasting metabolic rate for the pinnipeds in Figure 6.11 are plotted on a mass-specific basis.

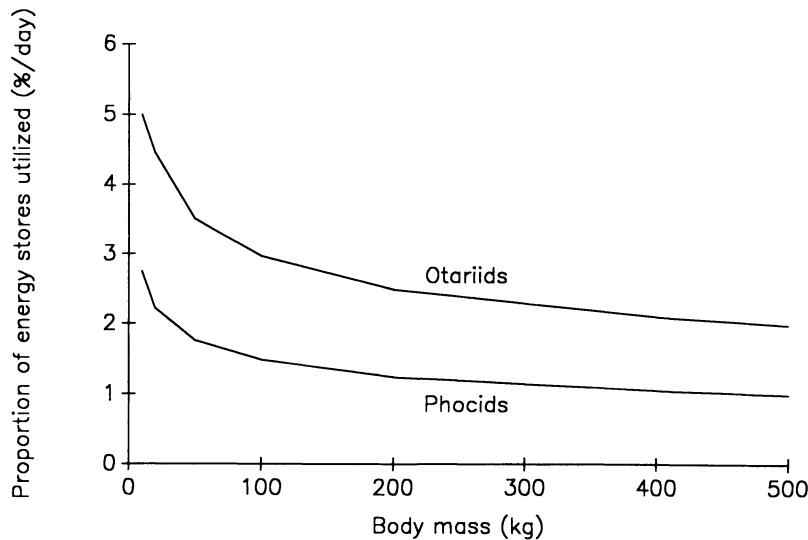


Figure 6.13 The theoretical metabolic overhead given as the proportion of the fat stores that would be utilized per day spent fasting are plotted as a function of maternal body mass (a phocid composed of 40% fat and an otariid composed of 20% fat). The metabolic rates were taken from the least-squares relationship given in Figure 6.11.

smaller pinnipeds (Figure 6.12). Therefore just due to the larger size of phocids, as a group, they exhibit lower mass-specific metabolic rates than otariids. The ultimate consequence of large body mass and low metabolic rate is the ability to reduce the metabolic overhead during fasting. Metabolic overhead, which can be assessed as the relative proportion of energy stores utilized per day fasting declines in a non-linear manner with decreasing mass (Figure 6.13). This implies that smaller pinnipeds have a disproportionately higher metabolic overhead as a result of differences in mass. Furthermore, phocids have a lower metabolic overhead due both to their greater adipose stores and their larger size than otariids. Most otariid females are smaller than 100 kg (only Steller's and Hooker's, *Phocarctos hookeri* and southern *Otaria byronia* sea lion females are larger than 100kg), whereas most phocid females are larger than 100 kg. It is interesting that the ringed seal, the smallest phocid at 62 kg, apparently feeds during lactation (Frost and Lowry, 1981). From Figure 6.13 it can be seen that the ringed seal's small body size would cause it to have a metabolic overhead 2–3 times that of larger phocids. It is likely that due to its small size it is incapable of storing all of the energy and material required for successful lactation. Successful reproduction may then require augmentation of the maternal energy budget by feeding during lactation.

It is important to note that metabolic rates are also affected by activity. Decreases in onshore metabolism may be achieved by reductions in activity by both phocids and otariids and by apneustic breathing in phocids (Costa *et al.*, 1986; Costa and Trillmich, 1988).

In summary, the ability of phocid seals to store most if not all of the maternal energy and nutrients prior to arriving onshore appears to be related to their large body size, low metabolic overhead and their greater lipid reserves.

6.3.6 Energy investment and trip duration

So far the total amount of energy invested in the offspring has been examined, but this ignores differences in the timing and patterning of energy and nutrient investment. For example, many phocids fast throughout the lactation interval, whereas otariid females spend 0.5–7 days at sea foraging between visits to suckle the pup on the rookery (Table 6.1). How do otariid mothers modify the timing and patterning of energy and nutrient investment to accommodate for such different trip durations?

A plot of trip duration and mass-specific energy delivery per trip indicates that otariid mothers that make short feeding trips provide their pups with a lower amount of energy than mothers that make long trips ($r = 0.934$, $n = 4$, $p < 0.10$) (Figure 6.14). Such a pattern

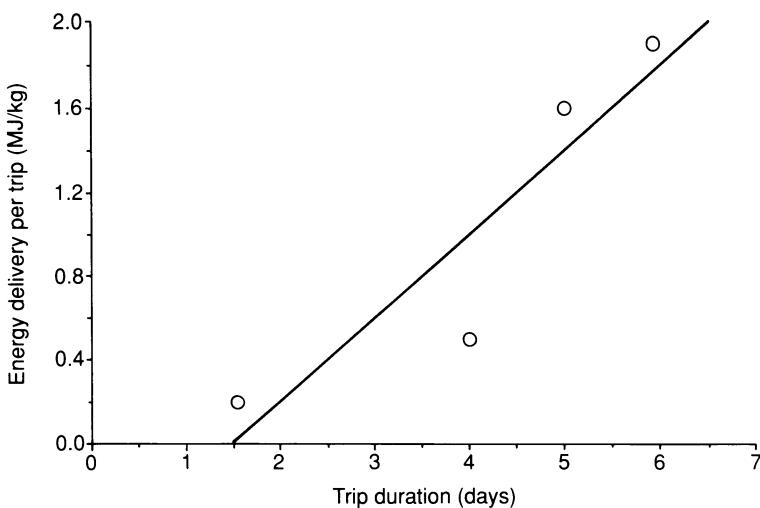


Figure 6.14 The amount of energy delivered per rookery visit corrected for maternal mass is plotted against the duration of a foraging trip for otariids ($r = 0.93$).

is consistent with the predictions of central place foraging theory (Orians and Pearson, 1977). This theory predicts the optimal behaviour of animals foraging at varying distances from a central place, such as a nest or rookery. For example, when foraging a long distance from the rookery a parent should make few trips of long duration and return with a greater quantity of energy per trip. In contrast, parents feeding close to the rookery (nearshore) should make many short trips, with a comparatively lower energy return per trip. Otariids like Steller's sea lion, make trips of relatively short duration (36 h), feed nearshore and thus travel short distances to the feeding grounds (Higgins *et al.*, 1988), whereas northern fur seals feed up to 100 km offshore and make trips of 7 days duration (Loughlin *et al.*, 1987). As predicted by the model, Steller's sea lions deliver considerably smaller amounts of milk energy (0.2 MJ/kg) per visit to their pup than northern fur seals (1.9 MJ/kg) (Table 6.3). Within fur seals a similar pattern exists, where inshore feeding species, like the Galapagos fur seal, often forage less than a day between shore visits to suckle their pups (Trillmich *et al.*, 1986). Offshore feeding species, like Antarctic and northern fur seals, spend 5–7 days foraging at sea (Gentry and Holt, 1986; Doidge *et al.*, 1986).

Such optimization of foraging behaviour is also consistent with the phocid reproductive pattern. In this case, some island-breeding phocid seals are an extreme example of an offshore feeder that utilizes highly dispersed or distant prey resources, where the optimal solution is to make as few trips as possible per reproductive event.

Table 6.3. For each pinniped the maternal mass, mass and energy of milk consumed by her pup per shore visit is given along with data on the mean foraging trip duration. Data on age and relative mass of pup at weaning are given for comparison. Milk fat values followed by an * indicate that the data are suspect because only a few milk samples were analysed

	Maternal mass (kg)	Milk fed to pup per trip			Time at sea (days)	Milk composition		
		g	MJ	MJ/kg		Fat (%)	Protein (%)	
Galapagos fur seal	27	n.a.	n.a.	1.5	29.4	12.1	[1]	
Antarctic fur seal	39	3600	63.7	1.6	4.3	42	12.3	[2]
Northern fur seal	37	3460	68.9	1.9	6.9	41.5	14.2	[3] [12]
South African fur seal	57	n.a.	n.a.	2.9	19*	56.3	9.6	[20]
Galapagos sea lion	80	n.a.	n.a.	0.5	19	10.0	10.0	[1]
Australian sea lion	84	n.a.	n.a.	2.4	19	7.3	7.3	[1]
California sea lion	85	2800	39.9	0.5	1.4	25.8	9.5	[17]
Steller sea lion	273	4420	52.1	0.2	1.5	31.7	9.8	[4] [13] [23]
Harp seal	135	39700	808	6.0	24*	7.8	7.8	[5]
Grey seal	174	57500	1274	7.3	51.8	7.8	7.8	[14] [16]
Hooded seal	179	34100	678	3.8	52.2	11.2	11.2	[15] [16] [21]
Weddell seal	447	159300	3320	7.4	61.4	4.9	4.9	[8] [7]
Northern elephant seal	504	149800	2700	5.4	53.6	8.9	8.9	[16]
Southern elephant seal	506				54.4	9.0	9.0	[10] [24]
Bearded seal					46.9	7.4	7.4	[18]
					49.5	6.8	6.8	[22]

Numbers in parentheses refer to the source of the data as follows: [1] Gentry *et al.*, 1986a; [2] Costa and Croxall, 1988; [3] Costa and Gentry, 1986; [4] Oftedal *et al.*, 1987a; [5] Higgins *et al.*, 1988; [6] Stewart and Lavigne, 1984; [7] Oftedal *et al.*, 1985; [8] Bowen *et al.*, 1988; [9] Tedman and Green, 1987; [10] Costa *et al.*, 1986; [11] Dodge *et al.*, 1986; [12] Gentry and Holt, 1986; [13] Weaning mass, Worthy and Costa, unpublished data; [14] Oftedal *et al.*, 1987b; [15] Fedak and Anderson, 1982; [16] Kovacs and Lavigne, 1986; [17] Costa, Kretzmann, Thorson and Higgins, unpublished data; [18] Peaker and Goode, 1978; [19] Trillmich and Lechner, 1986; [20] Ashworth *et al.*, 1986; [21] Amoroso and Mathews, 1952; [22] Fay, 1982; [23] Ono *et al.*, 1987; [24] Reidman and Ortiz, 1979.

At one extreme, elephant seals and grey seals have essentially separated feeding from onshore lactation. The reproductive pattern of these phocids has the advantage of being less constrained by the time it takes to travel and exploit distant prey, and may allow utilization of a more dispersed or patchy food resource. For example, since the acquisition of prey energy required for lactation is spread over many months at sea, northern elephant seal females need to increase their daily food intake by only an estimated 12% to cover the entire cost of milk production and maternal metabolism during lactation (this assumes that the food energy needed for lactation is consumed over the entire trip to sea, which may not be the case) (Costa *et al.*, 1986).

In contrast, lactating northern fur seal females consume 80% more food than non-lactating females (Perez and Mooney, 1986). It may be that the increased food intake of lactating fur seals (and probably otariids in general) can only be sustained in the highly productive water characteristic of upwelling environments. The lack of a truly tropical otariid may be related to the lower productivity of these warmer waters. The Galapagos fur seal and sea lion are not truly tropical species, since they exist in a highly productive equatorial upwelling region (Maxwell, 1974). In contrast, monk seals (*Monachus*) do exist in a truly tropical, warm-water, non-upwelling environment. It may be that otariids have a reproductive pattern that is optimal for prey that is concentrated and predictable, whereas some phocids have a reproductive pattern better suited for dispersed or unpredictable prey or prey that is located at great distances from the rookery. The long-distance foraging ability of some phocids, which would allow them to utilize a more dispersed or distant food resource, is achieved by reducing the importance of feeding during lactation.

What enables otariids and phocids to forage at sea for such variable intervals and yet supply their pups with an appropriate amount of energy? The answer is that lactation enables pinnipeds to process and concentrate the material fed to the young, with some independence from prey quality, or distance or time spent away from the rookery. It is well documented that marine mammals in general and pinnipeds in particular produce milk extremely high in lipid (Pilson and Kelly, 1962; Bonner, 1984; Oftedal *et al.*, 1987b). Furthermore, lactation enables the mother to provide her pup with food (milk), that compared to other vertebrates is independent of the composition of prey consumed (Pond, 1977). This is because although the milk reflects the basic constituents consumed by the mother, she can process, concentrate or utilize stored reserves in the production of milk. For example, California sea lions feed on fish, Antarctic fur seals feed on krill, northern fur seals feed on fish or squid and the hooded seal feeds on fish, yet they all provide their offspring with

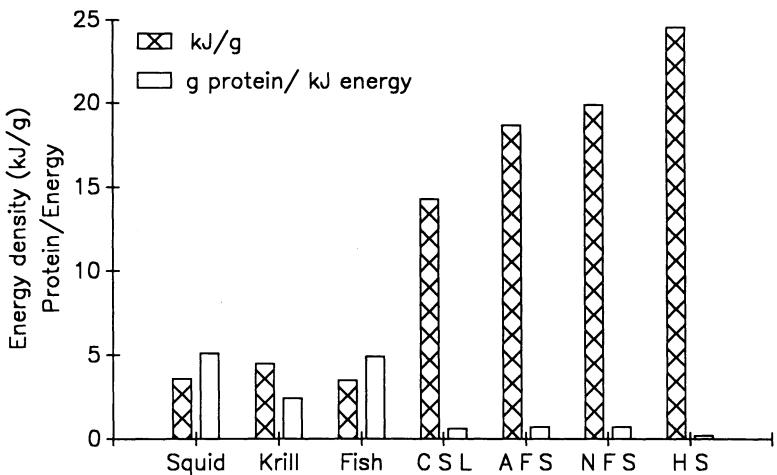


Figure 6.15 The energy density and protein energy ration of squid, nototheniid fish, krill and milk of California sea lions (C.S.L.), Antarctic fur seal (A.F.S.), northern fur seal (N.F.S.) and hooded seal (H.S.). Data on squid and fish are from Perez and Mooney (1986), krill from Clarke (1980), C.S.L. from Oftedal *et al.* (1987), A.F.S. from Costa *et al.* (1985), N.F.S. from Costa and Gentry (1986), and H.S. from Oftedal *et al.* (1988). Sea lions mostly eat squid and fish, fur seals eat krill and hooded seals eat fish.

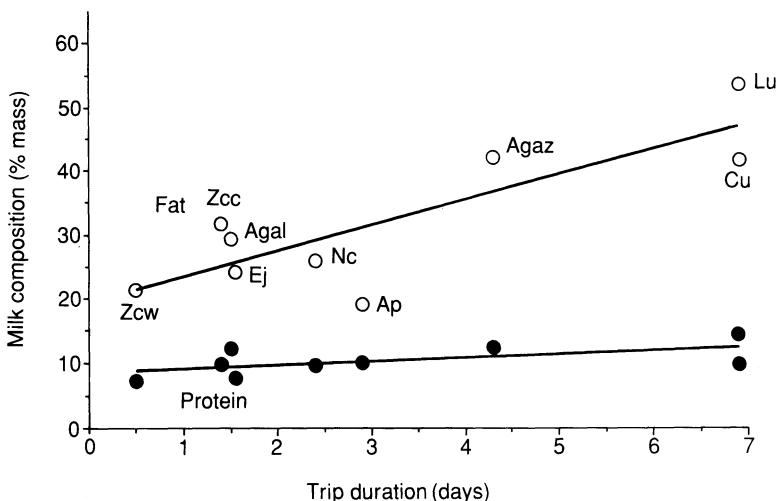


Figure 6.16 The relative milk fat and protein content (% of mass) of otariid milk is plotted as a function of the length of the female's foraging trip to sea ($r = 0.83$, $p < 0.01$). (Data are from Table 6.3.)

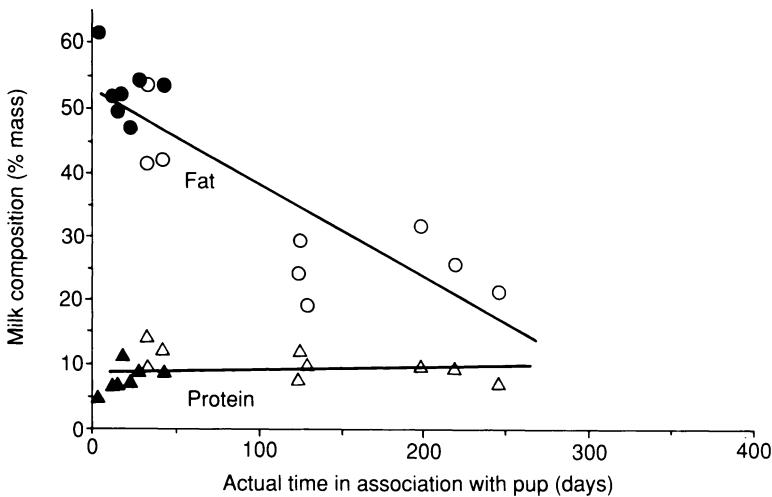


Figure 6.17 Milk fat (circles) and protein (triangles) content (% wet mass) of otariids (open symbols) and phocids (solid symbols) are plotted against the time the mother is available to suckle her pup on the rookery [milk fat: $r = 0.86$, $p < 0.01$; protein: $r = 0.66$, $p < 0.01$]. Data from Table 6.3 and percentage of time available for California sea lions from Ono *et al.* (1986); for Australia sea lions from Higgins (unpublished); all other otariids from Gentry and Kooyman (1986).

milk of significantly greater energy density than the prey consumed (Figure 6.15).

Increasing the lipid content to modify the energy density of milk has a disadvantage. The high energy density of pinniped milk is achieved by increasing the lipid content, with a reciprocal decrease in water content, but no corresponding change in protein content (Figures 6.16 and 6.17). Therefore, the protein to energy ratio of pinniped milk is lowest in the most energy dense milk (Figure 6.15). As will be seen later this limits the total amount of protein pinniped pups may receive during lactation, which constrains growth of lean tissue.

6.3.7 Variation in milk composition

Otariids are able to optimize energy delivery to their young by adjusting the lipid content of their milk in response to variations in trip duration. Lipid and therefore energy content of the milk of otariids has been shown to increase as trip duration increases (Trillmich and Lechner 1986). This pattern is displayed in Figure 6.16, along with the milk protein content. Notice that even though there is considerable variation in milk fat content there is relatively little change in the protein content. Recently, Trillmich (pers.

comm.) found that the milk lipid content of Galapagos fur seal females making long feeding trips (3–4 days) was higher than that of females making normal trips of short duration (1 day). This implies that the relationship between milk composition and trip duration is applicable within as well as between species.

Correlations of milk fat content and trip duration are complicated by the fact that otariid females with short trip durations are low-latitude species and those with long trip durations are high-latitude species. High latitude environments are highly seasonal and may force species to have shorter lactation periods than low latitude species (Oftedal *et al.*, 1987b). Furthermore, high latitude species are generally migratory whereas low latitude species are not (Gentry *et al.*, 1986a). Migratory species tend to have high population densities on small island rookeries. Higher population size requires access to a larger resource base and therefore individuals are more likely to forage farther at sea. A smaller resource base could support a low-density resident population and thus allow a nearshore foraging behaviour.

Females with short lactation durations should produce milk of higher fat content in order to deliver equivalent amounts of energy in a shorter interval. Consistent with this prediction, a significant negative correlation exists between milk fat content and the total amount of time spent by females ashore with their pups ($r = 0.86$ $p < 0.01$) (Figure 6.17). The hooded seal, with the shortest lactation interval, has the highest milk fat content of any pinniped (Oftedal *et al.*, 1988) and the milk fat content of the two polar otariids (Antarctic and northern fur seals) with short lactation intervals is very high. However, this relationship does not appear to be linear and other factors may become important as time available for suckling increases.

The increased energy density of pinniped milk may limit the amount of protein or other essential nutrients available to the offspring. The increased energy content of pinniped milk is achieved by increasing its lipid content with negligible changes in its protein content (Figure 6.17). Thus young may be provided with more than sufficient energy to fuel metabolism, but may be limited in their ability to grow due to the reduced protein intake. This is especially important in species that have shortened lactation intervals. In such species pups would receive similar amounts of total energy in a smaller quantity of milk. However, since the protein content of milk is independent of lactation duration these pups would get less total protein. This constraint can be seen by the fact that most of the post-natal growth of phocid seals is due to the accumulation of adipose tissue stored as blubber, with little growth in lean tissue (Bryden, 1968; Worthy and Lavigne, 1983; Costa *et al.*, 1986; Oftedal *et al.*,

1989). For example, at birth, northern elephant and harp seal pups are born almost without fat and upon weaning are composed of approximately 50% lipid (Worthy and Lavigne, 1983; Ortiz *et al.*, 1984; Oftedal *et al.*, 1989).

6.4 FORAGING BEHAVIOUR

The previous section examined energy partitioning to the pup, but did not examine the relationship between prey energy acquisition and subsequent investment in the pup. Otariids and phocids possess unique physiological differences in their diving abilities, which translate to differences in their foraging capabilities. Utilization of different foraging behaviour and prey resources may determine the rate of energy expenditure and acquisition, which may ultimately influence the divergent reproductive patterns of pinnipeds.

6.4.1 Foraging behaviour data

Diving patterns of free-ranging animals have been measured in a variety of ways from using small dye-filled capillary tubes or other devices (Kooymann, 1965; Wilson and Bain, 1984) to larger and more expensive instruments which employ a variety of analogue and digital electronic, and photomechanical transducers (Kooymann *et al.*, 1976; Kooymann *et al.*, 1983a; Hill, 1986). An example of such a unit deployed on an Australian sea lion can be seen in Figure 6.18. The results of these investigations with respect to dive duration and depth are summarized in Figures 6.19 and 6.20.

Several general patterns on maximum recorded dive depth and duration become apparent in Figures 6.19 and 6.20. First, phocid seals, and in particular elephant seals, are exceptional among all groups in their deep and long duration diving pattern. This is not unexpected because phocids can store more oxygen per kilogram body mass than otariids due to a larger blood volume and higher muscle myoglobin concentration (phocids 60 g O₂/kg; otariids 40 g O₂/kg; Kooymann, 1985). Second, with the possible exception of the New Zealand sea lion (a large otariid), otariids are shallow, short-duration divers. Third, the larger the mass of the animal, the longer its potential dive time, which enables it to dive deeper. This observation is explained by a more efficient utilization of stored oxygen and a greater proportion of stored oxygen with increasing body mass (Kooymann *et al.*, 1983b; Gentry *et al.*, 1986a).

If large pinnipeds can dive deeper than small ones, it is interesting that so many of the larger sea lions and fur seals make relatively shallow dives. Furthermore, the considerable difference between

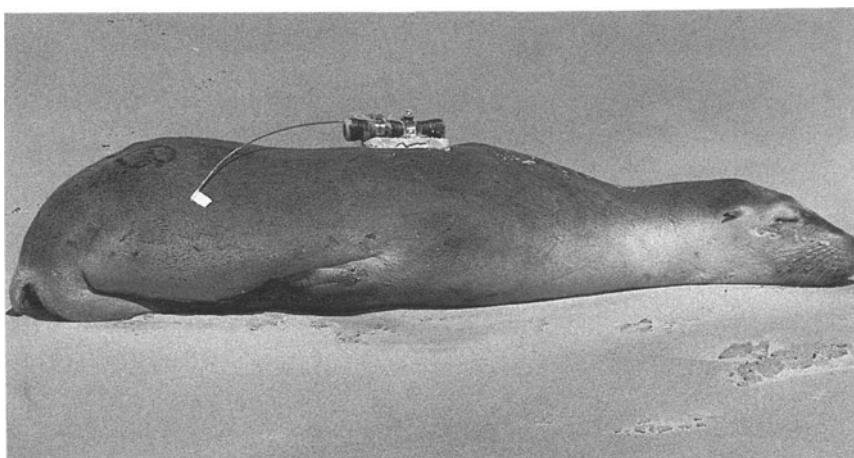


Figure 6.18 An example of an Australian sea lion with a smaller microprocessor-controlled time-depth recorder attached (Wildlife Computers, Woodinville, WA). This is an example of the type of device used to obtain the dive data displayed in Figures 6.20 and 6.21.

mean dive depth and duration, and maximum recorded dive depth or duration suggests that the typical diving behaviour of pinnipeds is considerably less than their physiological capability (Castellini and Kooyman, 1989). For example, Antarctic fur seals should be able to reach the depths achieved by similar sized northern fur seals. This implies that in some cases seals might only rarely reach their potential maximum diving depth or duration. Physiological limitations are probably only part of the story and it is likely that other factors, such as prey type, prey behaviour, prey energy content and size, influence the cost and benefit of pursuing prey at different depths.

Analysis of the influence of the above factors on foraging behaviour requires an examination of diving behaviour as a function of prey type. Research of this type is in its infancy and it is likely that many new and exciting patterns will emerge as new studies are completed. A preliminary analysis of available data and their implication to optimal foraging behaviour are discussed below.

6.4.2 Single-species foragers

Many Antarctic marine mammals prey upon krill and several of these do so exclusively (Laws, 1984). Unfortunately detailed studies of foraging behaviour exist only for Antarctic fur seals (Croxall *et al.*, 1985; Kooyman *et al.*, 1986; Fraser *et al.*, 1989). These investigators found that fur seals made most (75%) of their dives at night and that

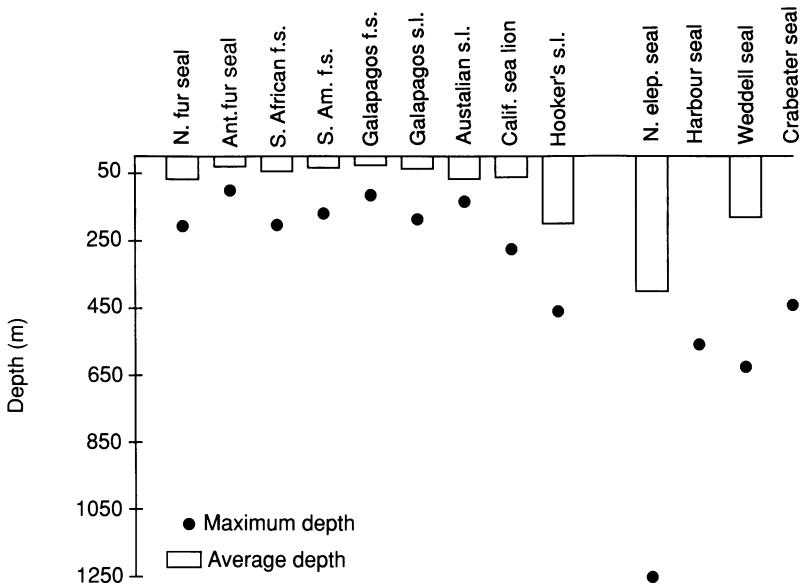


Figure 6.19 Maximum (dots) and mean (histogram) diving depth for 13 pinnipeds. Body mass of pinnipeds increases from left to right for otariids and than phocids. Data are from Galapagos fur seal, Trillmich *et al.* (1986); Antarctic fur seal, Kooyman *et al.* (1986); South African fur seal, Kooyman and Gentry (1986); northern fur seal, Gentry *et al.* (1986b); South American fur seal, Trillmich *et al.* (1986); Galapagos sea lion, Kooyman and Trillmich (1986); California sea lion, Feldkamp *et al.* (1989); Australian sea lion, Costa *et al.* (1989b); Hooker's sea lion, Gentry *et al.* (1987); harbour seal, Kolb and Norris (1982); Weddell seal, Kooyman (1981); northern elephant seal, Le Boeuf *et al.* (1988); Crabeater seal, Bengston (1986).

these dives were consistently shallower (dive depth < 30 m) than dives during the daytime (mostly 40–75 m). This pattern closely followed the vertical distribution of krill, which during daylight hours occur below a depth of 50 m, but at night are found in substantial quantities above 50 m. Furthermore, even though more than 40% of the krill was below 75 m depth at any time of day, fur seal dives seldom (3%) exceeded this depth. It was concluded that krill are captured only from shallow waters, since this is when they are most efficiently obtained. Similar patterns have been observed for other krill predators such as macaroni, chinstrap and gentoo penguins (Croxall *et al.*, 1988; Fraser *et al.*, 1989).

6.4.3 Dive patterns of multispecies foragers

Unlike Antarctic fur seals, female northern fur seals exhibit three distinct diving patterns, two of which appear to be specific to the type of prey consumed. Gentry *et al.*, (1986b) found that during a

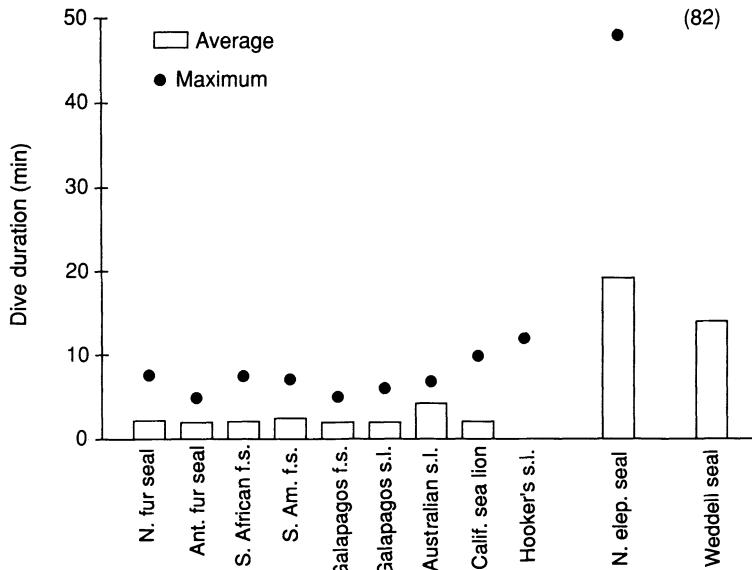


Figure 6.20 Maximum (dots) and mean (histogram) dive duration for 11 pinnipeds. Body mass of pinnipeds increases from left to right for otariids and than phocids. Data are from Galapagos fur seal (Trillmich *et al.*, 1986); Antarctic fur seal (Kooyman *et al.*, 1986); South African fur seal (Kooyman and Gentry, 1986); northern fur seal (Gentry *et al.*, 1986b); South American fur seal (Trillmich *et al.* (1986); Galapagos sea lion (Kooyman and Trillmich, 1986); California sea lion (Feldkamp *et al.*, 1989); Australian sea lion (Costa *et al.*, 1989b); Hooker's sea lion (Gentry *et al.*, 1987); Weddell seal (Kooyman, 1981); northern elephant seal (Le Boeuf *et al.*, 1988). The number in parentheses in the maximum dive duration recently recorded for Weddell seals (Castellini, pers. comm.)

foraging trip fur seals exhibited one of the following patterns: those composed exclusively of deep dives, having a mean depth of 185 m, those composed exclusively of shallow dives with a mean depth of 50–60 m, and those with a mixture of both deep and shallow dives. Deep-diving fur seals did not exhibit diurnal fluctuations in dive depth, suggesting that they might be feeding on demersal or benthic species. However, shallow divers exhibited a striking diurnal fluctuation in diving pattern quite similar to that observed for krill-feeding species. Recent data present the possibility that these deep-diving seals are feeding on demersal fish, such as pollock, on the Bering Sea Shelf, whereas shallow-diving seals feed on vertically migrating squid over deep water beyond the Bering Sea Shelf (Loughlin *et al.*, 1987). Like krill, squid are available throughout the day, and comparable to krill predators northern fur seals wait for squid to move into shallow water before preying on them. Finally, northern fur seals pursue fish with four times the energy value of squid, to considerably deeper depths than when diving for the latter (Costa, 1988a).

When combined with estimates of the number of prey that must be captured per dive to meet the predators' energy expenditure, the data suggest a relationship between the number of prey taken and dive depth. Deep divers should take prey that is large, which only requires the capture of a few individuals per dive. Conversely when small prey are taken, many individuals must be captured per dive and these dives should be limited to shallow depths. For example, it has been estimated that to meet their energy requirements deep-diving northern fur seals need only capture one pollock every other dive, whereas shallow diving Antarctic fur seals need to capture 70 krill every dive (Costa, 1987; Gentry *et al.*, 1986a).

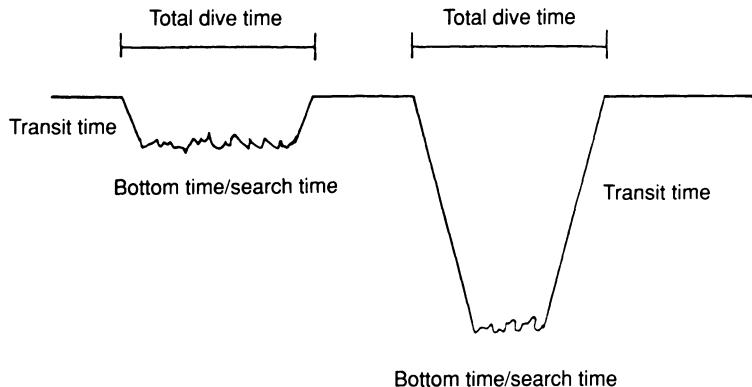
This suggests that deep diving in northern fur seals may only be economical when the predator is foraging on large prey which can supply a significant fraction of the energy requirement with each dive. In contrast, predation on small prey, where many individuals must be captured per dive, is limited to shallow depths. The terms shallow and deep are relative to the diving capability of the predator. For example, 'shallow' to an elephant seal may be 300m, whereas 'shallow' to a northern fur seal is 30m.

What constraints may be associated with depth that account for these different depths of foraging? First, let us examine a hypothetical predator making deep and shallow dives of equivalent duration, on which oxygen is utilized at the same rate, and in which no anaerobic debt is incurred. Although incorporation of an anaerobic debt while diving is a possibility, it is presumed to be unlikely. Due to the disproportionate amount of time that must be spent on the surface to clear lactic acid from the blood, it is an inefficient diving strategy (Kooyman *et al.*, 1980; Castellini and Kooyman, 1989). With the assumption that foraging occurs only when the seal reaches maximum depth for a given dive, a diagram of these diving patterns suggests that shallow dives use relatively little time in transit, which leaves proportionately more time to search for or pursue prey (Figure 6.21(a)). Alternatively, as a deep diver spends relatively more time in transit getting to the foraging depth, it has proportionately less time remaining to search for or pursue prey, and fewer prey can be obtained per dive.

If the same amount of time is spent per dive, and there is less time available to capture prey, it would be prudent to pursue prey of greater size and energy content (a similar relationship would follow with greater prey density). Likewise, if dives are of the same duration and prey is captured at a consistent rate per dive, more dives would be required when pursuing the prey of lower energy content. Shallow dives have short transit times so that many short dives with a lower premium on energy return per dive would be economical. For deep dives where transit time is long, few dives of long duration with a high energy return per dive would be favoured.

A

When Swim Velocity and Total Dive Time are Constant



B

When Swim Velocity Varies With Dive Depth

Bottom Time is Constant

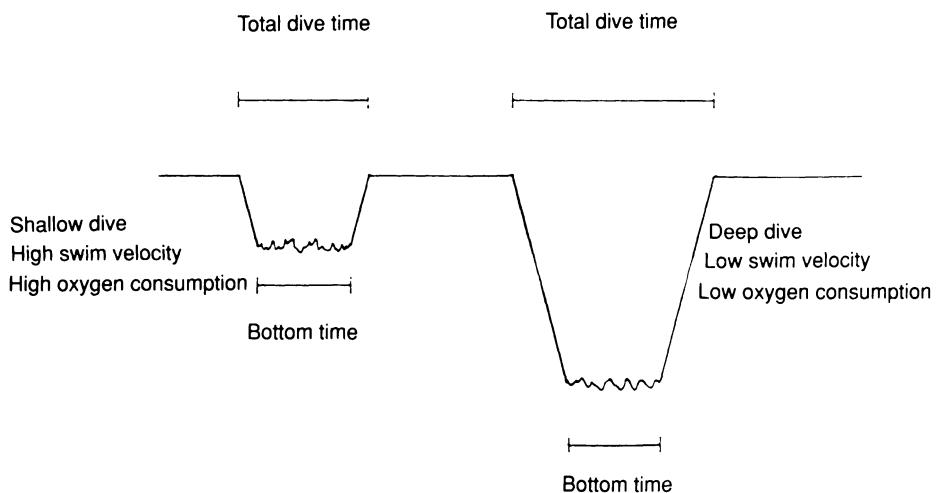


Figure 6.21 (a) A schematic representation of the diving pattern of a deep-and shallow-diving predator when oxygen utilization is constant and total dive durations are equivalent. (b) Diving pattern where the rate of oxygen utilization is greater for shallow dives than for deep dives. In this case total dive duration is not constant.

If oxygen stores are constant but the rate of oxygen utilization is a function of the animal's swimming or search and pursuit speed (Figure 6.21(b)), a fast swimming animal should utilize its oxygen stores faster and would thus be limited to shallow dives or 'spiked' dives with minimal bottom time. A slow-swimming animal should utilize oxygen more slowly and thus could make dives of long duration. It is possible that the pursuit of many small prey requires fast and agile swimming with high rates of oxygen consumption. Such a high rate of oxygen consumption would thereby constrain the predator to many short dives. However, for a shallow-diving predator this may not be a serious constraint since transit time to foraging depth is brief. In this case, since transit time is relatively low, most of the dive would be spent in pursuit and acquisition of prey. For deep dives, however, the opposite is true. If a deep diver were to swim fast, most, if not all, of the oxygen stores might be utilized in transit to depth, with little left over for the search and pursuit of prey. Such a situation probably results in the 'spiked' dives observed in many pinnipeds (Gentry *et al.*, 1986a; Le Boeuf *et al.*, 1986, 1988). Since some searching and pursuit of prey may be desirable at depth, an alternative would be to reduce oxygen consumption and swim slowly. This would allow greater bottom time at depth but might limit the predator to obtaining slow-moving prey or prey that is only encountered occasionally. If this were the case the predator would have to pursue prey that was of large size and high energy content. Consistent with this behaviour are the flat-bottomed dives observed for deep diving northern elephant seals (Le Boeuf *et al.*, 1988) and New Zealand sea lions (Gentry *et al.*, 1987). A corollary of this pattern would be to limit the pursuit phase to slow methodical swimming at least until the prey has been spotted. Switching to a rapid high-energy swim speed would result in rapid utilization of oxygen which could limit the dive to a single capture before oxygen stores were depleted. If deep divers can only capture a few individuals per dive, then in order to maintain energy balance they should pursue prey that contains a greater amount of energy per capture.

6.4.4 Foraging energetics

It is likely that different dive patterns are associated with a different cost (Costa, 1988a). The energy consumption of four species of lactating otariids has been measured using the oxygen-18 doubly labelled water method and indicates that while at sea they expend energy at five times the predicted basal level (Costa and Gentry, 1986; Costa *et al.*, 1989a, 1989b; Costa *et al.*, 1990). Unfortunately, data using this method are not yet available for phocid seals. However, metabolic rates of diving elephant seals estimated from

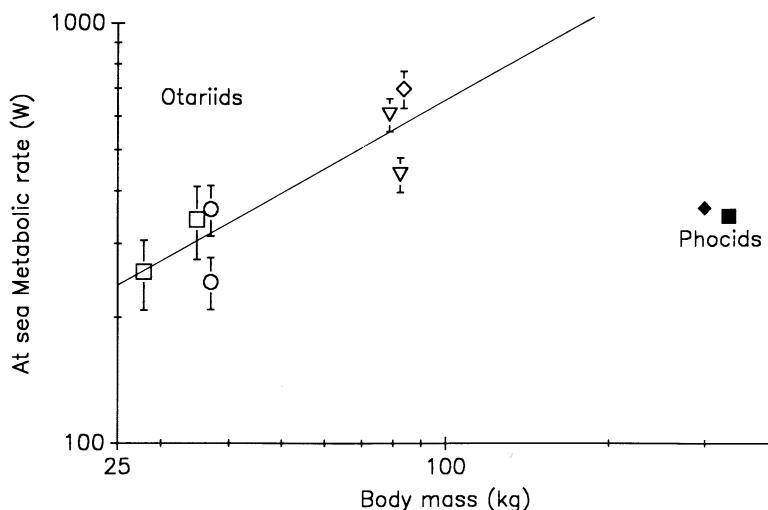


Figure 6.22 Open symbols are measurements of metabolic rate at sea determined with the oxygen-18 doubly labelled water method and are plotted as a function of body mass for northern, open circles (Costa and Gentry, 1986), and Antarctic, open squares (Costa *et al.*, 1989a), fur seals and Australian, open diamond (Costa *et al.*, 1989b), and California sea lions, open triangles (Costa *et al.*, 1990). Solid symbols are data for diving metabolic rates determined on Weddell seals, solid diamond (Kooyman *et al.*, 1973) or estimated for northern elephant seals solid square (Le Boeuf *et al.*, 1988). Error bars represent the 95% confidence interval.

measurements of dive duration and available oxygen stores estimate that their metabolism while at sea is only 1.3 times the predicted basal rate (Le Boeuf *et al.*, 1988). Similarly, metabolic rates (indirect calorimetry) of Weddell seals freely diving from a hole in the ice revealed a diving metabolism of between 1.5 and three times the predicted basal level (Kooyman *et al.*, 1973).

A comparison of the metabolic rate of pinnipeds while at sea can be seen in Figure 6.22. Notice that as a group otariids appear to have significantly higher metabolic rates than do phocids. This suggests that there might be a fundamental difference in the way otariids and phocids go about obtaining their prey. There are other well established differences between the two families in connection with their diving physiology. For example, phocids have increased blood oxygen storage capacity due to an increased proportion of red blood cells (haematocrit) (Lenfant *et al.*, 1970). Elevated haematocrit increases the blood viscosity in such a way as to reduce the ability of phocid blood to optimally transport oxygen (Hedrick *et al.*, 1986 and in press). Maximum oxygen-carrying capacity would not be an issue if as suggested in Figure 6.22 phocids maintain low metabolic rates while diving. Further support comes from the suggestion that

phocids have a low aerobic scope, a limited ability to increase their metabolic rate above resting (Elsner and Ashwell-Erickson, 1982; Elsner, 1987). In contrast otariids have a lower haematocrit, which is optimal for efficient oxygen transport (Hedrick *et al.*, *in press*). Lastly, there are many behavioural differences between otariids and phocids which support differences in the costs of foraging. For example, otariids typically travel at the surface porpoising, while phocids tend to surface quietly and descend before swimming. Hydrodynamic theory tells us that surface swimming is considerably more costly than sub-surface swimming (Vogel, 1981). All of these factors support a slow conservative foraging pattern for phocids versus an energetically costly foraging style for otariids. Finally, the proportion of time at sea spent underwater for phocid seals has led to their being considered surfacers rather than divers, while otariids may be considered more traditional divers (Kramer, 1988; Kooyman, 1989; Castellini and Kooyman, 1989).

How do these different diving patterns and energy expenditures affect the ability of pinnipeds to obtain prey and the efficiency with which they acquire energy? A summary of the available at-sea data from independent measurements of food intake derived from water influx, species-specific diving patterns determined with time-depth recorders and measurements of metabolic rates are presented in Table 6.4. Although these data are quite preliminary and are based on many assumptions (see Costa, 1987) they provide some interesting insights into differences in foraging energetics of pinnipeds. For example, although elephant seals obtain more prey biomass per dive (332 g v. 115–163 g) than northern fur seals, they take more time to do it, acquiring less energy per minute (19 min v. 2–4 min) (Table 6.4). Fur seals obtain more energy per unit time, but at a somewhat lower rate of energy expenditure. Even with an elevated metabolic rate, fur seals capture more prey energy per unit energy expended than elephant seals. Most importantly, elephant seals achieve a similar ratio of foraging success (energy gain/energy expended) with a considerably lower metabolic rate (Figure 6.23). This suggests that they expend less energy to obtain a similar amount of prey, which may enable them to subsist on a poorer or more dispersed prey resource than the fur seals and sea lion. However, the dramatic performance of northern fur seals, also suggests that in the right circumstances otariids may be able to better utilize resources when they are plentiful.

Since these data are preliminary, one must be careful not to extrapolate too much. If such a pattern is typical of phocids and otariids, it suggests that phocids have a conservative foraging mode that can net similar amounts of energy to that obtained by otariids, but at significantly lower costs. It might be argued that the phocid

Table 6.4 Dive rate and duration, rate of prey capture and energy acquired, energy expenditure and metabolic rate of three otariids and a phocid are summarized. Data on prey intake were estimated from water influx and metabolic rate of the sea lion and fur seals from oxygen-18 doubly labelled water measurements (Costa and Gentry, 1986; Costa, 1988b; Costa *et al.*, 1989a; Costa *et al.*, 1990). Metabolic rate of northern elephant seal was estimated from dive behaviour (Le Boeuf *et al.*, 1988)

breeding pattern allows a conservative foraging mode, which enables them to occupy habitats where productivity is lower. Otariids have a foraging and reproductive pattern which might be more costly, but optimal in highly productive regions where prey resources are not limited. Such a hypothesis is consistent with pinniped distributions and global productivity. Otariids are only found in locations where global productivity is high, whereas phocids breed in both the highly productive regions of the world and in areas of poorer productivity, like the Hawaiian Islands, the Mediterranean and historically in the Caribbean.

6.5 SUMMARY AND CONCLUSIONS

Pinnipeds have adapted to the constraints of marine feeding and terrestrial parturition in a variety of ways and have apparently achieved optimal results with different life histories. In otariids, lactation and feeding are coupled and conform to the predictions of central place foraging theory. This limits their utilization of prey in time and distance, such that they can spend no more than about 8 days at sea and forage about 100 km offshore of the rookery. In turn this limits them to an abundant prey resource that is predictable in time and space. Nevertheless, the otariid reproductive pattern allows greater investment of energy and protein into the offspring, which in turn allows young to be nutritionally independent at a greater relative body mass. Furthermore, weaning is gradual and may allow the pup a greater opportunity to learn to survive on its own, which may confer greater juvenile survival. However, this increased maternal investment requires more trips to sea, which results in greater exposure to predation and more time and energy spent travelling versus foraging.

In contrast, phocids possess a much shorter lactation period which has allowed them essentially to separate feeding from reproduction on shore. Such a pattern allows them to feed far offshore and utilize a dispersed or less predictable prey resource. Furthermore, females are not encumbered by the presence of their pup while they are foraging. However, fasting or reduced feeding during lactating places a limit on the total amount of energy and protein that can be invested in the young, which results in a smaller relative mass at nutritional independence. Finally, weaning is abrupt, which reduces the potential for the pup to learn from the mother. The attenuated breeding pattern also allows utilization of an unstable breeding substrate. Lactation has enabled both groups to compensate for the harsh seasonality of high latitudes.

It is interesting to ponder how such a difference in the breeding

pattern of pinnipeds evolved, since relative to otariids phocids have an exceedingly attenuated lactation interval (Bonner, 1984). Stirling (1975, 1983) has speculated that this breeding pattern was the result of all phocids being descended from an ice-breeding ancestor. He argued that a common pagophilic existence would require an attenuated lactation interval to enable pagophilic seals to successfully rear young on unstable pack ice. However, island-breeding monk seals are one of the oldest extant phocid groups and apparently never had an ice-breeding ancestor, yet they exhibit the typical phocid reproductive pattern (Repenning *et al.*, 1979).

An alternative hypothesis based on the differences in foraging and reproductive energetics discussed here is that phocids evolved their unique reproductive pattern as a way to utilize a patchy, highly dispersed or distant prey resource. Utilization of such a resource would have forced phocids to forgo a lactation pattern that alternates between feeding at sea and suckling the pup onshore. Acquisition and storage of all the material and energy needed to successfully rear the young in advance of parturition would allow phocids to forage over a wider oceanic area and utilize a more dispersed or distant food resource. Once attained this breeding pattern would then enable phocids to secondarily inhabit seasonally variable environments like unstable ice. Further attenuation of the lactation interval would then follow from the utilization of such a habitat as originally suggested by Stirling (1975, 1983).

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Sensory reception and processing in Phocidae and Otariidae

Deane Renouf

7.1 INTRODUCTION

In his 1934 monograph *A Stroll Through the Worlds of Animals and Men*, Jacob von Uexküll coined the term 'Umwelt' (translated by Claire Schiller (1957) as 'phenomenal or self world') to describe the sensory, spatial, temporal and functional world unique to each species. Pinnipeds must experience a different Umwelt in the ocean than on land, since the ways in which sensory information is received, attended to and processed are likely to be dissimilar in each place. Not only are the properties of physical energy transmission altered as the animal switches environments, the frame of reference for all sensory interpretation changes time scale because the speed of the animal's movement and of sound energy transmission is much faster in water. In the sea where they feed, their locomotion is swift in gravity-reduced space, allowing them to travel long distances and move rapidly in three dimensions to capture prey or escape the few predators they must avoid in the ocean. On land where they breed, they move with clumsy heaviness, needing only to know the location of their slow-moving pups, mates and competitors, and sense the approach of terrestrial enemies in enough time to escape into the adjacent water where pursuit ceases. In this chapter I will review what is known about sensory function in seals, sea lions and fur seals, and use this information to explore the nature of their Umwelt in the ocean and on land.

Insofar as phocids are less dependent on land than are otariids, the sensory worlds of each group should be different in some respects. The distinctions between true seals and eared seals are many. The

latter are substantially more agile out of water since their hind limbs are able to rotate forward for quadrupedal locomotion, while the former must travel caterpillar-like on their bellies. All pinnipeds give birth to their young on land or ice and nurse them there. Otariids lactate for 5-12 months (*Arctocephalus galapagoensis* for 2-3 years) continuing to nurse a yearling or older offspring at the same time as a new pup (Bonner, 1984). The typical lactation duration for phocids is 4 weeks, but often less (e.g. hooded seals, *Cystophora cristata* wean their pup which gains 7 kg per day in as little as 72 h) (Bowen *et al.*, 1985). In maintaining an extended dependence on their mothers, otariid pups spend more time on land, staying ashore for months before first entering the water (Ridgway and Harrison, 1981a). However, some newborn true seals must swim when they are a few minutes old (Lawson and Renouf, 1985). Otariids organize all of their breeding rituals on the beach (Ridgway and Harrison, 1981a), and while two phocids (elephant seals, *Mirounga* sp. (Stirling, 1983; Le Boeuf, 1972) and grey seals, *Halichoerus grypus* (Boness and James, 1979)) copulate ashore, all others carry out their significant mating displays and hence important social interaction in the ocean (Ridgway and Harrison, 1981b). Phocids are deeper divers (Harrison and Kooyman, 1968; Gentry and Kooyman, 1986).

It is unfortunate, then, that otariids and phocids are so often lumped together as a single group, since it is likely that their sensory function has evolved in response to different pressures, both at the receptor level and in relation to the complex perceptual organization which determines the nature of each Umwelt. The role of movement should not be underestimated in this regard. It has been shown clearly in some terrestrial mammals that there is an important relationship between perceptual and motor development. For example, cats which have been restricted in their freedom of movement, and therefore their ability to manipulate their surroundings, do not develop the same visual skills as normal cats which have had essentially the same visual experiences acquired through free motor exploration of the environment (Held, 1965; Held and Hein, 1963). Since sea lions and fur seals stay so long on land as young pups, and are thus limited in the extent of their locomotion, the dynamics of their perceptual development must be unlike that of true seals which swim at an early age. Because otariids differ from phocids in so many fundamental ways, I will discuss each group in its own right.

Since pinnipeds undertake activities crucial for survival on land and at sea, their sensory systems must function effectively (though not necessarily equally well) in both environments. In most instances their receptor apparatus seems to have been adapted to operate primarily in one environment, but with modifications works well in the other. It is also likely that the relative weighting of modality

dependence and hence processing changes in water and on land, perhaps similar to the way the system copes with variations in light levels or background noise. I will begin by reviewing what is known about the mechanics of such adaptations in each modality, and discuss what we can and cannot explain about the sensory worlds of pinnipeds.

7.2 METHODOLOGICAL CAVEATS IN PSYCHOPHYSICAL THRESHOLD MEASUREMENT

It is necessary to preface my review of sensory function by noting that most of the thresholds I describe hold true only for the reinforcement and signal contingencies prescribed at the time the measurements were made. This is not of serious concern since threshold is a misleading concept which implies incorrectly that some minimum energy is required to activate a perceptual system, or that there exists some physical point at which sensory resolution ceases. Instead, as signal detection theory explains, the organism makes judgments about signal to noise ratios, and these judgments depend to a large extent upon factors external to the animal (Swets, 1973). In any case, relative thresholds are of most interest such as those found in air and water, so when constant errors occur because of the training exigencies described below they do not preclude valid comparisons.

To elaborate, in most psychophysical studies, seals, sea lions and fur seals were trained to indicate whether or not they detected a stimulus or a difference between two stimuli. Usually, the animals were trained to make one response in the presence of a signal (or when two stimuli were resolved) and another response when no signal (or difference) occurred. Absolute (or differential) thresholds were then ascertained by reducing the intensity of the signal (or magnitude of the stimulus difference) until the animal responded as if the signal (or difference) were not present, with near-threshold values administered in various psychophysical arrangements.

Before Schusterman's (1974b) discussions of signal detection theory, it was rarely taken into account that sensory judgments are altered by the probability and quantity of reinforcement, and the proportion of signal trials (Schusterman and Johnson, 1975; Schusterman *et al.*, 1975; Schusterman, 1976). Typically, when thresholds are measured, on half of the trials in a session a signal is presented, and the rest are catch trials with no signal. There are instances in which a signal cannot be detected because it is subliminal, and therefore the animal makes the 'no signal' response. This is treated as an error, even though from the animal's perspective the correct response was

made. The purpose of catch trials, then, is to prevent extinction of the 'no signal' response, and performance on catch trials is taken as an indication of the reliability of the animal's discriminations.

Prior to Schusterman's (1974b) observations, few errors on catch trials (in the jargon of signal detection theory, a low 'false alarm' rate) was interpreted as reliable performance, and therefore thresholds ascertained on the associated signal trials were valid. In order to guarantee low false alarm rates, subjects were often punished for errors on catch trials. Schusterman (1974b) showed that under such conditions animals adopt a conservative strategy in order to avoid false alarms. That is, when the animal is not sure whether a trial is a catch trial, or one on which a signal is below threshold, it uses a 'when in doubt say no' rule. The result of this response bias is an elevated threshold. This is probably exacerbated to some extent by the fact that from the animal's point of view there is a higher proportion of no signal trials in most sessions because many of the signal trials are judged by the animal to be catch trials.

For these reasons, many of the thresholds I describe below are probably 'incorrect'. This is not worrisome since the whole concept of an 'on/off' point in the sensory mechanism is misleading. Clearly the animal makes judgments about whether or not a sensory stimulus is present; whether or not a signal is discernible against physiological noise depends upon the consequences of missing the signal or falsely reporting that it is there. Since the most instructive use of the psychophysical data is in drawing comparisons, such as among the performance of different species in air and water, or sensitivity at various frequencies or luminance levels etc., as long as the same response biases are operating the comparisons can still be made.

7.3 VISION

The difficulties of sensory functioning in two media are most evident when vision is considered. The amphibious animal must be able to see in the dim, murky, colour-restricted underwater environment, where light absorption and scattering are exaggerated. Pinnipeds must also be able to use vision in air where light levels can run from low on foggy, moonless nights, to high on sunny days on the ice floes. When a mammalian eye adapted to see in air is submerged, it loses the refractive power of the cornea and encased fluids which have roughly the same refractive index as sea water. The result is an out-of-focus retinal image, hyperopia (principal focus behind the retina) obvious to any human who dives without a face mask. If this corneal protected, fluid-filled eye were instead designed to see in

water, it would operate myopically (principal focus in front of the retina) in air as light is refracted upon entering the eye. In readapting to an aquatic environment, marine mammals have developed a spherical lens which results in emmetropia (images focused on the retina) or slight hyperopia under water. However, pinnipeds have had to evolve some way of coping with the myopia which their water-adapted eye suffers in air as the refraction introduced at the cornea produces an image which focuses in front of the retina. Otariids and phocids may have developed different ways of obviating the need for extensive aerial accommodation.

In what follows, I will discuss what is known about the sensitivity, acuity, and colour function of the visual systems of phocids and otariids.

7.3.1 Phocidae

(a) Sensitivity

The phocid eye resembles that of a nocturnal mammal in that it is large both relatively and in absolute terms (Jamieson and Fisher, 1972; Walls, 1942), with a pupil which can dilate to dimensions which maximize light collection (Lavigne, 1973; Lavigne and Ronald, 1972; Walls, 1942). In addition, the predominant receptor is rod-like and there is no area centralis (Jamieson and Fisher, 1971; 1972), which is the seat of the fovea and characteristic of the diurnal eye. The tapetum lucidum, located in the choroid of many nocturnal animals, is a reflecting layer which typically increases sensitivity by reflecting light back through the visual cells. Seals have a more extensive tapetum (cellulosum) relative to eye size than in any land mammal (Walls, 1942; See Figure 7.1). Finally, Jamieson and Fisher (1971) and Nagy and Ronald (1970) reported that the ratio of receptor to bipolar to ganglion cells is 100:10:1, which these authors considered very high, and therefore indicative of enhanced sensitivity. However, as Landau and Dawson (1970) explain, this is not very different from the human receptor to ganglion cell ratio, which is 130:1.

Surprisingly little work on the absolute sensitivity of seals has been done directly. Wartzok (1979) reported rod-dominated spectral sensitivity curves for the harbour seal, *Phoca vitulina*, and the spotted seal, *P. largha*, using behavioural tracking methods. The best sensitivity of both species was near 530 nm (green) under a low and a high ambient light level. The absolute thresholds at this wavelength were virtually identical for each seal ($2.52 \times 10^{-5} \mu\text{W/mm}^2/\text{steradian/nm}$ at $10^{-7} \mu\text{W/mm}^2$ adapting radiance, and $1.63 \times 10^{-9} \mu\text{W/mm}^2/\text{steradian/nm}$ at $0.5 \mu\text{W/mm}^2$ adaptation level). Wartzok calculated that such sensitivity should allow the seals to detect



Figure 7.1 (a) The harbour seal's eye at night. The pupil is only partially dilated in response to the photographic flash, but the reflecting tapetum shines through. (b) The harbour seal's pupil is closed down further than in (a) illustrating the inverted tear-drop shaped stenopaeic pupil. When fully constricted, the pupil becomes a very tiny slit. (Photographs by E. Noseworthy.)

Table 7.1 Spectral sensitivity of some phocids and otariids

<i>Species</i>	λ_{max} (nm, hue)	<i>References</i>
PHOCIDAE		
Spotted seal	530 (green)	Wartzok (1979)
Harbour seal	530 (green)	Wartzok (1979)
Harp seal	495.7 (blue-green)	Lavigne and Ronald (1975a)
Grey seal	496.6 (blue-green)	Lavigne and Ronald (1975a)
Weddell seal	496.8 (blue-green)	Lavigne and Ronald (1975a)
	495-496 (blue-green)	Lythgoe and Dartnall (1970)
Southern elephant seal	485-486 (blue)	Lythgoe and Dartnall (1970)
OTARIIDAE		
Northern fur seal	499.9 (blue-green)	Lavigne and Ronald (1975a)
California sea lion	497, 501 (blue-green)	Crescitelli (1958)

a moving object at depths of up to 466m on a clear moonlit night, if the water were extremely clear.

The absorption spectrum of the rod visual pigments determines the scotopic or dark adapted sensitivity of the eye. Lavigne and Ronald (1975c) reported a 25-35 min time to full dark adaptation in a harp seal (*Phoca groenlandica*), compared to 30-40 min in humans (LaMotte and Brown, 1970). Scotopic spectral sensitivity proved to be similar in harp, harbour and ringed seals (*P. hispida*), with the best wavelength near 500 nm (Lavigne, 1973). Wartzok's 'greener' value may be a species difference, or might indicate that his seals were not operating scotopically, since dark adaptation is disrupted when the stimuli are presented. Spectrophotometric rod pigment analysis in harp and harbour seals revealed λ_{max} at 496-497 nm (Lavigne and Ronald, 1975a), and in an early study of grey seals λ_{max} was 497 nm (Collett, 1881; cited in Lavigne and Ronald, 1975a) and Lythgoe and Dartnall (1970) found λ_{max} of 495-496 nm in Weddell seals *Leptonychotes weddelli*, and 485-496 nm in southern elephant seals, *Mirounga leonina* (see Table 7.1). Lavigne and Ronald (1975a) interpreted these data to mean that pinnipeds fit the 'sensitivity hypothesis' which proposes that maximum scotopic sensitivity correlates with the spectral energy of light at the depths in the ocean at which the animal feeds (Lythgoe, 1972).

(b) Acuity

The resolving power of the eye is functionally important since it defines the amount of detail which can be seen at various distances. This acuity is affected by light levels, and by ocular refractive error and astigmatism. The phocid eye with its enlarged spherical lens and

cornea which is flattened centrally (Jamieson and Fisher, 1972) sees almost emmetropically under water, and in air suffers severe myopia and, according to the older literature at least, corneal astigmatism. Walls (1942) believed that the locus of this astigmatism was corneal, and Piggins (1970) concluded that this was true for harp seals. Johnson (1893) measured the astigmatism in *Phoca vitulina* and found 4 dioptres (D) in the vertical meridian and 13 D horizontally, rendering an overall astigmatism of 9D. Wilson (1970a, 1970b) found similar values for Weddell seals (4.5 D vertical and 12 D horizontal). Using static retinoscopy, Piggins (1970) reported values for harp seals of -12.5 D in the horizontal meridian, and -8 D vertically* (overall median astigmatic difference = 6, n=12 seals). Piggins later confirmed these measurements on six harp seals using the Placido disc (Piggins, pers. comm). Jamieson and Fisher (1970) confirmed that the axis of greatest corneal curvature was horizontal in *P. vitulina*.

It is important to note that all authors reported difficulty in making the refractions, citing large variability in their data. It is generally agreed that refraction with retinoscopy or ophthalmoscopy, techniques designed for clinical purposes with humans, can be difficult to use in other species (Abrams, 1978; Dawson *et al.*, 1987). Recently, West *et al.*, (1989) refracted the eye of the hooded seal and found no significant astigmatism (less than 1 D). This seal was slightly myopic in air (2-4 D), and somewhat hyperopic in water (2-3 D). Either the hooded seal is an unusual phocid, or the refractions performed on the other species need to be re-evaluated in light of methodological difficulties. West *et al.*, (1989) used photokeratoscopy, which is a more manageable technique than most. A recent refraction of an otariid (*Zalophus*, see p. 357) in which a similar method was used also found no regular astigmatism.

If the seal's eye does suffer astigmatism, with the horizontal axis having the greatest curvature as all studies prior to West *et al.* maintained, the ability to see in air with any acuity might be explained by the characteristics of the pupil. The vertically slit stenopaeic (*στένως*, little; *διά*, opening: Abrams, 1978) pupil can close down in bright light more than a large round one could. When this slightly key-hole or inverted tear-drop shaped opening constricts (see Figure 7.1) it leaves a small aperture at the top to permit pinhole focusing in the horizontal meridian, thereby producing good depth of field in spite of the large refractive error of this axis. As much light as possible is then admitted through the vertical pupil, which is aligned along the axis with the smallest error of curvature. However, since

* Piggins (1970) reports his refractive findings in optometric prescription form, with reference to the axes of the cylindrical refractive power, not the meridians of the eye.

phocid acuity has not been ascertained in varying levels of background luminance this mechanism remains untested for true seals (and see pp. 356-358).

Since the cornea is optically unnecessary in water, it is not clear why it would have developed axes of curvature which cause it to be aurally astigmatic upon readaptation to an aquatic environment. Jamieson (1971) proposed that it was for reasons of streamlining to protect the shape of the eyeball and hence the viewing surface. According to his arguments, the main water flow over the pinniped eye should be vertical, and the decreased curvature found in this axis should reduce water resistance in this direction. Otherwise, as the eye advances through water, there would be a pressure differential between the nasal and caudal edges of the eye as the animal swims, possibly resulting in distortion of the eyeball itself and therefore a reduction in visual performance.

The impact of aerial astigmatism (if it exists), and the myopia caused by the addition of corneal refraction in air has not been directly assessed in phocids. Uncontaminated behavioural measures of their visual acuity are few. Early methodologies which intended to measure acuity may have measured brightness discrimination instead. Jamieson and Fisher (1970) trained two harbour seals to distinguish between a black bar and two black lines separated by gaps of varying widths in an attempt to determine the smallest separation in the latter that the animals could resolve. However, the authors concluded that the seals were probably making their judgments on the basis of the brightness of the white space between the lines, rather than on the width of the separation. From a distance of 1.7m, the seals could detect a gap as small as 1 mm, and could do so equally well in air and underwater. Since there was no difference in performance in the two media, the authors suggested that the 15.9-20.7 candela/m² brightness of the white patch separating the lines was what the seals attended to, a confound which had been identified in other studies using similar methods (Riggs, 1965).

Feinstein and Rice (1966) trained two *Phoca vitulina* to discriminate underwater between discs differing in size to varying extents. They found that the seals were able to distinguish between two black discs which differed in size by between 1.03:1 and 1.06:1. However, the possibility that the animals were making their decisions on the basis of brightness was not eliminated. Schusterman and Balliet (1970) used gratings of black and white stripes of various widths, equated in brightness to similarly sized grey stimuli to measure the acuity threshold of a harbour seal underwater. This method prevented the seal from using brightness cues to solve the discrimination task, thereby correcting the methodological difficulties of the earlier studies. With 85-130 mL ambient light, the

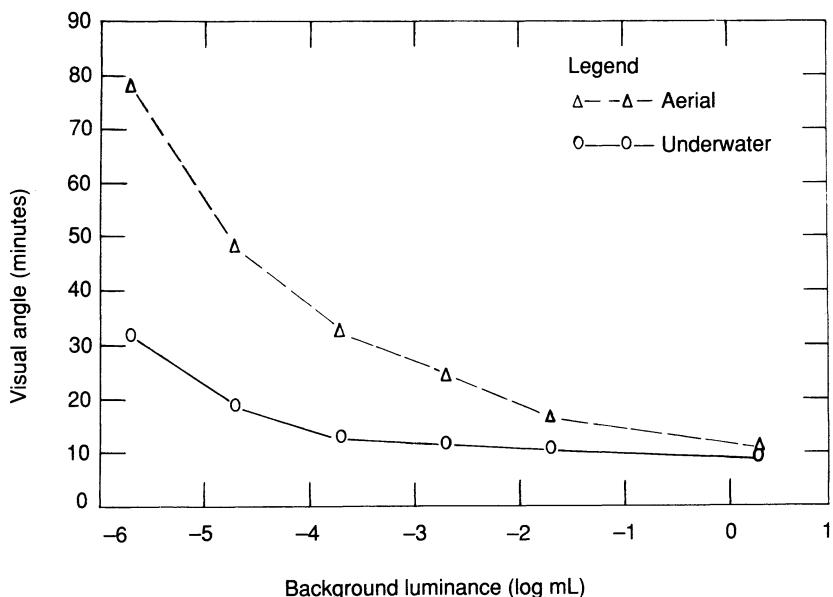


Figure 7.2 The aerial and underwater visual acuity thresholds of a California sea lion as a function of increasing luminance. Adapted from Schusterman and Balliet, 1971.

harbour seal revealed 8.3 minutes of visual angle underwater. Though this is poorer performance than the human in air (0.7 minutes of arc, Keesey, 1960), it compares favourably with the 5.5 minutes of arc thresholds of the cat (see Schusterman, 1972). Unfortunately, the study has not been repeated in air with varying levels of background luminance, so the putative role of the stopped down stenopaeic pupil cannot be assessed (see Figure 7.2 for luminance functions in Otariidae).

Wartzok and Ray (1976) reported psychophysical data from *P. largha* which suggests this seal's acuity in water is similar to the human's in air. The human Weber fraction* for line length discrimination is 0.029 and the spotted seal's fraction for judging the difference between the sizes of discs was 0.026 (they argued that brightness differences between the discs were too small to be used as cues). These tasks may not be equivalent since deciding area differences between discs does not necessarily entail the same acuity

* Wartzok and Ray (1976) found that the seal's visual processing obeyed Weber's law $\Delta M = kM + C$ (where ΔM is the just-noticeable-difference, M is the stimulus magnitude, c is a constant reflecting the absolute threshold, and k is the Weber fraction) which roughly holds true in all species and modalities tested. This law states in effect that the ability to distinguish between stimuli (in this instance visual acuity) is a constant proportion of stimulus magnitude. This proportion is the Weber fraction.

process as discriminating between lines of different lengths.

(c) Colour vision

Whether or not seals have colour vision has been debated ever since the similarity between the seal's eye and that of nocturnal animals was recognized. Landau and Dawson (1970) found no evidence of cones in the retina of harbour seals and northern elephant seals, but described the presence of cone-like receptors which were also reported by Nagy and Ronald (1970) in the harp seal retina. Jamieson and Fisher (1971, 1972) suggested that the traditional classification of retinal receptors into rods and cones might be inappropriate for the seal eye, and proposed instead that the three-receptor classification of Pedler (1969) might be applicable. They suggested that the cone-like receptors they found in harbour seals, and those reported by those investigating other species, might in fact be Pedler's Type B cell, a relatively sensitive polysynaptic receptor described in the fovea of the monkey.

Lavigne (1973) presented indirect but compelling arguments that seals have two photoreceptors. He found a 25 nm Purkinje shift, i.e. a shift in peak spectral sensitivity from 550 nm in the photopic eye to 500-525 nm in the scotopic eye of harp seals. This implies that there are two receptor types with different absorption spectra, one evident in the lightened and the other in the darkened condition. In addition, when the amount of light of various wavelengths needed to constrict the pupil area by 50% was ascertained in harp, harbour and ringed seals during the course of dark adaptation, a rod/cone break became apparent when the data were plotted in probits against log luminance. Lavigne interpreted this transformation of what was originally a sigmoid function to indicate a change from cone to rod operation. In another study, when dark adaptation thresholds to 450 nm (blue), 560 nm (yellow) and 600 nm (orange) light were ascertained in a harp seal, an apparent shift in improving sensitivity during the course of dark adaptation was in evidence (Lavigne and Ronald, 1975c; Lavigne *et al.*, 1977). This change midway through dark adaptation to a larger, but more gradual increase in sensitivity occurs in species known to have rods and cones, and argues for two separate receptor systems for light and dark in seals.

Bernholz and Matthews (1975) used the critical flicker fusion frequency (CFF) to ascertain a separate function for rods and cones underwater. In other mammals, the rate at which a stimulus must flicker before it is perceived as being a constant is higher for cones than rods, so that when the CFF is plotted against stimulus intensity two separate functions emerge. Bernholz and Matthews discovered in harp seals a clear change in this fusion threshold at $-3.77 \log \text{mL}$,

thus providing further indirect support for at least two retinal receptors.

The only direct demonstration of colour vision in a pinniped has been that of Wartzok and McCormick (1978) with a spotted seal. In ambient light bright enough to saturate the rods, the animal was trained to discriminate in air between orange and blue targets produced using 440 nm and 600 nm λ_{\max} Wratten filters. The relative brightness of each stimulus was varied in such a way that it could not be used as a discrimination cue. The task was considered learned once the animal made only six errors in 30 trials. Though this criterion is unusually lenient, the seal reached it after 360 trials of training, which is quite fast.

7.3.2 Otariidae

(a) Sensitivity

Very little study has been made of visual sensitivity in otariids. Their retina, like that of phocids, is rod dominated, with no area centralis, and the ratio of receptors to ganglion cells is high (200:1 in northern fur seals (*Callorhinus ursinus*) and California sea lions (*Zalophus californianus*) (Landau and Dawson, 1970). There is also a reflecting tapetum (Walls, 1942; see Figure 7.1). Spectral sensitivity in *Callorhinus* (Lavigne and Ronald, 1975a) and *Zalophus* (Crescitelli, 1958) showed a 3–5 nm shift in λ_{\max} to 500 nm in comparison with some phocid measures (see Table 7.1). Lavigne and Ronald (1975a) indicated that both otariid estimates were highly variable, and need confirmation. The sensitivity hypothesis would predict green-sensitive pigment for the shallow coastal waters inhabited by these species. Lavigne and Ronald (1975a) suggested that a λ_{\max} near 500 nm may simply be 'terrestrial' rhodopsins.

(b) Acuity

Visual acuity is well documented in some otariids thanks to the work of Schusterman and his associates. As was the case in phocids, early measures of size discrimination, and hence indications of acuity, may have unintentionally been measures of brightness (Baldwin, 1966; Schusterman, 1968; Schusterman et al., 1965). Later studies which used gratings to measure visual angle reported a 7.1 minutes of arc threshold for Steller's sea lions (*Eumatopias jubata*) underwater (Schusterman and Balliet, 1970a). These investigators also compared aerial and underwater acuity of *Zalophus* using a novel conditioned vocalization technique in which two sea lions were trained to emit a burst of clicks when a resolvable grating was

presented (Schusterman and Balliet, 1970b). They tested the animals at three distances from the targets: 1.9 m, 3.1 m and 5.5 m. Thresholds were equivalent in air and underwater, except at 3.1 m, in which case acuity was poorer in air. Schusterman (1972) felt that this may have been because this was the first distance at which thresholds were measured, and therefore difficult judgments were required of the animals. Overall, however, a visual angle of 5.5 minutes of arc was obtained in both media.

The equivalent performance in air and water may have been a result of the ambient light level being high since the animals were tested each morning out of doors. In a later study (Schusterman and Balliet, 1971) in which visual angle was determined with different levels of background luminance, aerial acuity was much poorer than that shown underwater when luminance was low. However, in bright light, thresholds in air were equal to the best sensitivity in water (see Figure 7.2). Schusterman and Balliet (1971) interpreted the more rapid deterioration of acuity with falling luminance in air to mean one of two things. Either the pupil dilates under low light levels and acuity is reduced by corneal astigmatism, or the pupil constricts under such conditions, resulting in reduced light entering the eye and therefore reduced performance. Jamieson and Fisher (1972) showed in *Phoca vitulina* that pupil dilation is affected only by light intensity, not by a change in medium *per se*. Therefore, until 1987 the accepted explanation of the luminance data of Schusterman and Balliet (1971) was that the animal overcomes corneal astigmatism in bright light in air by closing down to a stenopaeic pupil.

A refraction of the *Zalophus* eye led to a different understanding. Johnson (1901) was the only report of refraction of an otariid eye in which *Eumatopias jubata* showed myopic astigmatism equivalent to the harbour seal of 13 D horizontally and 4 D vertically. Dawson *et al.* (1987), in the first examination of the cornea of an otariid eye since Johnson, found that in fact there is no regular (meridional) astigmatism, but the eye is instead bifocal. They found a 6.5 mm diameter circular region near the centre of the cornea which is essentially optically flat (less than 2D), refraction through which revealed emmetropia. Dawson *et al.* suggested that this functions as an aerial cornea through which *Zalophus* looks when the head is out of water. Decreased luminance would still reduce acuity in aerial vision as Schusterman and Balliet (1971) found, for as the pupil dilates the focused image which passes through the corneal window would be 'diluted' by the defocused light passing through the remainder of the cornea (Dawson *et al.*, 1987). They cited Schusterman's (1972) comment that *Zalophus* made 'special postural adjustments' when looking at targets in air, which they suggested supports the

postulation that different corneal regions are used for viewing in air and underwater.

Whatever the mechanism which allows effective aerial vision, Schusterman (1975) calculated that, underwater, sea lions should be able to recognize small surface fish at depths of 200 m on cloudy nights and slightly more than 1000 m under ideal viewing conditions with the fish well silhouetted.

(c) Colour vision

The high sensitivity of the otariid retina, and their habit of fishing at night, led as it did in the phocid literature to the probably faulty assumption that the animals do not have colour vision because they should not need it. Since otariids are more dependent on the terrestrial environment than phocids, this kind of argument is even less acceptable. Baldwin (1966) tried to train *Zalophus* to discriminate between orange and red tennis balls without success, and otariid colour vision has not been demonstrated directly since.

Lavigne and Ronald (1975b) re-analysed the data of Schusterman and Balliet (1971). They plotted log visual angle against log luminance, and showed that the data fitted Hecht's (1937) theoretical photochemical equation for visual angle well enough to suggest the responses of two receptor systems. Further derivations of the relationship between visual angle and background luminance using multiple regression analysis also suggested a rod/cone break, though the location of the break was shifted from $-2 \log \text{mL}$ in water to 0.00 log mL in air. Lavigne and Ronald (1975b) suggested that this shift occurred because the large loss in aerial acuity as a function of pupil dilation with decreasing luminance obscured the loss suffered by cones at the same light level. To date, these data are the only support of colour vision in otariids.

7.4 HEARING

The adaptations that vertebrate sensory systems evolved upon leaving the water have become handicaps for functioning in that medium. I have already described the problems encountered by the terrestrial eye when the corneal interface becomes optically non-existent under water. In audition, the middle ear faces analogous difficulties. This transformer is not only unnecessary underwater but also introduces a hearing impediment.

The strength of sound as it travels the route to the cochlea of the terrestrial ear would be reduced in water because of the impedance mismatch between the aqueous medium surrounding the animal and

the air-adapted middle ear apparatus. The latter acts as a transformer, amplifying airborne sounds sufficiently so that they can be transmitted through the liquid-filled, hair-lined inner ear designed originally to work in water. Upon return to the ocean, pinnipeds are, in theory, disadvantaged by this air adapted transformer which they must retain because of their amphibious requirement to be able to hear in air as well. Furthermore, since sound is transmitted about 4.5 times more quickly in water, the mechanism for directional hearing which relies on differences in sound reception at each ear ought in theory to have receptors which are 4.5 times further apart. Instead, at worst, the submerged head is sound transparent and the effective interaural separation is reduced to that between the cochleas instead of the ear openings. As was the case with vision, otariids and phocids may have reached different solutions to these problems of amphibious operation.

7.4.1 Phocidae

(a) Frequency response

Gross anatomy would have one believe that the seal ear has not developed any major re-adaptations for functioning underwater, retaining the basic vertebrate pressure difference design. Apart from some modifications to enhance directional hearing which will be described below, the most obvious distinctions between the phocid ear and that of the typical land mammal are that the mass of the ossicles has been increased, and there is cavernous tissue in the middle ear cavity and the meatus, the external entrance to which in seals is capable of closing voluntarily (Møhl, 1967, 1968b; Repenning, 1972).

These modifications are as likely to be in response to the need of the ear to withstand increased pressure underwater as to auditory functioning *per se*. Presumably as the animal dives, the pressure differential on an air-filled middle ear and meatus would be eliminated if these cavities fill with blood. If this occurs, enlarged ossicles would be needed to drive the now denser middle ear medium, assuming that in water the route to the cochlea is via the middle ear. The ossicles should be able to operate in a liquid (Repennning, 1972). They are firmly attached to the epitympanic wall by a loose mucosal fold, which should allow the stiffness of ossicular suspension to increase as the middle ear fills with blood, and possibly improve its high-frequency sensitivity (Ramprashad, *et al.* 1972). This would also eliminate the impedance mismatch between the surrounding medium and the middle ear, but create problems for the cochlea if sound is then amplified (Repennning, 1972). Collapsing and sealing the meatus upon submerging should also prevent impedance

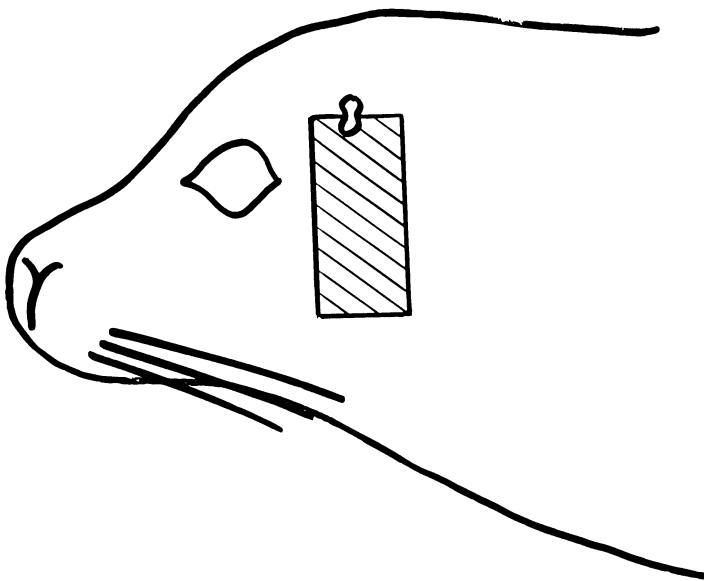


Figure 7.3 The hatched area ventral to the meatal opening indicates the route of sound to the cochlea when the seal's head is submerged. Adapted from Møhl and Ronald, 1975.

mismatches with this cavity and the surround (Terhune and Ronald, 1971). Possibly more importantly, this would eliminate the meatal 1/4 wave resonance which at least in humans boosts sounds in the 4 kHz region by 12 dB (Weiner and Ross, 1946).

Møhl (1964, 1968b) suggested various models to account for seals' amphibious hearing. One proposed that there is a single input which operates in both media, and a variable transformer in the middle ear which can alter impedance from high for operation in air to low for underwater function. A second model predicted that there are two separate input terminals, one for each medium. In a cochlear microphonic study with harp seals, Møhl and Ronald (1975) found that when the head is in air sound is transmitted via the meatus, but underwater sound enters the head in an area immediately ventral to the ear opening (see Figure 7.3). The data suggested further that the two inputs merge before they reach the middle ear. Perhaps a combination of Møhl's two models might be most appropriate, i.e. a middle ear transformer with two parallel inputs. A candidate for the transformer might be the cavernous tissue, which could adjust the middle ear resonance and overall signal volume depending on the extent of tissue engorgement. Another candidate might be the middle ear reflex which occurs in seals in response to loud sound (Møhl and Ronald, 1975). This reflex results in muscular stiffening which should decrease sensitivity in air but increase it in water (Møhl, 1964).

There are some other anatomical peculiarities of the phocid ear. In many species, the ratio between the area of the tympanic membrane and the oval window is smaller than in terrestrial mammals (Repennig, 1972). Since sound is amplified when the oval window is smaller than the tympanic membrane (Yost and Neilson, 1977), Repenning suggested that the ratio reduction which occurs in seals protects the cochlea from excessive stimulation when the tissue on either side of the tympanum is engorged when the animal is submerged. The round window is about three times bigger than the oval window, both membranes being larger overall than in fissiped carnivores, in which the two are roughly equal. Repenning (1972) proposed that the size difference between the two windows would amplify bone-conducted sound. There is an unexplained articulation between the malleus and the incus in harbour seals (Møhl, 1968b) reported also in harp seals as an anterior concavity on the malleus by Ramprashad *et al.* (1972). The lack of a pinna, a definitive characteristic of Phocidae, is thought to be for reasons of streamlining. The major auditory consequences of this pertain to directional hearing, and the loss of the ability to turn the pinna toward a sound source to improve the signal to noise ratio of high frequencies (Møhl, 1968b). The inner ear has undergone some alterations in that the basal whorl is enlarged, and the cochlear aqueduct is proportionately wider than that found in the terrestrial ear (Ramprashad *et al.*, 1972). It has been suggested (Møhl, 1968b) that the enlarged aqueduct would facilitate inertial bone conduction, wherein the entire cochlear capsule is moved, and its fluids are set in motion relative to the organ of Corti by inertial lag. These enlargements may also be a consequence of having to deal with greater pressures if the middle ear is boosting sound free of impedance losses.

If the phocid ear were a terrestrial mechanism, calculations of the energy loss as sound travels between two media of different acoustic impedances predict that there ought to be a 30 dB (power reference) hearing loss in water (Møhl, 1968a, 1968b). If the ear were fully water adapted by some means not obvious anatomically, the same hearing loss should occur in air. However, behavioural measures of the sensitivity of the auditory system do not unequivocally support either prediction. Audiograms (absolute intensity thresholds at various frequencies) have been ascertained in behavioural studies with harbour, harp and ringed seals (see Table 7.2), and electrophysiological measures of sensitivity have been reported in grey and harbour seals and there is fair agreement across species and methodologies.

Thresholds have been measured in air between 1 and 22.5 kHz in harbour seals (Møhl, 1968a), and 1 and 32 kHz in harp seals (Terhune and Ronald, 1971). Harbour seals showed the typical U-shaped

Table 7.2 Psychophysical determinations of the audiograms of some phocids and otariids in air and water

Air (dB re: 20 µPa)			Water (dB re: 1 µPa)			
Frequency (kHz)	Harbour seal ^a	Harp seal ^b	Harbour seal ^a	Harp seal ^c	Ringed seal ^d	Hawaiian monk seal ^e
0.76			77			
1	36	33	84	78	75	
1.4	34	39		69	79	
2	19	33	75	68	79	97
2.8	22	37		68	80	
4	26	29	73	75	75	92
5.6		34		74	74	
8	19	38	67	69	77	99
11.3	16	35		69	70	
16	26	41	64	71	70	65
22.5	58					
22.9		41		66	72	
24						67
30						87
32		42	63	74	75	
40						128
44.9				76	72	
45			72			
48						>141
55				81	87	
64			106	103	110	
90			120	114	115	
100				156		
128			125			
180			133			
Air (dB re: 20 µPa)			Water (dB re: 1 µPa)			
Frequency (kHz)	Northern fur seal ^f	California sea lion ^f	Northern fur seal ^g	California sea lion ^g		
0.25					114	
0.5	27				94	
1	29	41	94		85	
2	9	19	69		81	
4	22	26	59		86	
8	13	16	61		81	
16	7	28	64		79	
24	22	37			84	
28			60		84	
32	34	61	76		91-113	
36					127	
42			77			
48					137	
64					145	

^a (Mohl, 1968a). ^b (Terhune and Ronald, 1971). ^c (Terhune and Ronald, 1972). ^d (Terhune and Ronald, 1975a). ^e (Thomas *et al.*, 1990). ^f (Moore and Schusterman, 1987). ^g (Schusterman *et al.*, 1972).

* Averaged over two seals. † Thresholds averaged over two animals except at 500 Hz in air. ‡ Abstracted in Schusterman and Moore (1980). § Abstracted in Schusterman and Moore (1978a).

function (range = 42 dB), with best sensitivity at 11.25 kHz and with another trough at 2 kHz. Bullock *et al.* (1971) recorded evoked potentials from the inferior colliculus and adjacent brain stem regions of a harbour seal in a study which dealt primarily with 12 *Zalophus*. They reported best sensitivity between 4 kHz and 6 kHz in air, with no response able to be elicited above 30 kHz. However, the sea lion and harbour seal data were not clearly differentiated so the details of the harbour seal response were obscured. The harp seal's aerial audiogram was flatter (range = 13 dB) than that of the harbour seal, with the lowest threshold at 4 kHz. The flatness of the harp seal audiogram and the higher thresholds suggest that some masking by the background noise may have occurred. However, Terhune and Ronald (1971) claimed that the audiogram was free from masking on the basis of their calculations of the seal's critical ratio.

Grey seal cortical evoked responses were obtained in response to sounds presented in air between 20 kHz and 30 kHz (Ridgway and Joyce, 1975). In spite of questionable use of evoked potentials as indicators of absolute hearing (cf. Saunders, 1971) 'thresholds' thus obtained agree well with those from the behavioural studies of other seal species. Electrodes were surgically implanted on the left temporal region, posterior to the external meatus of four seals. The cortical potentials were transmitted telemetrically on FM carriers, and the minimum sound intensity at which a recognizable evoked response occurred was noted. These intensities plotted against frequency formed a U shaped curve, with best sensitivity at 4 kHz (10^{-15} W/cm², taken from a graph).

Five species have been tested in water (see Table 7.2) above 1 kHz (0.76 kHz for *P. groenlandicus*) and four showed a relatively flat audiogram below 64 kHz (ranges = 21 dB for harbour, 17 dB for ringed, 18 dB for harp and about 20 dB for grey seals as extracted from a graph). The Hawaiian monk seal (*Monachus schauinslandi*) exhibited a much narrower range than the other phocids, with relatively poor bearing at 8 kHz and below, and at 30 kHz and above. Best sensitivity was at 32 kHz for harbour (Mohl, 1968a), 22.9 kHz for harp (Terhune and Ronald, 1972), at 11.3 kHz and 16 kHz for ringed (Terhune and Ronald, 1975a) at 16 kHz for monk seals (Thomas *et al.*, 1990), and between 20 and 25 kHz (60 dB re: 1 μ Pa taken from a graph) for the grey seal, as indicated by its cortical response (Ridgway and Joyce, 1975). With the exception of the monk seal, thresholds increased abruptly at 64 kHz, but revealed the ability to detect the highest frequencies tested (180 kHz, harbour; 100 kHz, harp; 90 kHz, ringed; and 150 kHz, greys). In an underwater study by Terhune (1988), *Phoca vitulina* showed higher thresholds for short-duration (≤ 50 ms) repeating signals than for longer ones (≥ 100 ms). With the exception of the physiological measurements of Ridgway

and Joyce (1975) in which repeating 100ms tones were used, the signal durations in all of the above reports were all longer than this.

Comparisons of aerial and underwater hearing reveal a 15 dB (power reference) loss in air for harbour seals (Møhl, 1968a), and a 28 dB loss for harps (Fobes and Smock, 1981). The grey seal's evoked responses showed better hearing in water; however, the precise extent of this hearing difference cannot be ascertained from Ridgway and Joyce's graphical presentation of the data. The deviation appears to be of the same magnitude as in the behavioural studies, but less pronounced at low frequencies. Terhune (1989) proposed that if the middle ear and meatal cavernous tissues were still engorged when a seal surfaced to listen in air, the 30 dB hearing loss predicted by Møhl (1968a, 1968b) would be evident. However, once these tissues drain, thereby lowering the acoustical impedance, aerial sensitivity would be enhanced. The aerial thresholds of the harp seal which showed a 28 dB loss were obtained with the animal able to submerge between trials. When Terhune tested a harbour seal which was similarly given access to water between trials, aerial thresholds differed from under water ones by 27–40 dB between 1 and 8 kHz. Unfortunately Møhl (1968a, 1968b) gave no indication of the amount of time the harbour seal he tested (15 dB loss) kept its head out of water between trials. Interestingly, the cochlear microphonic study of Møhl and Ronald (1975) suggested an overall 20 dB reduction of sensitivity in air, but also found occasional sudden decreases in sensitivity as the seal was raised toward the surface, as if vascular adjustments were occurring in preparation for impending aerial function. In any event, the more sensitive underwater hearing over a broader frequency range indicates, in spite of anatomy, an auditory system designed to operate best in water.

(b) *Upper hearing limit*

Though the detection of very high frequencies in water was reported for all but one species examined, it seems likely that the effective upper limit of hearing is in the vicinity of 60 kHz. At this point, all but the monk seal's audiograms showed sudden losses in sensitivity which flatten out somewhat near 100 kHz. It is likely that, in water, hearing above 60 kHz is mediated primarily by bone conduction. The shape of the curve agrees well with human data which revealed that when sounds were transmitted underwater and conducted via bone all frequencies above about 15 kHz are perceived as being the same pitch. The human sensitivity curve showed a similar flattening near the upper frequencies tested (Corso, 1963).

Precise determinations of the ability to discriminate between frequencies were made with harbour and ringed seals underwater and, as expected from the audiograms, above 60 kHz the difference

threshold increased abruptly. In harbour seals, for example, a signal which changed every second in frequency from 57 kHz to 57.54 kHz was perceived as a fluctuating tone, but at 62 kHz the seal behaved as if a signal with a 16 kHz frequency modulation were a constant pitch. Had larger deviations been employed, intensity cues could probably have been used to make the discrimination (Møhl, 1967). Ringed seal data were to some extent contaminated by difficulties in producing constant-amplitude signals and problems with motivation of the two seals used in the study. Terhune and Ronald (1976) believed that the higher difference thresholds they found were attributable to this. However, assuming that these errors were constant across all frequencies tested (which may not be fair since the authors did not randomly vary the FM signal intensity to prevent the seals from discriminating on the basis of loudness cues), both seals showed roughly a threefold decrease in their ability to distinguish constant from modulated tones at 60 kHz.

In air, the harbour seal showed a 32 dB hearing loss at 22.5 kHz (Møhl, 1968a), suggesting an aerial upper hearing limit near 20 kHz for this species. Since the harp seal's audiogram in air is relatively flat (see Table 7.2), judgment about its upper hearing limit in air should be reserved.

(c) Masking

Audiograms are determined in the quiet, but the animal must function in the noisy environment of the real world. Masking has been investigated in harp, ringed and harbour seals, and the parameter ascertained was the critical ratio, which is essentially the amount by which a threshold is raised by a given noise level. Not all frequencies in white noise raise a particular threshold, just those within a critical bandwidth surrounding the test frequency; the total energy of the noise in this critical bandwidth equals the amount by which the threshold at the centre frequency is raised. The results obtained are comparable in all species of seals tested in air (see Table 7.3), and are somewhat lower than the general mammalian result. A harp seal (Terhune and Ronald, 1971) indicated a 23 dB critical ratio at 2 kHz, and 26 dB at 4 Hz. At 8.6 kHz the seal's behaviour was apparently unstable, and the authors felt that the 35 dB critical ratio they measured was possibly not reliable. Since this seal's false alarm rate was lowest at this frequency, its threshold was likely raised for this reason if for no other. Harbour seals showed critical ratios ranging from 21 dB to 26 dB (Renouf, 1980a; Turnbull and Terhune, 1990) when tested in air between 2 kHz and 16 kHz.

Underwater measurements were made with two ringed seals and a harbour seal (Terhune and Ronald, 1975b; Turnbull and Terhune,

Table 7.3 Critical ratios of some phocids and otariids in air and water

Air			Water		
Species (Reference)	Signal (kHz)	Critical ratio	Species (Reference)	Signal (kHz)	Critical ratio
PHOCIDAE					
<i>Harbour seal</i> (Turnbull and Terhune, 1990)	2	25	<i>Harbour seal</i> (Turnbull and Terhune, 1990)	4	19
	4	23		8	22
	8	21		16	25
	16	23		32	27
<i>(Renouf, 1980a)</i>	2	24			
	4	26			
	8.6	25			
	15	26			
<i>Harp seal</i> (Terhune and Ronald, 1971)	2	23	<i>Ringed seal</i> (Terhune and Ronald, 1975b)	4	30
	4	26		8	32
	8.6	35		16	34
				32	35
OTARIIDAE					
			<i>Northern fur seal</i> (Moore and Schusterman, 1987)	2	23
				4	19
				8	21
				16	25
				32	27
			<i>(Moore and Schusterman, 1978; given in Schusterman, 1981)</i>	4	20
				8	20
				16	25
				32	27

1990). Between 4 kHz and 32 kHz, the critical ratios varied from 30 dB to 35 dB in ringed seals, and from 19 dB to 27 dB in harbour seals (see Table 7.3).

This consistency of the aerial measurements is not surprising since the critical bandwidth is supposed to be related to the architecture of the cochlea (Greenwood, 1961), representing equal distances along the basilar membrane. This has been taken as an indication that the inner ear processing mechanism of seals is similar to the general mammalian design (Terhune and Ronald, 1971; Fobes and Smock, 1981). If Greenwood's contention is correct that the structure of the basilar membrane is a major determinant of masking effects, there would be no reason to expect differences between air and water. Harbour seal critical ratios are similar in air and water, and of comparable magnitude to the underwater values for northern

fur seals (see p. 371); however, the higher underwater critical ratios of ringed seals are difficult to explain. Signal detection theory would predict the highest masked thresholds in the harp seal study in which the animal was punished for errors (false alarms and misses) by administering jets of compressed air which the animal apparently found disturbing. Reinforcement was withheld for errors in all studies, and Renouf (1980a) employed salient signal catch trials in addition to silent ones, to offset the response bias created by signal probabilities. Nonetheless, the ringed seals' critical ratios were larger than all other measures which were in fair agreement. It is unfortunate that the aerial critical ratios have not been ascertained in ringed seals to rule out the possibility that this species is idiosyncratic.

The critical bandwidth allows some calculation of the practical hearing abilities of seals in the noisy environments in which they must operate. If both background noise and signal levels are known, the distances at which the seal ought to be able to distinguish signal from noise can be estimated. The harbour seal mother, for example, seems to monitor the continuous vocalizing of her pup to keep track of the youngster when the two are at sea. The mother should be able to hear a 70 dB re: 20 μ Pa pup call (aerial), in 25 dB (spectrum) noise, which is moderately quiet, at distances up to 8 m. Fortunately, the pup shows an imprinting-like predisposition to follow its mother more closely than this (Renouf, 1984; Perry and Renouf, 1988).

(d) *Directional hearing*

The mechanism responsible for directional hearing in mammals is the differential reception of sound by two spatially separated ears. Comparisons of phase and arrival time differences govern the perception of the location of the source of low-frequency signals whose wavelength is large in relation to the size of the interaural distance (at least twice as large). Intensity differences become important at the smaller wavelengths of higher frequencies. In all of this, the distance separating the receptors is critical.

The poor ability of human divers to locate sound underwater without extensive experience is well known (Feinstein, 1966, 1975; Hollien, 1973), and is attributed to the reduced interaural separation resulting from bone conducted sound in water. It was of interest to discover whether seals are similarly impeded by the use of bone conduction underwater, which reduces the effective interaural separation to the 6 cm or so between the cochleas, instead of the 12 cm between the external surfaces. Although the bullae are not as extensively attached to the skull as they are in terrestrial mammals, they are still attached, so bone transmission is possible. If the critical separation is between the external orifices in both air and water, the

Table 7.4 Directional hearing (minimum audible angle (MAA), calculated as cited) of some phocids and otariids

Air			Water		
Species (Reference)	Signal	MAA (degrees)	Species (Reference)	Signal	MAA (degrees)
PHOCIDAE					
<i>Harbour seal</i> (Møhl, 1964) (Terhune, 1974a)	500 Hz Click	4.8 3	<i>Harbour seal</i> (Møhl, 1964) (Terhune, 1974a)	2 kHz Click	3.1 9
OTARIIDAE					
<i>California sea lion</i>					
			(Gentry, 1967)	3.5 kHz 6 kHz Click	15 10 6-9
			(Moore, 1975) (Moore and Au, 1975)	0.5 kHz 1 kHz 4 kHz 8 kHz 16 kHz	12 4 42.4 13.5 18

directional hearing of seals should be poorer in water because of the differences in sound transmission speed, and hence wavelength, in both media. If sound is bone conducted in water, location ability should be even worse. Preliminary behavioural measures of the directional hearing skills of *Phoca vitulina* in both media show comparable minimum audible angles (MAA) in each (see Table 7.4). Møhl (1964) tested one seal in an enclosure in Strib harbour, and used signals of 500 Hz in air and 2 kHz in water. He employed these frequencies because phase would be the same in air and water if the interaural separation were the equivalent in both places. The similarity of the MAAs found by Møhl in both media suggested that phase is the important cue for localizing low frequencies, as it is in most mammals, and that the interaural separation is the same in air and water.

Terhune (1974a) tested the directional hearing of a harbour seal using click train signals in water (130 dB re: 1 µPa). In air, band-limited noise (55-85 dB re: 20 µPa) and tones (60-65 dB) were presented in addition to repeated clicks (80 dB). The MAA in water was $9^\circ \pm 4$, and in air was $3^\circ \pm 4$ for click trains (see Table 7.4). In air, clicks, and 1/3 octave noise bands above 3 kHz were better localized than low frequency sinusoids. Terhune interpreted the click localization results to mean that time differences were more important than intensity and/or phase cues. Since clicks are broad band, Terhune felt intensity and phase differences would occur in both media, and MAA should be the same in each. Instead, the differences he found

between the MAA in air and water were those predicted by the 4.5 times increase in sound transmission speed in water.

Terhune's (1974a) results further substantiate the hypothesis that the seal's head is not functionally sound transparent in water, since the 6 cm separating the bullae would result in an MAA which is nine times that in air, not the threefold difference he found, assuming the same neurological mechanism in each medium. The hypothesis that the effective separation between the receptors is external was given its best support by a cochlear microphonic study of Møhl and Ronald (1975) with two harp seals. They found that in water the cochlear potential in response to short clicks was greatly reduced when a 7 cm long rectangular region just ventral to the external orifice was shielded with sound opaque material (see Figure 7.3). Such attenuation did not occur when the meatus was plugged, or when other regions adjacent to the effective rectangle were shielded. Furthermore, when clicks originated from one side of the head or the other in water, average time delays from the signal's onset to that of the cochlear potential was 0.47ms on the close side and 0.58ms on the far side. Møhl and Ronald (1975) used these data to calculate a 15 cm interaural difference.

7.4.2 Otariidae

(a) Frequency response

The eared seals have to cope with functioning in water in spite of the middle ear, as do phocids. A 30 dB hearing loss across media is similarly predicted if the otariid ear is entirely water or air adapted. Anatomy is again of little help, though the eared seals' adaptations seem to be less geared for their aquatic medium. Their ossicles are much smaller than those of phocid seals, as are the tympani and bullae. For example, equally sized *Zalophus* and *Phoca vitulina* had ossicles weighing 18mg and 204mg respectively (Møhl, 1968b), and Repenning (1972) reported that otariid ossicles are comparable in relative size to those of terrestrial fissipeds. Otariids have smaller tympanic membranes than phocids, and in most cases have a smaller tympanic membrane to oval window ratio. In both families, this ratio is smaller than that shown by terrestrial carnivores (Repennning, 1972), and as mentioned above may be an adaptation to avoid excessive amplification at the cochlea when the head is submerged.

Aerial and underwater audiograms have been obtained in two species of otariids, *Callorhinus ursinus* and *Zalophus californianus*. Overall, their hearing loss in air is not as extensive as that of phocids. *Callorhinus* is more sensitive at all frequencies tested in air, and at 4 kHz, 8 kHz and 28 kHz underwater, than is any other pinniped

thus far investigated. Underwater, both otariids' audiograms are down-shifted in frequency range compared to phocids (see Table 7.2). Using the conditioned vocalization technique and a staircase-like method of signal presentation, a California sea lion was tested in air and water (Schusterman, 1974a). In air, what were believed to be unmasked thresholds were obtained between 4 kHz and 32 kHz, and revealed a relatively flat audiogram between 4 kHz and 24 kHz (< 10 dB range), with best sensitivity at 4 kHz (about 32 dB re: 20 μ Pa, taken from a graph). The animal displayed a 20 dB/octave loss beyond 24 kHz, and 60 dB/octave loss above 28 kHz. At the same time as Schusterman undertook this study, Bullock *et al.* (1971) recorded evoked potentials from the inferior colliculus and adjacent regions in 12 *Zalophus* specimens in air. The evoked potential (as assessed by eye) was most easily elicited between 4 and 6 kHz, with no response evoked above 30 kHz even with 100 dB re: 20 μ Pa, which is 60 dB higher than should have been required.

In a later study of *Zalophus*, Schusterman and Moore (1980) and Moore and Schusterman (1987) extended the low frequency end of the aerial audiogram to 1000 Hz, and found more of a U shape function than in the earlier study (See Table 7.2) with thresholds rising at 32 kHz. They claimed that the thresholds reported in Schusterman's 1974a paper must have been masked by noise. This seems likely since the early audiogram was quite flat below 24 kHz and measurements were made in an outdoor tank, whereas in the later studies, an acoustic chamber was employed. In the more recent study, reminiscent of *Phoca vitulina*, two sensitivity peaks (See Table 7.2) were found in the aerial audiogram of *Zalophus* (2 kHz and 8 kHz) and *Callorhinus* (2 kHz and 16 kHz).

In water, *Zalophus* was tested using conditioned vocalization between 250 Hz and 64 kHz (See Table 7.2). The audiogram was relatively flat over five octaves (7 dB, 1 to 28 kHz), with best sensitivity at 16 kHz. From 28 kHz to 36 kHz, there was an abrupt loss of 60 dB/octave which flattened out to 14 dB/octave above 48 kHz (Schusterman *et al.*, 1972). This audiogram differs by about 3 dB from the corrected aerial one (Watkins and Wartzok, 1985). Similarly, two northern fur seals showed maximum sensitivity between 2 kHz and 28 kHz, falling off in sensitivity thereafter up to 42 kHz (120 dB/octave) (Schusterman and Moore, 1978a; Moore and Schusterman, 1987). Their aerial and underwater audiograms are similar below 2 kHz, and reconverge at 16 kHz. However, their underwater thresholds are as much as 20 dB re: 1 μ W/cm² better in water at 4 kHz. Moore and Schusterman (1987) interpreted the aerial insensitivity at this frequency to be a consequence of the resonant properties of the extensively modified pinna and meatus in pinnipeds.

(b) Upper hearing limit

A major difference between otariid and phocid hearing is the fact that the eared seals have a lower high frequency limit in water, but possibly a higher limit in air (Schusterman and Moore, 1978b). The steep rise in the aerial audiogram of *Zalophus* at 28 kHz led Schusterman (1974a) to project a 36 kHz effective upper hearing limit in air. Moore and Schusterman (1987) reported increasing hearing losses in air at 24 kHz and 32 kHz in *Callorhinus* and *Zalophus* (See Table 7.2). This does not have the same implication as the upper hearing limit in water, where a switch to bone conduction is thought to occur, resulting in the ability to detect very high frequencies without concomitant spectral recognition. However, the underwater audiogram (Schusterman *et al.*, 1972) indicated the same 36 kHz cut-off, since an abrupt loss of sensitivity occurred between 28 kHz and 36 kHz. This slope flattened out above 48 kHz, which is typical of the shape of the upper region of the human bone conduction curve (Corso, 1963). Intense (i.e. more than 138 dB re: 1 μ Pa) 192 kHz signals were detectable (Schusterman, *et al.* 1972). The audiogram of *Callorhinus* falls off in sensitivity above about 40 kHz underwater (Schusterman and Moore, 1978a; Moore and Schusterman, 1987).

The only study which actually measured difference thresholds in water (Schusterman and Moore, 1978b) revealed that a California sea lion was able to discriminate a 2% frequency difference in an FM tone between 16 kHz and 28 kHz but at 38 kHz this increased to 11.2%. The authors took this as evidence that the effective upper hearing limit is in the vicinity of 32 kHz.

(c) Masking

The only direct investigations of critical ratio in a otariid undertaken underwater with *Callorhinus* (Moore and Schusterman, 1978; Moore and Schusterman, 1987). Thresholds were measured between 2 kHz and 32 kHz in the presence of three levels of masking noise (See Table 7.3). The critical ratios ranged from 19 dB to 27 dB.

(d) Directional hearing

If otariids function with a sound transparent head in water, they will suffer the disadvantages described above which phocids seem to have so nicely obviated by arranging a separate input in air and water. Similar to phocids, otariids have cavernous tissue in the middle ear, and a collapsible external meatus, with the pinna sealing as it folds in on itself (Ramprashad *et al.*, 1972).

Unfortunately, the questions of sound routes and directional

hearing have not been examined to the extent that they have been with phocidae insofar as the requisite cochlear microphonics and measurements comparing performance in air and water have not been made.

The minimum audible angle in water has been ascertained in *Zalophus*, both to pure tones and clicks (See Table 7.4). Gentry (1967) found that in water, a California sea lion demonstrated a MAA of 10° for 6 kHz tones, and 15° at 3.5 kHz. To investigate the suggestion of these data that location performance improves as frequencies increase, Gentry held the angle between the sea lion's head and the transducer constant, and varied the tone in 1 kHz increments from 1.5 kHz to 6.5 kHz. This confirmed the improved performance at smaller wavelengths, the animal showing the most difficulty at 2.5 kHz. Gentry proposed that the sea lion's ability to locate sound in water may be a consequence of neurological adaptations which allow the animal to cope with the smaller interaural differences resulting from bone conduction. It is possible, however, especially in light of the correlation between location performance and wavelength, that the lower frequencies were more affected by reflections of the tank boundaries, and therefore more difficult to localize.

Moore and Au (1975) tested *Zalophus* in a pen floating in a harbour, which would reduce boundary effects substantially. They measured the MAA from .5 kHz to 16 kHz, and found that 1 kHz pulsed tones were located most easily (MAA = 4°). Similar to Gentry, the sea lion showed great difficulty at 2 kHz, so much so that a MAA based upon 70% correct responses could not be ascertained because the animals behaviour became erratic. Performance was almost as bad at 4 kHz, MAA being 42.4°. However, opposite to the trend Gentry found, localization ability worsened as frequency increased thereafter (See Table 7.4). At 500 Hz, 8 kHz and 16 kHz, MAAs were 12°, 13.5° and 18°, respectively. They suggested that performance between 2 kHz and 4 kHz was so poor because this is the range at which there is a switch between the usefulness of interaural phase and intensity cues. Empirical measurements at various frequencies using a *Zalophus* skull showed that intensity differences decreased with frequency, such that below 4 kHz they were very small. The authors concluded that in their study, phase differences were probably the most important localization cues below 1 kHz, since arrival time differences are not likely to be useable with 20msec pulsed signals with 5 msec rise and fall times, and performance was best at the longer wavelengths where intensity could not be used (Moore, 1975). Moore and Au (1975) found with their measurements of intensity differences with the sea lion skull, that above 4 kHz, there were intensity differences between the two bullae of approximately 3 dB. The use of intensity differences above 4 kHz was further confirmed

by Moore and Schusterman's (1976) measurements of underwater intensity difference threshold in the same sea lion that was used in the location studies. The animal was trained to bark to the louder of two 16 kHz tones, and revealed a difference limen of 3.19 dB.

Moore and Au (1975) maintained that the sea lion's head cannot be strictly sound transparent in water since the animal was able to locate sound. They agreed with Gentry's proposition that adaptations allowing localization underwater are likely to be neurological. This hypothesis seems even more likely if the inter-receptor difference is the distance separating bullae as the similarity between the behavioural and skull measurements might be taken to suggest.

Overall localization performance of sea lions in water is about the same as an untrained human who showed MAA's of 21.5° at 3.5 kHz and 14.5° at 6.5 kHz. After training, the human divers performance improved dramatically to MAAs of 11.3° and 11.5° at 3.5 and 6.5 kHz, respectively. Their ability to localize broad band signals was better overall, with a 9.8° MAA before training, and 7.3° after (Feinstein, 1973). Moore (1975) used click stimuli with the same sea lion he employed in the study of underwater localization of pure tones, and reported better performance with a 9° threshold. It is unfortunate that there are no measurements of click location in air, since a 2° or 3° MAA in that medium would indicate as it did in harbour seals, that time of arrival cues permit the best location (Terhune, 1974a).

7.5 TACTILE SENSATION: VIBRISSAE

The only facet of tactile sensation which has been directly investigated in pinnipeds is that mediated by vibrissae, though the possibility of very sensitive tongue and upper lip tissue in the walrus was revealed serendipitously in a study of whisker function in this pinniped (Kastelein and van Gaalen, 1988; Kastelein *et al.*, 1990). Apart from this work, and one anatomical study with *Zalophus* (Stephens *et al.*, 1973), all work has been done with phocids, so *per force* all groups will be discussed together. This is not to suggest that they are the same, since there are obvious differences evident even after cursory examination. For example, the otariids lack the rhinal vibrissae which phocids have (Ling, 1977), and of those species studied thus far, only phocid whiskers have regular lobulations along the length of the hair (Scheffer, 1962; Yablokov and Klevezal, 1969; Ling, 1966, 1972; Miller, 1975;). More striking is the extreme length of some otariid vibrissae, for example those of the Antarctic fur seal (*Arctocephalus gazella*) can reach 41 cm (Ling, 1966). The benthic feeding walrus with its prominent mystacium in which objects can be moved among the whiskers is clearly quite different from the



Figure 7.4 A harbour seal mother and her pup, demonstrating the prominent vibrissae of pinnipeds.

other two pinniped families.

Though nearly all mammals possess these vibrotactile sensors, they are best developed in pinnipeds (Ling, 1966; and See Figure 7.4), and it is tempting to speculate that this is somehow functionally related to the fact that these mammals are not likely to use their reduced forelimbs as tactile agents. *A priori* consideration of the physics of vibratory transmission in water would predict that a rapidly adapting, displacement sensitive organ could be very useful. Because water is virtually incompressible, when an object oscillates it creates a displacement wave in addition to the compressional one. This is true for any type of sound generator, for example a pulsating monopole (eg. fish's swim bladder), or the more complex dipole which propagates a signal without changing volume (eg. fish's tail beat). The intensity of the transverse component is large near its source, but falls off more rapidly than the concomitant pressure wave: the more complex the oscillation, the more rapid the attenuation. Within roughly $\lambda/2\pi$ (where λ is the wavelength of the signal) of the source, the displacement wave predominates, beyond which distance the longitudinal wave retains the greatest amplitude (van Bergeijk, 1964). The area inside this boundary is referred to as the near field, and the water movements in this region should be detectable by a displacement sensor which is innervated by units which can adapt quickly enough to encode vibration. For example, it has been shown that the fish's lateral line is sensitive to the near field and is no doubt important in the co-ordination of schooling (Harris and van Bergeijk, 1962). By this logic, a submerged vibrissa could theoretically detect a vibration without having to touch the source as it must in air. Therefore, regardless of whether or not pinniped whiskers are specialized in comparison to those of terrestrial mammals, they should operate well in water.

Most differences between the structure and underlying anatomy of seals' whiskers and those of terrestrial mammals are quantitative rather than qualitative. The enlargement of the whiskers themselves in seals is accompanied by increases in the extent of innervation (Dykes, 1975; Hyvärinen, 1989) and increased development of the cortical trigeminal sensory area in the sylvian gyrus (Alderson *et al.*, 1960). The hair itself is stiffer than that of land mammals, and for most of its length is flattened to be almost oval in cross section. As mentioned above, in most phocid species the hair shows regular thickenings, the function of which is unknown (Ling, 1966; Hyvärinen, 1989). The follicle is surrounded by three blood sinuses, as opposed to two in terrestrial species (Ling, 1966, 1972, 1977; Stephens *et al.*, 1973; Hyvärinen, 1989). The receptors found in the follicle are similar in *Zalophus* (Stephens *et al.*) and the ringed seal which lives in Lake Saimaa in Finland (Hyvärinen, 1989). Neurites were found which

terminated in association with Merkel cells which have been shown to be mechanoreceptors in other cutaneous preparations (Iggo and Muir, 1963). A lancet shaped termination was also described, and was felt by Stephens *et al.* to be a mechanoreceptor since it was close enough to the glassy membrane of the dermal capsule to be activated by movement of the vibrissa. These workers identified a lamellated corpuscle which they felt resembled the vibration sensitive pacinian corpuscle found in the skin of other mammals (Werner and Mountcastle, 1965). Hyvärinen (1989) described encapsulated end organs in the lower cavernous sinus of the ringed seal, but concluded they were more like 'Ruffin's corpuscles' than the smaller pacinian corpuscles.

In terrestrial mammals there is a field of barrel cells somatotopically organized in the thalamus (Waite, 1969, 1973 a,b) and another of similar distribution in the cortex (Weller, 1972; Van der Loos and Woolsey, 1973; Welker, 1971, 1976, Hinrichsen and Stephens, 1977) each cell driven by its own whisker. This makes the trigeminal circuit and its higher articulations an excellent model for neurophysiological study, especially in pinnipeds where circuitry is so extensive. It is not known whether this arrangement occurs in seals, but it is likely given the other similarities to land mammals, and since Dykes (1975) reported somatotopic arrangement at the peripheral nerve.

To date, the only neurophysiological investigation in pinnipeds was done with grey and harbour seals in air (Dykes, 1975). Single unit recordings at the infraorbital branch of the trigeminal nerve revealed responses of fibres in seals similar to those recorded from cats in the same study. One third of the units were slowly adapting and responded to maintained deflection. The rest of the units were rapidly adapting and therefore able to respond to vibratory stimulation. These units were categorized according to their tuning points into three groups, those which were sensitive to signals which displaced the whisker by as little as 10μ , a second group which required a larger vibration amplitude (at least 70μ) to fire, and those whose tuning points were frequency dependent. All units were similar to most tactile systems in that they showed no indication of being able to respond to frequencies above 1000 Hz.

Psychophysical measurements of the absolute threshold of whiskers to vibration have been made twice in seals, and in both cases thresholds differ from those predicted by the neurophysiological findings. Harbour seals were trained in air to protract their whiskers onto a rod projecting from the surface of a vibration exciter, and they were required to indicate whether or not it was vibrating. Sensitivity increased with frequency, and in the preliminary study the seals were able to detect displacements of less than 1μ at 1000 Hz, the highest frequency tested (Renouf, 1979). The second study

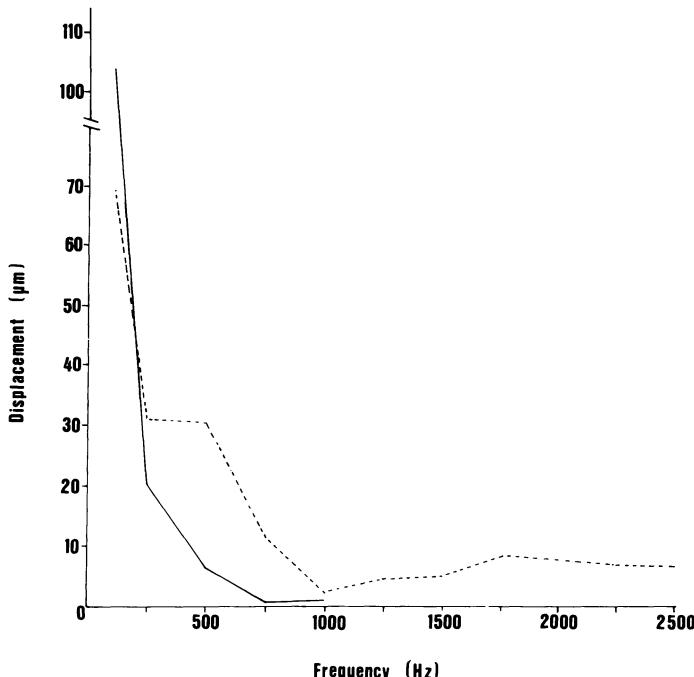


Figure 7.5 The thresholds of harbour seals' vibrissae to sinusoidal displacement of various frequencies. The dotted line illustrates the data from Mills and Renouf (1986) and the solid line is from Renouf (1979). Adapted from Mills and Renouf, 1986.

confirmed the findings of the first, and extended the range to 2500 Hz, beyond which the equipment could not produce a clean signal of sufficient amplitude. At 2500 Hz, the vibrissae showed no indication of becoming less sensitive, so the upper limit of vibrissae sensitivity remains unknown (Mills and Renouf, 1986).

The reason for the differences between the behavioural and neurophysiological findings is unclear, but it may be related to two factors. First, the latter work examined the response of single fibres, whereas the psychophysical measurements were the result of the collective response of the entire physiological network. Second, the vibrissae of the anaesthetized animals used in the physiological study were retracted, whereas the seals in the psychophysical work were required to fully extend their whiskers. It is possible that protraction may somehow alter the frequency response of the hairs, perhaps through sinus filling. This might operate as a mechanism to reduce the enormous low frequency noise which must be created as the animal swims.

Psychophysical studies were undertaken with a male walrus which was trained out of water to use its mystacial vibrissae to discriminate

between 3 mm thick triangles and circles of equivalent surface areas. The animal was able to distinguish both on smooth backgrounds (Kastelein and van Gaalen, 1988) and rough surfaces (Kastelein *et al.*, 1990) a triangle from a square with surface areas of as little as 0.4 cm². When the objects were 0.2 cm² in surface area, the walrus became frustrated and was unable to make the discrimination, attempting occasionally to do so with its tongue and upper lip. The central vibrissae showed superior resolution to the lateral ones which appeared to be used for detection rather than identification of objects.

All of the measurements of vibrissae sensitivity have been conducted with the animal's head in air. Since in each case the stimulus objects made direct contact with the vibrissae, it is likely that the thresholds would not change in water, at least as a consequence of the physics of signal transmission. However, the possibility that cavernous sinus engorgement in stiffening the hair might also increase its sensitivity to vibration and bending has not been investigated. If this sinus fills in water, as do other cavernous tissues in response to diving, underwater thresholds might be lower than those obtained in air.

Though it seems probable that the walrus employs its vibrissae to discriminate relatively immobile food objects from the substrate having made the water very turbid by furrowing with its tusks (Kastelein and van Gaalen, 1988), the context in which pinnipeds use their vibrissae is not well understood. Calculations of the intensity of the near field displacement suggest that the wave propagated by a herring for example, remains above the threshold of the seals vibrissae for a distance of about 0.5 m from the fish. Therefore it seems possible that vibrissae may be used at some stage during fish capture (Renouf, 1979). There is some circumstantial support for this insofar as experienced seals with vibrissae removed, initially take longer to catch live fish (Renouf, 1980b). It has been suggested that vibrissae, in their sensitivity to continuous deflection, might act as a speedometer in seals (Montagna, 1967), since the degree of hair bending should be correlated with the animal's swimming speed. However, a test of this hypothesis revealed that though a harbour seal could be taught to swim at a predetermined speed, performance was not altered when vibrissae were clipped. Though the whiskers may impart sufficient information for speed sensing, it is apparently not necessary that they do so (Renouf and Gaborko, 1982). The hairs are prominently protracted during social encounters (Miller, 1975 and this volume; Renouf, unpublished data) and likely form a component of social display. Unfortunately, nothing else is known about the manner in which pinnipeds use these receptors.

7.6 CHEMORECEPTION

Olfaction is likely to play a substantial role in pinniped behaviour while the animals are on land, having been proposed as an important social indicator and as a means of mother-pup recognition in several otariid and phocid species (Peterson and Bartholomew 1967; Evans and Bastian, 1969; Ono, 1972; Ross, 1972; Kaufman *et al.*, 1975). However, smell would be of dubious value when the animals are underwater. There have been no direct investigations of this sensory channel in pinnipeds apart from the olfactory epithelium having been described as typically mammalian in the fur seal (Kuzin and Sobolevsky, 1976 cited in Lowell and Flanigan, 1980), and the olfactory apparatus as reduced, more extensively so in phocids than otariids (Harrison and Kooyman, 1968). Four taste papillae have been identified in the tongues of various pinnipeds (Bradley, 1971), and there has been one report of taste discrimination in *Zalophus*. Nachtigall *et al.* (1981) presented preliminary results which showed sea lions can taste citric acid in solutions with molarities of 0.025M. Unfortunately further data have not appeared in the literature to date.

7.7 MAGNETIC RECEPTION

Since some pinnipeds seem to be able to function in the absence of conventional sensory input, the possibility that they might be able to detect magnetic fields presents itself, but it has only been investigated so far in harbour seals. After extensive training of harbour seals, I ended in adding to the list of failures to demonstrate magnetic reception. I trained three adults to swim through a Helmholtz coil which shifted the horizontal field eastward by 60 degrees. The seals were trained to touch one buoy upon emerging from the coil if the field inside it were deflected, and to touch a different buoy if the field were unaltered (See Figure 7.6). After between 900 and 2000 training trials, none of the animals gave any indication of learning the task, behaving instead as if they could not tell the difference between a normal and a shifted field (Renouf, 1989).

Sensitivity to the earth's magnetic field has supposedly been established in migrating birds (Keeton, 1971; Wiltschko and Wiltschko, 1972; Walcott and Green, 1974; Visalberghi and Alleva, 1979). However, in spite of numerous attempts, it has only twice been demonstrated in the lab in avians (Reille, 1968; Bookman, 1977) and once in mammals (Mather and Baker, 1981). Since many studies failing to find magnetic sensitivity have recently emerged (Kreithen and Keeton, 1974; Beaugrand, 1976; Griffin, 1982; Alsop, 1987; Carman

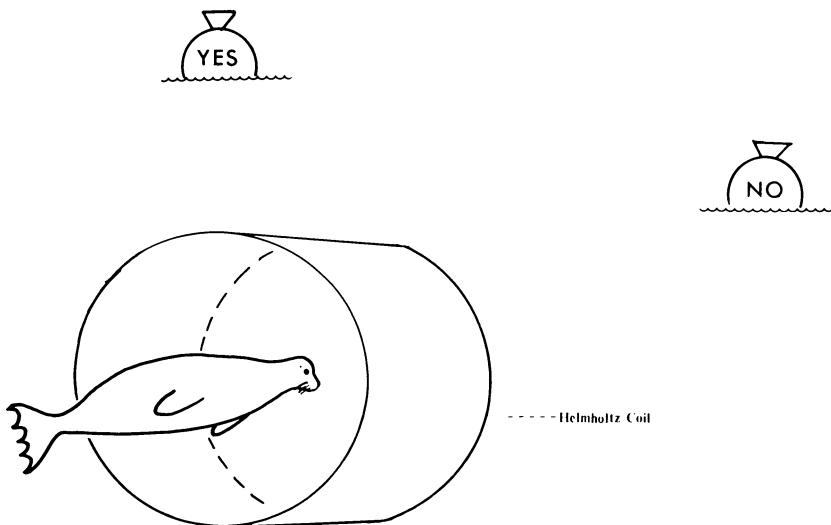


Figure 7.6 The seals were trained to swim through this Helmholtz coil which shifted the earth's magnetic field eastward by 60° . Upon emerging from the other side of the coil, the animals were required to swim to the buoy on the left if the field were shifted (YES), but to the buoy on the right (NO) if the field were unaltered.

et al., 1987; Madden and Phillips, 1987; McIsaac and Kreithen, 1987; Moore *et al.*, 1987), some researchers (see Griffin, 1987) have begun to question the proposal of magnetic orientation, especially since the two studies demonstrating it in birds have not been able to be replicated. It has been suggested that the organism might have to be moving through the field in order to detect it (Kreithen and Keeton, 1974), since in many of the failures to show a magnetic sense, the animals remained stationary performing some operant response like key pecking. By moving through a magnetic field, a marine mammal could, in theory, produce a current flow or maintain a static field (Faraday's law; see Gould, 1984) in a manner similar to some elasmobranch fishes (Kalmijn, 1978). The harbour seals we tested moved freely through the coil, but were still unable to learn the difference between a normal and horizontally shifted condition. These results do not necessarily mean that magnetic reception does not occur, but at least that all the variables affecting it have not been identified. For instance, it has been suggested that there might be tuning to specific field intensities or that the magnetic reception system is turned off if the behavioural context is inappropriate (McIsaac and Kreithen, 1987).

Negative results are always difficult to interpret because it can always be argued that they are attributable to methodological errors and omissions. The fact that harbour seals could not learn a magnetic

discrimination task does not prove that they cannot detect magnetic fields. Biological constraints (Shettleworth, 1972) could have limited the seals learning. That is, they may not have been able to use the magnetic cues we provided because the context may have been unlike that which they normally encounter. It is also possible that they use the vertical instead of the horizontal axis. The training paradigm was a simple discrimination of the kind they have been shown capable of learning in many psychophysical studies of other sensory modalities. Normally, correct response rates of 90% or better are required in such discriminations before they are considered learned (Schusterman, 1974b). My seals showed response rates near 50% in all sessions of training in spite of the fact that the magnetic shift which occurred when the coil was powered should have been very salient, unless the animals are specifically tuned to a particular sector of the compass or field intensity.

7.8 DISCUSSION: OTARIIDS VERSUS PHOCIDS

In spite of the predisposition in science to treat all things equal until proven otherwise (which is not evidence that they are equal), there is some *a priori* justification for expecting that otariids and phocids do not operate in the same sensory worlds. Until recently, the consensus was that the two groups evolved from separate terrestrial ancestors, otariids from a bear-like stock, and phocids emerging from an otter-like line. The arguments of Wyss (1988, 1989) have re-energized the monophyly/diphyle debate, but regardless of its outcome, there is no reason to expect each group to have acquired the same adaptations for sensory function in water. Apart from evolutionary origins, the fact that true seals are more aquatic in their habits, and eared seals more terrestrially bound, argues for differences in sensory design in each.

Unfortunately, sensible comparisons are precluded by large gaps in the data. Audition has been the best studied modality in each family, and otariids and phocids differ in many respects in this regard. Apart from the lack of pinnae in phocids, there are obvious anatomical differences attributable to the more aquatic existence of true seals, such as their heavier ossicles, and larger tympanic membrane and bullae, and their greater tympanic membrane to oval window ratios. In the seven species which have been studied in psychophysical experiments (see Table 7.2), the otariids' underwater audiogram is tuned to a lower range of frequencies than phocids', insofar as the upper hearing limit in that medium is in the vicinity of 36 kHz in the eared seals and 60 kHz in all but one true seal. The otariids' aerial and underwater audiograms are, overall, more similar than those of phocids,

showing the former's superior adaptation to an amphibious existence. In both groups, there is less of a hearing loss in air than Møhl (1968b) predicted for a fully water adapted ear. It would be of great interest to understand the mechanism by which otariids are at some frequencies able hear equally well in each medium, whether or not as do phocids, they use two separate inputs. The role proposed by Terhune (1989) of engorged cavernous tissue in the external and middle ear when the animal is listening in air needs to be ascertained directly.

The phocids and otariids which have been studied (see Table 7.4) are able to locate click signals underwater with a minimum audible angle of about 9° . Otariid directional hearing has not been quantified in air, but harbour seals show an aerial MAA of 3° to clicks, a difference Terhune (1974a) explained by the faster transmission of sound in water. As is the case in humans (Terhune, 1974b), both groups of pinnipeds perform more poorly when the stimuli employed are pure tones, otariids apparently more so than phocids. Both pinnipeds appear to locate sound underwater by relying on the same interaural cues as most mammals in air (Mills, 1972). Otariid MAAs increase to some extent with frequency, suggesting that the intensity differences typically employed at shorter wavelengths are less useful than phase cues. Møhl's (1964) study suggested that the harbour seal might rely on phase cues as well, and though Terhune (1974) reported that the harbour seal had great difficulty localizing sinusoidal signals, he found no deterioration at shorter wavelengths, presenting the possibility that intensity and phase cues are equally effective. Whether otariids employ the same means as phocids to cope with faster sound transmission in water, and possible reduced interaural separation because of the sound transparency of much of the head, remains to be seen since aerial measurements have not been made in the former. For this reason, Gentry's suggestion that there are neurological adaptations which permit otariids to discriminate smaller differences in water cannot be assessed.

Critical ratios of both groups are similar in both media except for the anomalous ringed seal masked thresholds in air (Table 7.3). This is not surprising if such similarity is a product of the architecture of the cochlea.

Otariid and phocid visual apparatus is ostensibly similar insofar as they both share features expected of a nocturnal eye, that is a reflecting tapetum, a rod dominated retina with no area centralis, and a high receptor to ganglion cell ratio. Some putative functional differences between eared and earless seals might be accounted for by variations in methodology, for example the 'greener' spectral sensitivity in the only otariids examined, *Zalophus* and *Callorhinus* (See Table 7.1). Lavigne *et al.* (1977) argued that Lythgoe's (1972) sensitivity hypothesis would predict this peak wavelength band for

an organism which lives in shallow coastal waters and depends to a significant extent on a terrestrial habitat. They then maintained that the peak wavelengths for the phocids which have been investigated can similarly be explained by the spectrum of the waters in which they feed. However, Wartzok's (1979) report of maximum spectral sensitivity at 530 nm in the spotted seal, which is much greener than the peak found in the other pinnipeds, encourages the re-evaluation of all measurements. The biggest problem in the behavioural determinations is the extent to which stimulus presentation itself alters the degree of the eye's scotopic function so that variations in the manner in which stimuli are presented could alter the threshold's location.

Statistical manipulations by Lavigne (1973) and Lavigne and Ronald (1975b) suggest duplex vision for both pinnipeds. It is unfortunate that the otariid retina has not been examined for cone-like receptors, and that critical flicker fusion thresholds and direct tests of colour vision have been made only in phocids. The rod/cone break identified in Lavigne's re-analysis of Schusterman and Balliet's (1971) acuity data in *Zalophus* occurred between -1 and -2 log mL. Comparable indications of a shift from rod to cone function were made by measuring pupillary diameters in the harp, harbour and ringed seal as a function of luminance. The rod/cone break in these instances occurred near -1 log mL as well. However, a break at -3.77 log mL in the harp seal using critical flicker fusion measurements is difficult to explain especially in light of the fact that this method is considered to be the best indication of retinal duplicity (Dodd, 1967; Lavigne *et al.*, 1977). Lavigne *et al.* (1977) suggested that '...differences in methodology including vast differences in stimulus size and stimulus presentation may be involved.'

A sensitive nocturnal-like visual system with two receptor types is not surprising in any two groups of mammals which have to see in both bright and dim light. Perhaps the best indication of separate visual worlds is a comparison of resolution in air and water. Disappointingly, acuity measurements have only once been obtained in a phocid using methods uncontaminated by brightness cuing, and this was done only underwater and did not incorporate systematic variation of background luminance. The visual angle thus obtained for a harbour seal at 85-130 mL was 8.3 minutes of arc. Comparable results were obtained in the same ambient light levels from the Steller's (7.1 minutes of arc, aerial) and California sea lion (5.5 minutes of arc, aerial and underwater). Any differences between the two families of pinnipeds would probably emerge at lower levels of light, where the aerial and underwater performance of *Zalophus* separates.

The extent of corneal astigmatism had been reported as similar in the two groups of pinnipeds, based upon the otariid measurements of Johnson (1901) of the *Eumatopias* eye. Dawson *et al.*'s (1987) report of no regular astigmatism in *Zalophus*, but instead an optically flat window for aerial vision calls for a re-examination of the generally accepted view of how the eye relies on the stenopaeic pupil for aerial resolution. As Dawson *et al.* explained, the poor acuity of *Zalophus* in low luminance may occur because the dilated pupil admits nonfocused light through areas adjacent to the aerial window. The findings of West *et al.* (1989) of no significant astigmatism in the hooded seal suggests that before the stenopaeic explanation of aerial acuity in bright light is accepted for true seals, phocid refractions need to be replicated using more reliable methods. An aerial window like that proposed for *Zalophus* has never been observed in any phocid eye, however, it should be noted that Wilson (1970a) reported a 'flattened' area in the Weddell seal cornea. He could not identify this flattening in all of his corneal plaster castings, and reported that it was not located in the same regions of the few eyes he found it in. It might be that this observation was an artifact of the mechanics of the casting procedure. However, the existence of an optically flat region should not be discounted until further phocid refractions are undertaken. The possibility of a separate otariid and phocid mechanism for aerial and underwater acuity awaits the outcome of such investigations.

The other modalities have not been studied well enough to make similar comparisons, though there is every indication that differences will occur. The more terrestrial social behaviour of otariids predicts more olfactory sensitivity than in phocids. There are also at least superficial differences between the vibrissae of each group. However, data based analysis requires the further accrual of information. In general, however, all modalities considered, when there is no reason to expect the mammalian characteristics to change as a result of amphibious and/or aquatic function, otariids and phocids are similar such as in the case of auditory masking or a sensitive duplex retina. However, where differences would be predicted because of different environmental constraints, either both groups have been shown to differ as in the tuning of their audiograms, directional hearing thresholds, and pattern of corneal astigmatism or the data have not been yet acquired, as in the absence of aerial and underwater luminance acuity functions in phocids.

7.9 UMWELTEN: BEYOND THE RECEPTOR

The data reviewed in this chapter pertain primarily to the functioning of receptor systems. The organism's Umwelt is also determined by the nature of the stimulus, and the manner in which it is processed, neither of which necessarily predict the same thing as does the receptor mechanism. For example, even though we know that the water adapted eye has good resolution in that medium, many pinniped species inhabit murky coastal water where visibility is seriously restricted by turbidity. Similarly, the mechanisms which permit good aerial acuity in bright light are useless on the dim foggy beaches which many pinnipeds use in the breeding season. However, acuity thresholds do not necessarily give an indication of the extent to which visual cues are used. The amount of visual detail which is necessary for information processing might be quite small, that is, a clear picture may not be necessary for the seal to acquire a large amount of information about an object, such as its size, trajectory of movement, identification etc. Studies of human perception have shown that the properties of objects can be ascertained on the basis of very little detail, the perceptual mechanism being capable of 'filling in' large gaps in information. For instance, clear impressions of human movement postures can be perceived when only ten or twelve points of the moving figure are visible (Johansson, 1973). Dolphins are able to make visual discriminations on the basis of very meagre cues, so much so that Herman (1987) referred to them tendentiously as 'visual animals'.

Clearly, more information about cognitive and perceptual processes is needed to explain the manner in which sensory stimuli are employed. For example, the broad range of auditory sensitivity in phocids, ranging well beyond 60 kHz in water, with peak sensitivity near 30 kHz is of unknown value in the species like the harbour seal which is essentially silent. The use of echolocation might account for the frequency range of the underwater audiogram, however, though sonar-like click vocalizations have been recorded in at least five species, the data supporting their employment in an echolocation system are scarce (Renouf and Davis, 1982; Renouf *et al.*, 1980). The cues pinnipeds use for orientation and navigation are a complete mystery even though there is ample demonstration of considerable skill such as in the relocation of breathing holes after lengthy under-ice excursions (Kooyman, 1969; Elsner *et al.*, 1989), the return each year to fog bound breeding beaches on tiny offshore islands (Norris, 1967), or the location of fish in darkness (Renouf *et al.*, 1980).

(See Wartzok, this volume).

In spite of the capability of their senses in water, there are many instances in which these animals appear to operate without much conventional sensory information because visual cues are obscured by turbidity, as far as we know auditory cues are absent, and vibrissae are out of range. Either all sensory channels have not been identified, or the animals require very little information for sensory/cognitive processing. The role of stimulation which the animal itself produces as it moves has not been examined, but it is conceivable that the apparent dearth of environmental input is compensated for by an ongoing record of changes resulting from the seal's own locomotion. For example, the animal might store a 'cognitive map' of its movement to which it refers for orientation and navigation. This map might be coded kinaesthetically, and/or a product of vibrations (auditory or encoded by vibrissae) produced by the seals swimming through the water.

The sensory world of pinnipeds must be influenced by their ability to move swiftly in three dimensions in the ocean, essentially unconstrained by gravity. In other mammals, the course of perceptual development is determined by an interaction between movement and the sensory information received during locomotion. This is presumably one of the chief means by which the organism acquires the ability to cope with pervasive discrepancies between the sensory data relayed by receptor and the real properties of the environment (eg. the retina tells the brain that receding objects shrink as they move away, or the cochlea records changes in frequency and amplitude as the organism alters position with respect to a sound source). This developmental interplay between movement and sensation might be an important feature of the underwater Umwelt of pinnipeds. If so, their sensory world must undergo a dramatic change as they endure the clumsiness of terrestrial travel. This perceptual change would probably be more extreme for phocids than otariids because the latter undertake most of their reproductive activities ashore.

Processing differences may be responsible to a greater extent than receptor modifications for pinnipeds' ability to function well on land and in the ocean. Not only might the amount of input needed to form useful percepts be different in each environment, but the importance of particular modalities or stimulus properties such as movement may shift depending upon changes in available sensory information. The particulars of receptor mechanisms are indubitably important, but to gain insight into the Umwelt of pinnipeds it is time to shift attention to cognitive processing mechanisms

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