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REPRODUCTIVE BEHAVIOUR OF SOUTHERN SEA LIONS

by

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(With 6 Figures)
(Acc. 20-VIII-1987)

Introduction

Sea lions and fur seals are attractive subjects for the study of sexual selection, the evolution of polygyny, and the evolution of sexual dimorphism (BARTHOLOMEW, 1970; ALEXANDER *et al.*, 1979). The reproductive behaviour of males and females has been reported for several species (*e.g.*, BARTHOLOMEW & HOEL, 1953; RAND, 1967; BONNER, 1968; GENTRY, 1970; MARLOW, 1975; ODELL, 1975; VAZ-FERREIRA, 1975; GISINER, 1985). These studies are important in understanding the evolution of mating strategies and polygynous mating systems (STIRLING, 1982). However, few of these otariids have been studied in depth, and some species, especially the three species of sea lions inhabiting the southern hemisphere, remain relatively unknown.

This paper deals with southern sea lions, *Otaria byronia*, (or *Otaria flavescens*, PINE *et al.*, 1978) one of the largest, most sexually dimorphic, and least known of the five sea lion species. Adult males have a large head and a distinctive massive neck adorned by long guard hairs. Females lack these traits, are smaller and about one-third the weight of adult males.

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Southern sea lions are widely distributed along the Atlantic and Pacific coasts of South America (KING, 1983). Most research on this otariid has focused on whole groups rather than on individuals, emphasizing aspects of breeding biology important for understanding population dynamics (HAMILTON, 1934, 1939; VAZ-FERREIRA, 1975, 1981; XIMÉNEZ, 1976; LEWIS & XIMÉNEZ, 1983; CAMPAGNA, 1985a). Social behaviour and the mating system has not been studied in detail.

HAMILTON (1934, 1939) provided the first general description of reproductive behaviour and natural history from observations in the Falkland Islands (Islas Malvinas). VAZ-FERREIRA (1975, 1981) described the chronology of reproductive events at Lobos Island, Uruguay. CAMPAGNA (1985a, 1985b) reported the timing of key events in the breeding cycle at Punta Norte, Argentina. We describe fundamental aspects of the reproductive behaviour of individual males and females. Specifically, we report on: (1) male aggressive behaviour used in territorial and female defence, (2) responses of females to male mating attempts, (3) mating success and variance in mating success among males, (4) the change in male mating strategy from territorial defence to a combination of site and female defence, and (5) the timing of key events in the female reproductive cycle (*e.g.*, parturition, mating, and foraging schedules). We compare our results on reproductive behaviour of southern sea lions with that on other sea lions. A companion paper (CAMPAGNA, LE BOEUF & CARPOZZO, in press) treats one aspect of male mating behaviour in detail.

Methods

Daily observations were conducted at Punta Norte, Península Valdés, Argentina, from 0800 to 2100 hrs, during six breeding seasons (1981-1986). We studied the agonistic behaviour of breeding males from 1981 to 1983, and the reproductive biology of marked males and females from 1984 to 1986. During these years, the size of the rookery at the peak of the breeding season was 400-450 breeding individuals (CAMPAGNA, 1985a), grouped just above the high tide line along a 200 m long, narrow stretch of an open pebble beach. We refer to this place as the central breeding area (CBA) (Fig. 1).

The tidal range at Península Valdés is five metres. Since breeding animals congregated just above the high water mark and did not move from this area in relation to tides or time of day, they were awash or in the surf zone twice a day during the highest tides. However, they were often exposed to high temperatures during the austral summer when low tides occurred at midday (air temperatures above 35°C and black-bulb temperatures above 50°C). The breeding location provided neither shade nor tidepools to cool off.

Observations were conducted from a cliff about seven metres above the colony and 30 m distant from it at its closest point. Binoculars and a spotting scope were used to census, identify marked individuals, and record behavioural data.

The entire area in view, about 500 m of the CBA and its periphery, was censused daily during low and high tides, differentiating adults, non-adults, and pups. Males were categorized as adults (about eight years old and older), or subadults based on overall size, size of the neck, and the length of the mane [see HAMILTON (1934) for a general descrip-

tion of age categories]. The number and identity of males associated with females in the CBA (resident males), and of itinerant males without females, were recorded several times per day. Females were considered to be associated with a male when they were closer to him than to any other neighbouring male, usually no more than two body lengths away. A census of females categorized by their estimated size (small, medium, or large) was taken three times per week by two observers. Sex ratios were determined from census data.

The tenure of a male was defined as the number of hours that he was observed in the CBA. We assumed that males remained on their territories at night when we were not conducting observations. All males that we saw lose their position in the CBA did not return to it for at least several days.

Serial records were kept of female arrivals, parturitions and copulations observed during daylight hours. Mean duration of parturition was estimated from the first appearance of the fetus or the embryonic sac to expulsion of the fetus. Copulation was defined as penile intromission. Intromission was indicated by rhythmic pelvic thrusting lasting at least one minute, performed by adult males mounting females on land. A copulation was judged unsuccessful if it was disrupted by a male neighbour within two minutes, or if it lasted less than five minutes and was followed immediately by another mating attempt by the same male.

Marking individuals.

About 30 females and 60 males were marked during each of three breeding seasons (1984, 1985 and 1986) with multicolored paint pellets (Nel-spot Paint Company) fired from a slingshot or a CO₂ pistol at a distance of 10-20 m from the animals. The paint marks lasted three to six weeks. The marking procedure did not cause visible disturbance to individuals or to the colony. Typically, males flinched but did not move. Females sometimes started to move when hit by a paint pellet but were kept in place by the males with whom they were associated.

Identification cards and serial records were kept of the presence and key activities of marked individuals. Intervals between parturition, copulation, departure on a feeding trip, duration of feeding trips and time on land after feeding trips, were calculated from data obtained from marked individuals.

Estimating stages of the oestrous cycle.

The number of daily births was estimated from the number of pups censused daily at high tide and from the number of births observed during daylight hours. From these data—and from the mean interval in days between parturition, first copulation, and female departure to sea on the first foraging trip—we calculated daily estimates of the number of females that: (a) gave birth but were not yet in oestrus (pre-oestrous females after birth), (b) were in oestrus, and (c) were in post-oestrus and at sea on their first foraging trip. The proportion of females expected to be in oestrus (oestrus being defined as the day a female was expected to copulate) was estimated by back calculating the number of pups born six days earlier. The daily number of females on land that copulated and were back from a foraging excursion (post-oestrous females on land), and that copulated and were at sea in subsequent foraging excursions (post-oestrous females at sea), was estimated based on the mean duration of feeding trips and subsequent intervals on land. The number of females that were on land but did not give birth (pre-oestrous females before birth) was estimated as the difference between the mean number of females censused during a week, and the sum of the mean number of females in pre-oestrus after birth, oestrus and post-oestrus on land. We were unable to calculate the number of primiparous females in the breeding area. Therefore, our proportion of females estimated to be in oestrus was a conservative figure.

Male-male competition.

The frequency, form, and consequences of male-male competition was studied by: (a) recording agonistic interactions among males, (b) recording samples of male agonistic vocalizations for the whole rookery, (c) describing the behaviour of males attempting to secure females, (d) counting copulations, and (e) maintaining a serial record of the presence and activity of marked males. Agonistic interactions (AIs) were defined as hostile contests between two males during which they threatened, chased, sparred with each other, or fought. The frequency of AIs was studied by taking focal animal samples (ALTMANN, 1974) of randomly chosen resident males. The samples lasted 15 minutes and were randomly distributed during daylight hours. Seven to 12 samples were obtained each day of the breeding season. During each sample, all agonistic interactions of a target male were recorded. To set the context in which AIs occurred, social and physical variables, such as the distance between the target male and his neighbours and tidal conditions, were recorded before the start of the fifteen-minute samples. The distance between males was estimated using one body length as a reference. The number of male threat vocalizations that occurred during two-minute samples was used as an indicator of general activity of the rookery. Typically, when a male issues a threat vocalization to another male he sits up, alert and ready to defend his position or his females.

The percentage of injured males and females was calculated by dividing the number of injured individuals observed during scan samples of the rookery (ALTMANN, 1974), by the number of individuals censused. For some male injuries (canines lost or broken, opacity of the cornea and locomotion problems), the percentage was estimated by dividing the number of individuals observed sustaining such injuries during the entire season, by the mean number of adult males censused on land at peak season.

Results

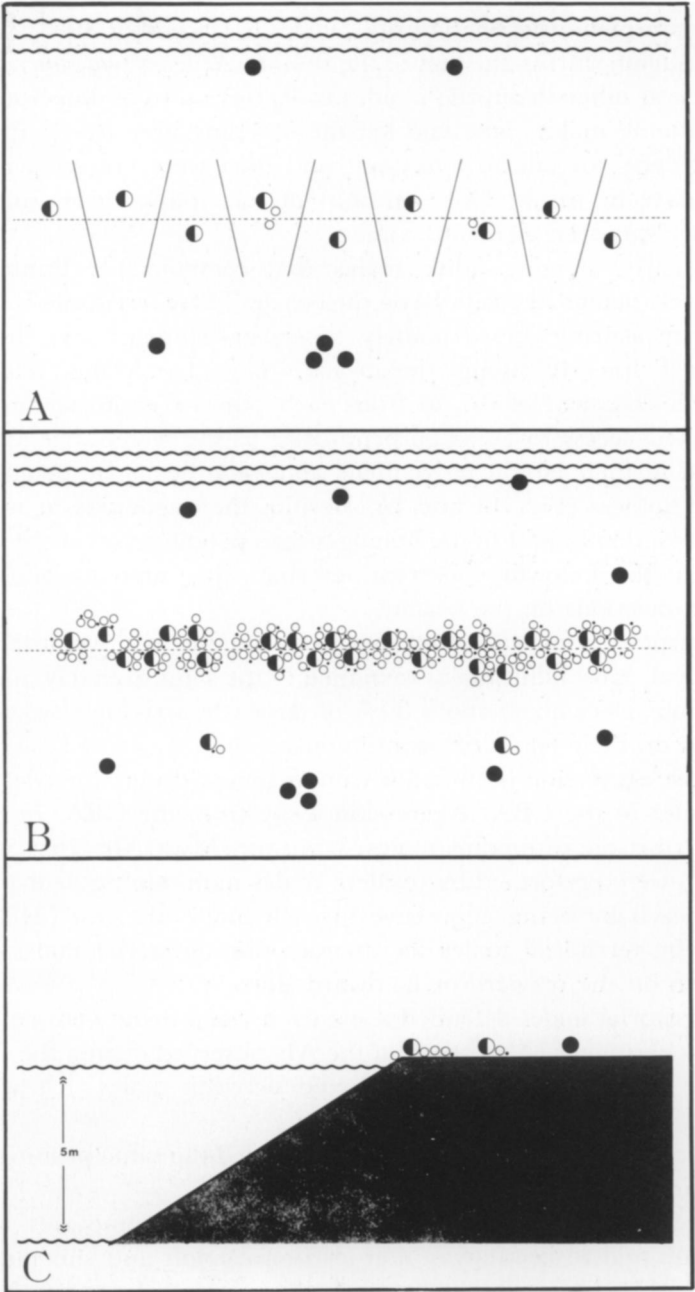
Male reproductive behaviour.

Male arrivals and establishment of positions.

Males arrived in December followed by females. All of these males were large adults; some of them came from a resting area located one km from Punta Norte. Males arrived singly and, anticipating the places where most females were going to be later in the season, took up a position on the beach near the high tide line (Fig. 1a and 1c).

Males appeared to survey the prospects at several breeding locations in Península Valdés. Some used Punta Norte as a relay station on their way to other breeding places, being seen resting on the beach for one to

Fig. 1. A schematic representation of the central breeding area at Punta Norte, Península Valdés, Argentina. Large half-filled circles denote territorial males, large solid circles indicate adult and subadult peripheral males, open circles indicate adult females and the small dots represent pups. Figure 1a and 1b is an aerial view of the central breeding area early in the breeding season (late December) and at peak season (third week in January), respectively; the dotted lines indicate the high water mark. The lines separating males in Figure 1a approximate the territorial boundaries. Figure 1c shows a sideview of a section of the beach; the tidal range and slope of the beach of ca 30° are indicated.



four days before leaving the area. Nineteen (61%) of 31 adult males marked conspicuously near Punta Norte in December 1984, were not observed again during the rest of the season. At least two marked males were seen at other Península Valdés rookeries up to 50 km from Punta Norte. Young males came and left the breeding area freely; they were seen regularly for one to five days, and then were not seen again for several days or at all. Only one out of ten young males marked in December was seen again in January.

Most early arriving adult males that remained at Punta Norte aggressively defended positions on the beach. These territories were large at first, measuring approximately 15 m in diameter and they were distributed linearly along the beach (Fig. 1). Males maintained individual distances of 6-7 m from each other. Territorial males had unrestricted access to areas perpendicular to the water, but they were restricted in their lateral movements along the beach by neighbouring territory holders (Fig. 1a and b). Despite the vagueness of territorial boundaries, due in part to the homogeneous pebble substrate, it was evident from the following observations that early arriving adult males defended positions on the beach:

1. Except for a few visits to the water during the first two or three days after arrival, most adult males remained in the same area day and night. Throughout December, about 80% of the early arriving marked males remained on their territories continuously.

2. Most aggression occurred in connection with territory defence by adult males in the CBA. Aggression away from the CBA, in all-male groups or between itinerant males, was rare. Most AIs (76% of 1,836 recorded) were performed by resident males maintaining their positions on the beach by being aggressive to each other; the rest (24%) were directed by territorial males to itinerant non-territorial males passing near them on the seaward or landward side.

3. Territorial males defended a site even when there were no females within its perimeter. About half of the AIs observed during the first two weeks of the breeding season occurred between males that were not associated with females.

4. Two males identified from scars defended the same position on the beach during two consecutive breeding seasons.

The result of site defence was to establish boundaries between neighbours and to keep away non-territorial adult and subadult males (Fig. 1a and 1b). All individual attempts by young males to approach and enter the CBA were rebuffed. When a new male tried to secure a position

in the CBA, he was vigorously attacked by the nearest resident males, each one acting alone and defending his own territory. After a few minutes of defending himself against 1-3 residents, the newcomer was usually chased out or relegated to the periphery, ten metres or more away from the CBA.

Territories were established and maintained by three types of AIs between males: (a) threat vocalizations (with and without simultaneous charge), (b) attack and retreat displays, and (c) fights. Males threatened another male by vocalizing while suddenly charging or bluffing a run toward the opponent. Threat vocalizations were characterized by short (about 0.3 sec), explosive, high frequency sounds (around 5,000 Hz), the

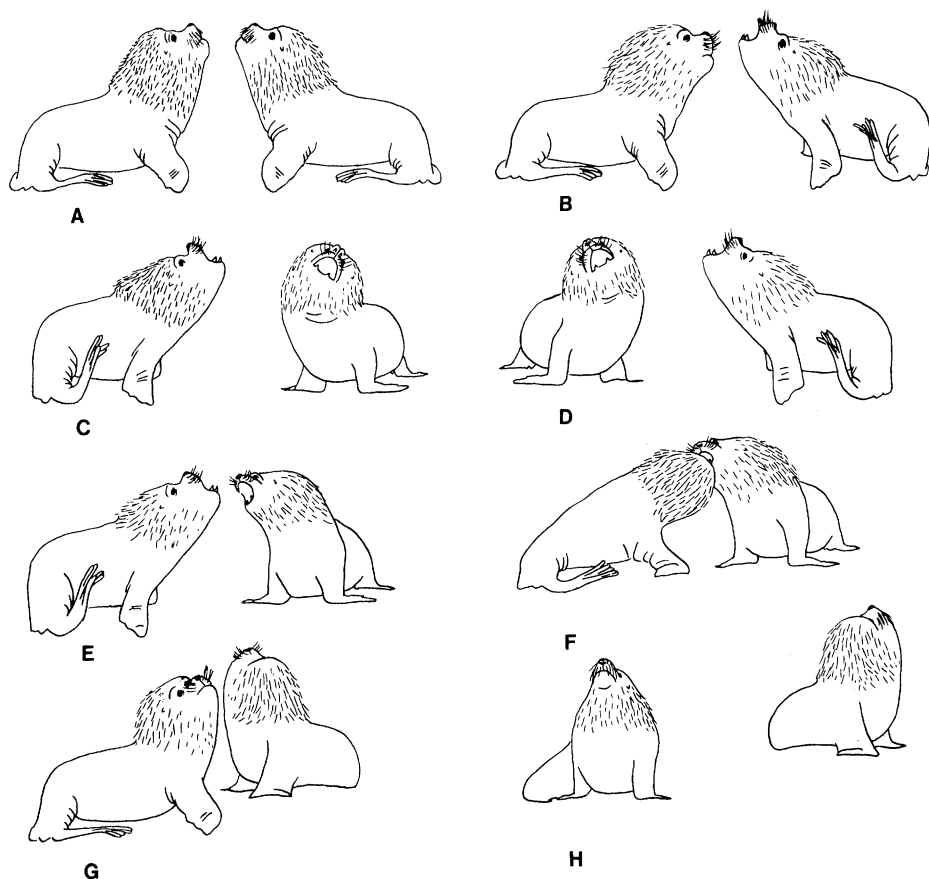


Fig. 2. A typical sequence of postures observed during agonistic interactions between territorial males.

result of forceful exhalations. When a threat vocalization was followed by attack, the charge consisted of a short rush toward the opponent with the neck outstretched, the jaws open, the vibrissae erected, and the eyes fully opened (Fig. 2a and 2b).

Fifty percent of the aggressive episodes did not go further than a vocal threat. In 41% of the threats, the attacker stopped abruptly before reaching his opponent, only to face away quickly, and rush back to his starting place. This charge and retreat behaviour alternated in synchrony with similar behaviour by the opponent (Fig. 2c to 2g). The cycle of alternating charge and retreat was repeated up to six times and lasted three to eight seconds. AIs between territorial males were a common event throughout the breeding season with peak numbers occurring during the third week in January (Fig. 3).

Fights consisted of quick biting of the neck and chest, violent shaking and twisting of the neck, and pushing. They resulted in large wounds, bloody tooth punctures and broken canines. Over the course of the breeding season, about 68% of the adult males sustained punctures, wounds or lacerations of the body (Table 1). Eleven percent of them lost or broke a tooth, usually an inferior canine. We did not confirm any male deaths due to fights. Fights between neighbouring males did not result in an increase of their individual distances. Males often ended up being closer after a fight than before.

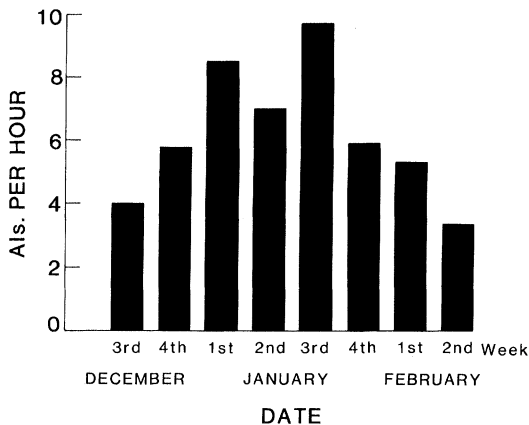


Fig. 3. A frequency distribution of agonistic interactions per hour per male observed during the 1981-82 breeding season.

TABLE 1. Percentage of males and females present in the breeding area that sustained injuries during the 1985 breeding season

Type of cost	Males		Females	
	Frequency	Percentage	Frequency	Percentage
Head injuries:				
- Tooth broken or lost	11	11	1	<0
- Cuts on eyelids	5	4.5	—	—
- Wounds around the mouth	29	26.4	—	—
- Wounds on the nose	11	10.0	4	<0
- Opacity of the cornea	3	3.0	2	<0
Punctures, wounds or lacerations on the body	75	68.2	113	26.3
Bloody wounds or wounds with loss of tissue	5	4.2	89	20.7
Infected wounds	3	2.7	2	<0
Locomotion problems (injured foreflipper)	7	6.4	9	<0

Some animals arrived on the rookery with broken or lost teeth or opaque corneas, indicating that these wounds were sustained previously.

Female arrivals and male-male competition for females.

The first females to arrive found about five to ten adult males defending positions on the beach just above the high tide line (the area that was to become the CBA), and about ten to fifteen adult and young males on the periphery of the CBA. Arriving females attempted to settle on the beach near established males. If itinerant males were not around at the time when a female arrived, or if these males were 100 m or more away from the arriving point, she joined a male in the CBA directly. If itinerant males were near, they usually approached and intercepted her. Females attempted to avoid itinerant males. When approached by them, some females returned to sea. Others approached the CBA slowly, stopping several times to rest, allowing males to explore their genitalia, and lying down when males attempted to mount, bite or butt them. Once an arriving female and the group of itinerant males got near the CBA, the closest territorial males chased away the intruding males, and the female entered the CBA. Other females approached the CBA as fast as possible, although often followed by groups of males. The latter were more aggressive in attempting to escape, fighting back, biting the male's flippers, lips and neck.

Itinerant males competed among themselves to hold an arriving female, cutting off her attempts to go into the CBA and sometimes mounting her. Females always resisted mating attempts by these males, shaking their bodies from side to side and biting them when mounted. In 73% of 337 female arrivals, at least one itinerant male intercepted the female before she reached the CBA (range = 1-30 males). In 9.5% of 126 female arrivals, the female was mounted at least once during her way to the CBA. We never recorded a copulation in this context. Some arriving females took advantage of the competition among males to escape to the CBA.

Female arrivals occurred throughout the day but females gained entry to the CBA most easily when they arrived during high tides. Females arriving during low tides had a greater distance to traverse (up to 50 m to reach the CBA) and they were easily spotted and chased by itinerant males, sometimes for several hundred metres. It took several hours for some of these females to escape and reach the CBA. About ten percent of the females arriving at low tide returned to the sea as soon as males rushed toward them. Males pursued females into the water up to three to four km off shore. About 50% of the females that arrived during high tide entered the CBA without being intercepted by itinerant males. Females tended to arrive at the breeding area more often during high tide than during low tides (55% *vs* 45% of 163 arrivals, respectively), but the difference was not significant (Chi-square test = 1.77, d.f. = 1, $p > 0.05$).

Most early-arriving females were small or medium sized, suggesting that they were young (HAMILTON, 1934). Early in January, only about 15% of the females in the CBA were categorized as large. By mid-January, about 30% of them were large. Fewer than 2% of the females arrived in the company of a yearling.

Females were often injured in the process of reaching the CBA. Itinerant males bit females in the neck, side or back as they tried to get away. Once in the CBA, resident males forced females to stay in certain areas by biting, pushing and even hurling them into place by lifting them in their jaws. By the end of the season, many females had fresh wounds (Table 1).

Early arriving males became associated with females by: (a) waiting for arriving females to approach them, (b) intercepting arriving females and herding them to their territories, and (c) carrying females away from other males. The first females to arrive were disputed by the first males to defend positions in the CBA. When these females gave birth they were often separated from their pups during male disputes to mate with them.

While one male held a female near him, another male held the female's pup precluding nursing. Every December, the first two to three pups that were born died a few days after being separated from their mothers by competing males.

Males that did not acquire females by defending a position in the breeding area early in the season, attempted to secure females by joining a raiding group composed of four to 40 males. During group raids into the CBA, one male sometimes succeeded in securing a position in the CBA and held and defended a female for a period ranging from a few minutes to several days. Raids affected male tenure, the mating success of males and the distribution of females within the CBA (see CAMPAGNA *et al.*, in press, for a detailed treatment of group raids).

Male defence of females.

As the season progressed, more adult males established positions in the CBA, the site defended by each male became smaller, the frequency of AIs between resident males increased, and more females arrived and became associated with resident males (Fig. 1a and 1b). The mean number of males in the CBA increased from about 15 during the last week of December to 100 during the third week of January, while itinerant males increased from about ten to about 40 (see CAMPAGNA, 1985a). The distance between CBA males decreased significantly from a mean of nine metres late in December (range: 3-50), to a mean of four metres in mid-January (range: 2-12) ($t = 10.1$, d.f. = 559, $p < 0.05$).

A decrease in distance between males was significantly correlated with an increase in the mean frequency of threat vocalizations (Pearson's $r = -0.89$) and fights ($r = -0.88$). These data are based on seven weekly means per correlated variable ($P < 0.01$). The mean number of AIs per male was not constant during the breeding season (ANOVA $F = 6.83$; d.f. = 7, 92; $P < 0.05$; Fig. 3), and was positively correlated with the mean number of males in residence (Kendall's tau = 0.76, $p < 0.05$, $n = 8$ weekly means).

The proportion of adult males observed in the entire area associated with at least one female in the CBA or on its periphery increased steadily from 20% in December, to 45% early in January, and up to 86% by the end of January (Table 2). The mean number of females located near a male increased significantly from 1.3 by the end of December to 3.4 by the end of January ($t = 10.73$, d.f. = 514, $p < 0.05$; Table 2). By the end of the third week of January the CBA was an almost homogeneous stretch of densely clumped females associated with resident males. Even

TABLE 2. Weekly changes in the male and female composition of the breeding group during January 1986

Week	Number of females associated with a male		Percentage of adult males associated with females	Adult sex ratio	Mean operational sex ratio
	Mean	Range			
1st	1.5	1-8	45	1:0.7	1:0.1
2nd	2.2	1-13	72	1:1.8	1:0.5
3rd	2.8	1-16	81	1:2.9	1:1.3
4th	3.4	1-18	86	1:3.3	1:1.2

All sex ratios are expressed as male to females. The number of females associated with a male ("harem size") is based on proximity (closer to male "X" than to neighbouring males and no more than two body lengths away). The adult sex ratio is the weekly mean of the number of adult males to adult females censused daily. The mean operational sex ratio is the mean number of adult males censused weekly to the total number of females estimated to have been in oestrus during that time.

at peak season, when the CBA was most crowded, the distribution of males remained virtually linear, with only one to three males making up the width of the CBA.

With the arrival of females, males began shifting their efforts from defending positions in the CBA exclusively to a combination of defending positions and defending or holding females. This was evident in the following categories of male behaviour:

1. CBA males were alert to the activity of the females located near them and prevented them from moving away. A resting male stood up, rushed toward a female that started to move away, blocked her movement, pushed her back, or prevented her from moving any further. At times, the male grabbed her in his jaws, lifted her in the air, and flipped her back over his head to a site where she could be more easily defended. This behaviour was common and occurred throughout the breeding season. Some males left their CBA position to follow a straying female. In pursuing a female, a male sometimes crossed the territory of another male and ended up in a new area of the CBA. We never saw a solitary female moving away from a CBA male without the latter attempting to stop her, except during group raids or when she was in post-oestrus and went to the sea to feed.

CBA males did not allocate equal efforts to defending all females located near them. They were particularly alert to the movements of some females, maneuvering them into defensible areas by pushing and

biting, while allowing non-receptive females to move freely within the CBA.

2. When females moved as a group, resident males followed them. Female movement was observed in response to high temperature and during raids. The first group movement occurred during over a period of several hours and was associated with an increase in temperature. Females moved from the high tide line to the wet substrate near the water's edge. This movement was observed during an unusually hot week in January 1986, when air temperature reached 34-36°C, black bulb temperature rose above 50°C, and these high temperatures prevailed for 4-6 hrs. Females apparently became heat stressed and, during midday hours and at low tide on four consecutive days, they moved 40-50 m toward the sea, with about 60% of the resident males following them. The resident males that did not abandon their positions were associated with females that did not move to the water. At high tide, females and males moved slowly back to the high tide water line.

During group raids, females rushed laterally from the point of attack. Females fled ten to 20 m from the male with whom they had been associated and from his territory, into neighbouring areas held by other CBA males. During these sudden events, resident males always left their territories and rushed after the departing females, alternately trying to check the stampede, while turning to threaten the onrushing raiders. Males that secured females after following them during a stampede, remained with them rather than returning to their vacated territory.

3. Most resident males did not stray far from their females and remained away from them for only a few seconds. The form and frequency of AIs suggests that males tried to maintain control of the females by reducing their time away from them; they compromised between keeping intruders away and keeping females from straying. During AIs, males alternated short threats or bites toward other males with quick movements back to the females. Fights were brief ($\bar{X} = 6.4 \pm 2.1$ sec, $n = 24$) and infrequent. Only nine percent of 1,055 AIs recorded during three breeding seasons ended in fights. Each season, we recorded fewer than five fights that ended in long bites, during which one male hung on the rival's mane, holding a bite up to one minute. Males no longer associated with females left their positions to chase itinerant males several metres away as they did early in the season. (HAMILTON (1934) stated that males with territories containing females were less likely to pursue human intruders as far as males that were without females).

4. Some CBA males that lost their females abandoned the CBA. This occurred at least ten times during two breeding seasons. Defence of females on the periphery of the CBA took precedence over defence of a site. When a female was abducted during group raids from the CBA to the inland or the seaside periphery of the CBA, she was defended against other males, and was prevented from returning to the CBA. Attempting to hold a female, a male sometimes moved 100 m or more from the CBA to the place where the female was finally held. Males associated with females on the periphery of the CBA always abandoned their positions when their females fled. This behaviour was recorded at least 15 times during three breeding seasons. Early in the season, the defence of a position was affected by the presence of females near the males. Solitary males that had defended positions during most of the day sometimes abandoned their positions for a few hours, while males associated with females in what would later become the CBA, never left them.

5. At the peak of the season, male fights occurred where females were present. We rarely saw adult or subadult males fighting outside of the CBA or in male resting areas. The rate of occurrence of AIs was positively correlated with the probability of associating with at least one female in oestrus (Pearson's $r = 0.77$, $n = 7$ weekly means for each variable, $p < 0.05$).

6. During raids, males invading the CBA did not fight for a position in the CBA but for females. While abducting a female, a male fought with other males to keep them away and hold her. If she fled from him, the raider left the CBA immediately and did not try to maintain his position.

Male mating success.

Adult males marked during the 1985-86 breeding season copulated a mean of 3.51 times ($s^2 = 10.43$, $n = 71$). Similar data were obtained from a smaller sample in 1984-85 ($\bar{X} = 3.09$, $s^2 = 8.08$, $n = 35$). The data for 1985-86 are presented graphically in Fig. 4a. The measure of variance in male copulatory success excludes sexually mature subadult males, a category that was not marked. However, subadult males who made up about 30% of all males present in the breeding area, were rarely observed to copulate. By adding 21 subadults to the marked adult sample (in the same proportion added as marked adults to total adults present) and giving each one zero copulations (Fig. 4a), we obtain an estimate of the mean number of copulations per male in the area (2.71) and of the variance in male mating success (10.23).

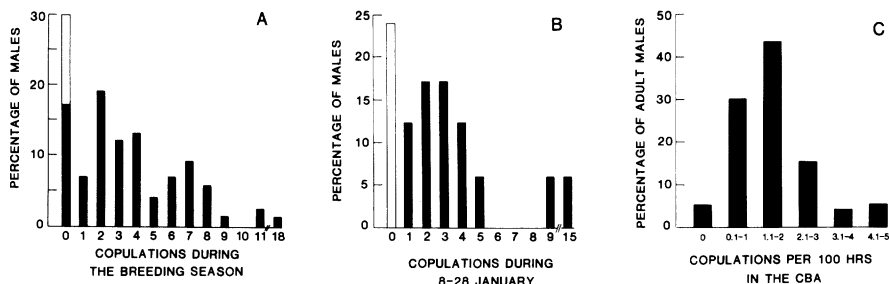


Fig. 4. Copulatory success by marked males observed during the 1985-86 breeding season: a) Total number of copulations recorded by 71 adult males (black bars) and by 21 subadult males (open bar). b) Number of copulations achieved by 13 adult males (black bars) and 4 subadult males (open bar) located in the breeding area between 8-28 January. c) Copulations by 32 adult males who were present in the central breeding area for at least 100 hrs.

Some of the variance in the distribution of copulations shown in Fig. 4a is due to the different amount of time that marked males were observed. Some were marked early in the season and followed for several weeks while others were marked at peak season and observed for only a few days before they left the area. We adjust for this bias by presenting the distribution of copulations for 13 marked adult males that were present in the breeding area at peak season, January 8-28, 1986. During this period, all marked adult males copulated at least once (Fig. 4b). A similar proportion of unmarked, subadult males outside the CBA ($N = 4$), all of whom obtained zero copulations, is indicated in Fig. 4b. This adjustment yields a mean of 3.76 copulations per male with a variance of 16.69.

Variability in male mating success is also indicated by the mating rate of adult males that arrived and were marked early (before January 7), and then spent at least 100 hrs in the CBA (Fig. 4c). The mean mating rate for this sample was 2.2 copulations per 100 daylight hrs spent with females in the CBA ($s^2 = 1.0$, range = 0-4.7, $n = 32$).

The number of copulations achieved by marked, adult males was positively correlated with tenure in the CBA (Pearson's $r = 0.58$, $N = 56$, $p < 0.05$). The mean tenure of early arriving males was 24.2 days ($sd = 5.3$, range = 15-57, $n = 33$). A mean of seventy six percent of this time was spent in association with one or more females. Assuming that these males did not go to sea at night (observations on moonlit nights indicated that they did not), they fasted throughout their stay in the

CBA. The maximum number of copulations observed for a male during the entire season was 18, achieved during 350 daylight hours in the CBA.

Male departure from the rookery.

The social structure of the breeding group broke down gradually, starting during the last week of January and ending by mid-February. Fewer adult males were present in the breeding area each day, and females and pups began to move around freely. Animals began to disperse on the beach. The homogeneous group of tightly clumped females, characteristic of the peak of the season, loosened up, dissolved and segregated into small groups of variable size. Groups of up to 100 females spent part of the day in the water swimming and surfing near the shore. Pups moved to tide pools where they spent most of the day. Males were seen abandoning the breeding area throughout the breeding season, but most adult males residing in the CBA abandoned it by the first week of February, after most females had completed oestrus. By contrast, itinerant males often abandoned the breeding area for a few days even during the peak of the breeding season. During January, itinerant males spent a mean of 27% less time in the breeding area than CBA males. Fifteen percent of 100 adult males left the breeding area to spend 1-8 days as solitary males in places near Punta Norte ($\bar{X} = 2.4$ days, $sd = 1.5$, $n = 28$). Of 97 male departures, 43 (44%) occurred during the first week of February. Some of these males went to the sea and were not seen again while others stayed near the breeding area resting for a few days before going to sea. Young males stayed in the breeding area with the females and behaved as if they were defending them, attempting to keep others away from them. These males attempted to mount females but did not succeed in mating.

Female reproductive behaviour.

Parturition.

Females gave birth about three days after arriving on the rookery ($\bar{X} = 3.3$, $sd = 0.3$, $n = 5$). Females in labor behaved in a restless manner and threatened other animals near them. Most pups were born cephalic (66% of 77 births), the rest (34%) were born in the breach position. The amniotic sac was ripped off during labor or the female tore it from the newborn. The placenta was expelled sometimes with the pup, or up to 40 min after parturition. Females did not eat the placenta.

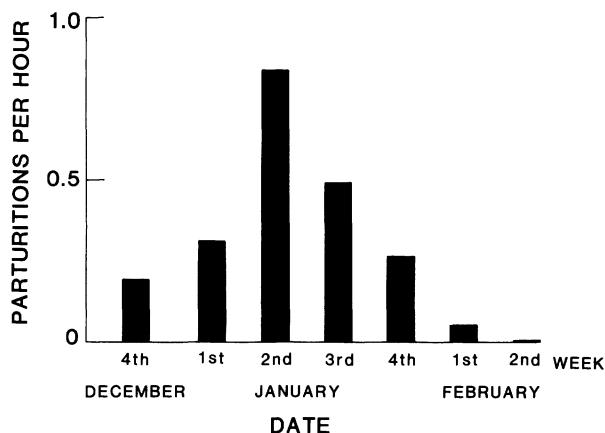


Fig. 5. Parturitions per hour as a function of week during the 1985-86 breeding season.

Birth duration varied greatly, ranging from 20-254 min ($\bar{X} = 38$, $sd = 18$, $n = 36$). Births in the breach position took longer ($\bar{X} = 97$ min) than cephalic births ($\bar{X} = 32.7$ min, $t = 2.62$, d.f. = 11, $p < 0.05$).

Births were observed from mid-December to early February (CAM-PAGNA, 1985a) and peaked during the second week of January (Fig. 5). During the fourth week of January we estimated that 21.6% of the females on land had not given birth yet (Table 3). Most of these females did not give birth subsequently because we observed few births after January.

TABLE 3. Weekly estimation of the breeding status of the females present in the breeding area during January

Date	\bar{X} Females censused	Daily percentage of the females censused					
		Pre-oestrus		Total	Oestrus		Post-oestrus
		Before birth	After birth			On land	Foraging
1-7	56.0	56.4	36.8	93.2	2.8	4.0	8.5
8-14	159.4	35.9	50.2	86.1	4.2	9.7	11.5
15-21	292.9	34.7	40.4	75.1	6.4	18.5	20.7
22-28	313.2	21.6	31.2	52.8	5.4	41.8	39.7

Figures represent the mean daily percentage of females censused that had not yet copulated (pre-oestrus), were expected to be sexually receptive (oestrus), and had already copulated (post-oestrus).

Mating.

Females nursed their pups daily until coming into oestrus, a mean of six days after parturition (Table 4). Males often sniffed or licked the females' genitalia before mounting. Males did not always copulate during their first mounting attempt. In about 30% of the copulations the male mounted the female up to ten times before intromission occurred. Once CBA males mounted a female, they usually ended up copulating with her (70% of 486 mounting attempts). About 5% of the copulations in the CBA were interrupted by AIs from neighbouring males.

TABLE 4. Duration of female reproductive events (in days) based on data from the 1985 and 1986 breeding seasons

	Parturition to copulation	Intervals Copulation to departure	Parturition to departure
$\bar{X} \pm \text{S.D.}$	6.0 ± 0.7	1.9 ± 1.0	7.6 ± 0.6
	23	30	25
Range	5-7	08-4.5	7-8

Departure refers to the first postpartum foraging excursion.

Most copulations (85% of 609 observed) took place on land in the CBA. The rest occurred on the periphery of the CBA, within five metres of resident males (4% on the inland side, 11% in the sea side). Females usually copulated laying on their belly but in about one percent of the copulations the female lay partially on her back. The mean duration of intromissions was 10.8 minutes ($sd = 3.3$, range 7-25, $n = 343$) and did vary during daylight hours ($F = 1.2$; $d.f. = 3, 214$; $P > 0.05$).

Most marked females (12 of 16 in 1985-86 and 10 of 18 in 1984-85) were seen copulating only once during the breeding season, but 13 of them (38% of the marked females) may have copulated two to three times during an interval of two hours to four days. However, only four of these females did it in the normal context (in the CBA, on land, with an adult male, without interruptions or unusual resistance, and for the normal duration). The rest (nine of 13) performed at least one of the copulations: (a) on the periphery of the CBA during a hot day, (b) in the water, (c) after resisting mounting attempts, (d) after a raid, (e) with a resident male after being copulated by a peripheral male, and (f) with a subadult male while going to or from the sea. The circumstances in which

multiple copulations occurred suggest that some of them may not have been complete. Fifty percent of the 13 marked females that copulated more than once did it with the same male.

The rate at which copulations occurred did not vary as a function of time of the day. About 22% of 596 copulations observed occurred between 0900-1200, while 26% occurred between 1201-1500, 1501-1800 and 1801-2100, respectively (Chi-square test = 3.07, d.f. = 3, $p > 0.05$).

The breeding status of the females in the CBA varied as a function of date (Table 3). Most of the females present were not sexually receptive on any given day. The mean operational sex ratio (a measure of sexual receptivity) in mid-January was 2.3 times lower than the adult sex ratio (the proportion of males to females on land). Every day of January, a mean of 4.6% of the females on land were expected to be in oestrus. The expected daily proportion of females in oestrus at the rookery and the frequency of copulations peaked during the third week of January (Table 3 and Fig. 6). The total number of females expected to be in oestrus during a week and the number of copulations recorded per hour of observation during the same week were positively correlated (Pearson's $r = 0.92$, $n = 15$, $p < 0.05$; combined data from three breeding seasons).

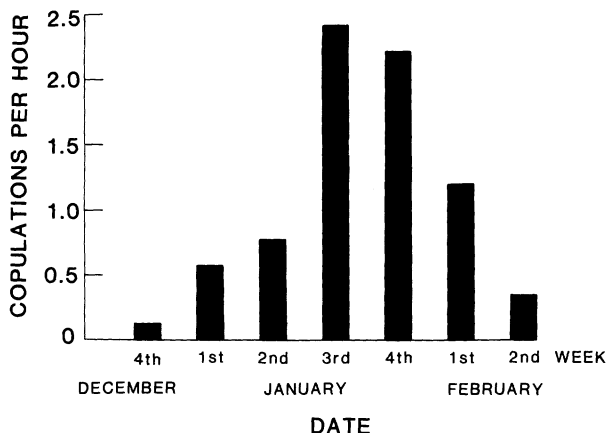


Fig. 6. Copulations per hour as a function of week during the 1985-86 breeding season.

Foraging.

After having copulated, females left their pups on the beach to go to the sea to forage. Females went to sea to forage for the first time a mean of 7.6 days after parturition, and 1.9 days after copulation (Table 4). Mean

TABLE 5. Estimated duration (in days) of consecutive foraging trips of females following parturition

	Successive feeding trips						
	1st	2nd	3rd	4th	5th	6th	7th
$\bar{X} \pm \text{S.D.}$	2.5 ± 1.0	2.8 ± 1.2	3.0 ± 1.0	3.1 ± 0.9	2.8 ± 0.9	2.8 ± 1.0	4.0 ± 1.0
(N)	(35)	(29)	(23)	(18)	(12)	(4)	(3)
Range	1-5	1-5	1-5	2-4	2-4	2-4	3-5

Data from the 1986 breeding season except for the first feeding trip, which also includes data from the 1985 breeding season.

foraging trips lasted 2.8 days ($sd = 1.1$, $n = 124$) (Table 5). The duration of the first seven feeding trips did not vary significantly ($F = 1.4$; $d.f. = 6, 117$; $p > 0.05$). Most females departed alone except at the end of the season when they left in groups of up to 25 individuals. Departures occurred throughout the day. During January, the mean number of females foraging at sea was estimated as 20% of the females on land. The proportion increased to 40% by the end of the season (Table 3).

Females alternated foraging excursions with mean intervals of two days spent on land nursing ($s = 0.8$, $n = 101$; Table 6). However, the mean duration of successive returns to the rookery was not constant ($F = 6.9$; $d.f. = 5, 100$; $p < 0.05$). A *posteriori* ANOVA comparisons of the means showed that the intervals following the first three trips to sea were shorter by 25% than the three subsequent intervals ($P < 0.05$). Females returning from a foraging trip vocalized and searched for their pups freely in the CBA.

TABLE 6. Estimate of days females spent on land with their pups between foraging trips (mean \pm one standard deviation)

	Successive intervals on land after feeding trip number					
	1	2	3	4	5	6
$\bar{X} \pm \text{S.D.}$	2.2 ± 0.9	2.8 ± 0.8	2.6 ± 0.8	1.9 ± 0.9	1.9 ± 0.8	1.8 ± 0.5
(N)	(27)	(24)	(19)	(17)	(9)	(5)
Range	1-3.5	2-5	2-5	1-3	1-3	1-2

Data are from the 1986 breeding season except for the first interval on land, which also includes data from the 1985 breeding season.

At least three females that lost their pups in December 1985 left the breeding area after copulating and did not return to the breeding area until February, when most of the breeding was over.

Discussion

The reproductive behaviour of all five species of sea lions is similar in its general form. Males defend territories from each other and from males without territories. Only territorial males breed and consequently there is great variation in mating success among males present during the breeding season. Females give birth, nurse their pups and copulate on the sites where males compete for territories. After parturition, females alternate nursing their pups onshore with feeding trips to sea.

However, there are significant deviations from this general pattern and the expression of some components are variable between species (GENTRY, 1975) and between different populations of the same species, e.g., California sea lions, *Zalophus californianus*, breeding in California (ODELL, 1975; BONESS, OFTEDAL & ONO, 1983; HEATH & FRANCIS, 1983) versus those breeding in the Galapagos Islands (TRILLMICH, 1986), and Steller sea lions, *Eumetopias jubatus*, breeding in California versus Alaska (GISINER, 1985). A comparison of key features of the reproductive behaviour of both sexes puts our results on *Otaria* in perspective and may shed light on the basis for the species differences.

Otaria males at Punta Norte differ from males of other species in several ways. One behaviour, sequestering females, leads to differences in other behaviours. Except in the case of group defection owing to a raid (VAZ-FERREIRA, 1965, 1975; CAMPAGNA *et al.*, in press), or of females that go to sea to forage, *Otaria* males prevent a female from escaping by blocking her with the neck and body or, by grasping her in their jaws, holding, shaking and hurling her into place. The injuries sustained and the relative absence of movement among females, suggest that females may learn to curb their movements. Among the other four species, only male Australian sea lions, *Neophoca cinerea*, herd females successfully. MARLOW (1975) reports that a *Neophoca* male will chase an escaping female across another male's territory and herd her back into his own.

A suite of other species differences follow from adopting a female-sequestering mating strategy:

- 1) The mating system changes from strict resource defence polygyny to one incorporating elements of female defence polygyny (EMLEN & ORING, 1977). As *Otaria* males on territory are joined by females, they switch from strict site defence to female defence to a combination of site

defence and female defence. A similar transition is not reported in any of the other species.

2) Males must remain near females to hold them. *Otaria* males do not move more than a few metres away from their females and they do not stay away long. This is reflected in the brief duration of fights and aggressive (boundary) displays. Fights among *Otaria* males are measured in seconds ($\bar{X} = 6.4$ sec) while those of males of other sea lion species are measured in minutes. For example, GENTRY (1970) reports a mean fight duration of 6.5 min in *Eumetopias* with some fights lasting up to 25 min. Boundary displays of *Otaria* are reduced to 3-5 sec in comparison with an average of 6 to 10 sec for *Eumetopias* (GISINER, 1985). *Zalophus* boundary displays are even longer because competing males often exchange several threatening displays as they walk parallel at the boundary of a territory (FRANCIS, pers. comm.).

3) Female defence is associated with fewer females being held per male. Harem size, the number of females with whom territorial males are associated, averages less than three females among *Otaria* at Punta Norte, in contrast to means of ten for *Eumetopias* (GENTRY, 1970), 27.5 for Hooker's sea lion, *Phocarcos hookeri*, (MARLOW, 1975), and 14 to 25 for *Zalophus* (PETERSON & BARTHOLOMEW, 1967; HEATH & FRANCIS, 1983). *Neophoca* males, who resemble *Otaria* in herding females, also exhibit a small harem size, a mean of 3.7 females per harem (MARLOW, 1975). Maximum harem size in *Otaria* may reach 18 females for a few hours at peak season at Lobos Island, Uruguay; however, it rarely exceeds eight females (VAZ-FERREIRA, 1975). In all sea lions species, mean harem size reflects male mating success in only a general way because not all females in harems are fecund. Moreover, the composition of harems varies with time of day, time of year and other factors such as terrain and temperature.

4) When few females can be defended successfully, the degree of monopolization of females by males is attenuated. A high proportion of males present in the area secure matings and the variance among breeders is reduced. Data on the number of individual males present on a breeding area are available for a few species because of differences in methodology, terrain and reporting. Among *Otaria* at Punta Norte, over 80% of the adult males present in the study area were associated with females at peak season (Table 2), a high figure relative to other polygynous seals, e.g., 61% of adult male northern elephant seals, *Mirounga angustirostris*, present at Año Nuevo Island, copulated during the years 1968 to 1973 (LE BOEUF, 1974). Most of the *Otaria* males (94.4%)

that held a territory in the CBA for five days or more, copulated. Copulation frequency among all tenured males, a good estimate of number of females mated because most females copulate but once, was remarkably uniform ($\bar{X} = 3.87 \pm 3.31$).

Copulations were observed throughout the entire CBA. The most successful male achieved 18 copulations, only 7% of the total observed. In contrast, copulation frequency of territorial male *Eumetopias* breeding at Año Nuevo Island California (GENTRY, 1970), was much more variable ($\bar{X} = 11.9 \pm 10.9$); 54% of the copulations occurred in an area making up only one quarter of the land available to females. Location of territories was highly correlated with male mating success; the best territories were located near females routes to and from water, or they contained tidepools. The most successful *Eumetopias* male achieved 21% of the copulations observed (GENTRY, 1970). GISINER (1985) reports that the most successful male at the same site in a later year accounted for 31% of the copulations observed. Mating success among *Otaria* at Punta Norte was more a matter of territorial tenure—time spent in association with females—than of quality or location of the territory.

Our data suggest that the mating success of *Otaria* males is constrained by holding females until they come into oestrus while defending them against neighbours who have their own females and groups of intruders without females. Since *Neophoca* is the only other sea lion besides *Otaria* in which males sequester females, one would expect the species to be similar in behaviours linked to female defence. Both species are characterized by small harem sizes and group raids. The latter, involving peripheral non-territorial males attempting to abduct females from territorial males, may reflect the failure of territorial males to rebuff intruders with force and threat of injury. To do so would be at the expense of attending to females, giving them the opportunity to flee. Raids reduce the mating success of some territorial males (VAZ-FERREIRA, 1975; CAMPAGNA *et al.*, in press).

Physical variables interact with social variables to further constrain the mating strategies of *Otaria* males. Temperature and tidal range set narrow limits within which males can defend and hold females. Breeding occurs during the peak of the austral summer when air temperatures exceeds 30°C for 4-6 hrs during a day during 25% of the days in January and, at times, rises to 39°C. Territorial males and females reduce heat stress by aggregating just above the high water mark where wallowing into the substrate gives access to the wet pebbles below. Male territories do not extend into the water, do not contain tidepools and offer no shade

from the sun. Twice a day, territorial males and their females and pups get relief from the heat as the high tide comes up to them. The majority of animals in the central breeding area get wet from the surf and spray, but neither males nor females enter the water. High tides prevent males from extending their territories seaward. Males that locate further down the berm would be awash at high tide and would not be able to hold females nor defend them from swimming groups of non-territorial males. The high temperatures, especially on days when low tide occurs at mid-day, prevent males from expanding territories to landward. Males that do this are exposed to the dry pebbly substrate and higher temperatures. Consequently, the territories of males at Punta Norte, and along the entire length of Península Valdés where the substrate is similar, are virtually linear; for the most part, they run one territory deep along the high tide mark of the shoreline. Each territory is bounded on two sides with neighbours and defended on the seaward and landward sides against potential intruders.

The substrate on which the other four species breed, the distribution of territories, and the options for reducing heat, vary greatly at the locations where they have been studied. *Eumetopias* at Año Nuevo breed on rocky shelves sloping to the sea. Females regulate their temperature by moving to and from the surf and spray (GENTRY, 1973). Male territories are semi-aquatic or terrestrial, with the latter containing tidepools. Terrestrial territories are two to three males deep along the shoreline; boundaries are sharply defined. *Eumetopias* at Marmot Island, Alaska, abandon waterless territories periodically to get wet, but they are able to return to these territories and defend them (GISINER, 1985). *Neophoca* territories are two to three deep in rocky gullies containing tidepools or access to shade; they are contiguous to one another and do not extend into the sea. *Zalophus* breed on sandy beaches and rocky shelves (PETERSON & BARTHOLOMEW, 1967; ODELL, 1975; HEATH & FRANCIS, 1983). Territories are linear along the beach like those of *Otaria* except that they extend into the water. At high temperatures, females move to the water's edge or enter the water. *Phocartos* territories are one to two deep on open sandy beaches where there are no physical features to function as boundaries (MARLOW, 1975). Males do not enter the sea but instead flip sand onto their bodies to cool themselves.

Otaria females differ from other species with regard to their minimal movements in the breeding area. Once peri-oestrous females enter a male's territory and are defended by him, they are prevented from moving away and are punished for attempting to do so. Post-oestrous females

are allowed to go to and from the sea. In contrast, all females move freely across territories in *Phocarctos* (MARLOW, 1975), *Zalophus* (HEATH & FRANCIS, 1983) and *Eumetopias* (GENTRY, 1970). In the latter, males may attempt to block the movements of females but to no avail. At Año Nuevo Island, 46% of 112 individually identified *Eumetopias* females copulated with a male other than the male on whose territory they had been an hour before or on whose territory their pup was located (GISINER, 1985).

Otaria females do not deviate from other sea lions species in temporal aspects of reproductive behaviour and copulation frequency (Table 7). Several points are notable: 1) Where data are available, species are similar and show only negligible variation in the interval between arrival to parturition, mean duration at sea, and attendance duration. *Phocarctos* females may spend more time at sea than females of other species (GENTRY, pers. comm.) but the estimates are preliminary and more data are needed. 2) Latency to go to sea after parturition is similar among all species studied with the exception of *Neophoca*, in which this interval is considerably longer (MARLOW, 1975). 3) *Otaria*, *Neophoca* and *Phocarctos* copulate less than a week after giving birth and before they go to sea for the first time after parturition (MARLOW, 1975). Most *Eumetopias* females copulate after the first trip to sea (HIGGINS *et al.*, in press). *Zalophus* females have the longest delay between parturition and copulation

TABLE 7. Temporal aspects of the reproductive behavior of sea lions (in days)

Genus	Arrival to parturition	Parturition to first trip to sea	Parturition to copulation	Mean duration at sea	Attendance duration
<i>Otaria</i>	3.3 ± 0.3	7.6 ± 0.6	6.0 ± 0.7	2.8 ± 1.1	2.3 ± 0.8
<i>Eumetopias</i>	@ 2.3	6.7 ± 0.6	12.4 ± 2.3	(1-4)	1.0
<i>Neophoca</i>	@ 3	@ 14	@ 7	@ 2	(1-2)
<i>Phocarctos</i>	?	?	@ 6.6	@ 8	?
<i>Zalophus</i>					
California	n.a.	6.5	@ 28	@ 3	2.1
Galápagos	1.5	6.8 ± 2.1	@ 21	0.5	0.6

The data consist of means ± one standard deviation, ranges (in parentheses), and approximations (@). The source of the data is as follows: *Otaria*: this paper; *Eumetopias*: GENTRY, 1970; GISINER, 1985; HIGGINS *et al.*, in press; *Neophoca*: MARLOW, 1975; *Phocarctos*: MARLOW, 1975, GENTRY (pers. comm.); *Zalophus* in California: ODELL, 1975; HEATH & FRANCIS, 1983, 1984; *Zalophus* in the Galapagos Islands: TRILLMICH, 1986b. n.a. = not applicable.

(HEATH & FRANCIS, 1983). This latency is unknown for *Phocarctos*. Most female sea lions copulate only once during oestrus; a small proportion of females copulate twice, e.g., 15% in *Eumetopias* (GENTRY, 1970). However, figures on multiple copulations are unreliable within and across species because of the difficulty of detecting intromission. This is especially true in *Otaria* when peripheral males attempt to force copulation. 4) *Zalophus* breeding in the Galápagos spend less time at sea and on shore feeding their pups than *Zalophus* breeding in southern California (TRILLMICH, 1986; HEATH & FRANCIS, 1983). Similar differences between populations of other species might be expected under conditions of extreme habitat variability. Many of the differences in attendance behavior—the pattern of delivering nourishment to pups by females—reflect maternal strategies. The latter are constrained by foraging economics—the nutritional value of available prey and the effort required to obtain it—as well as the cost of delivering nourishment to the pup on land. Little is known about foraging economics in sea lions but studies of diving behavior (FELDKAMP, 1985; KOOYMAN & TRILLMICH, 1986; GENTRY & KOOYMAN, 1986) and at-sea energetics using labeled water methodology (COSTA & GENTRY, 1986; COSTA, in press) offer a promising approach for elucidating species differences.

Summary

The reproductive behaviour of individually marked southern sea lions, *Otaria byronia*, was studied from 1981 to 1986, at Punta Norte, Península Valdés, Argentina.

Males defended territories along the high water mark early in the breeding season but switched to female defence as they were joined by females. Males defended females from neighbours and intruders, and forcefully held pre-oestrous females near them.

Males defended territories and females against neighbours and intruders with threat displays and by fighting. Males never strayed far from females. The frequency of aggressive interactions among males was positively correlated with the number of females in oestrus.

A mean of 2.8 females was associated with each male in the central breeding area at peak season, with some males being associated with 8-16 females for a few hours.

Ninety four percent of the males that held a territory for five or more days copulated. Copulations were not observed away from territories in the central breeding area. Mating success was positively correlated with tenure on territory. The first males to arrive had the longest tenures and achieved the most copulations. Mean tenure on territory was 24 days (range = 15-57 days). The mean number of observed copulations per marked adult male was 3.87 ± 3.31 . Variance among breeding males was low; the most successful male achieved only 7% of the copulations observed.

Females gave birth a mean of 3.3 days after arrival, copulated once six days later and then went to sea to feed 7.6 days after parturition. Thereafter, females alternated periods of feeding at sea ($\bar{X} = 2.8$ days) with periods of nursing their pups ($\bar{X} = 2.3$ days).

Males sequester pre-oestrous females. This mating strategy leads to differences in behaviour between *Otaria* and males of other sea lion species. These differences are evi-

dent in harem size, time away from females (as manifested by brief and infrequent fighting), the high percentage of males breeding, and the low variance in mating success among breeding males.

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Résumé

Nous avons étudié le comportement reproducteur chez des *Otaries méridionales* (*Otaria byronia*) à Punta Norte, Península Valdés (Argentine). Des animaux individuellement marqués ont été observés de 1981 à 1986.

Les mâles défendaient leurs territoires au niveau des plus hautes eaux pendant la première partie de la période de reproduction, mais passaient à la défense des femelles lors de l'arrivée de celles-ci. Dans la zone centrale de reproduction, les mâles défendaient les femelles contre voisins et intrus et maintenaient de force près d'eux les femelles pré-oestrales.

La défense du territoire et des femelles consistait en parades de menace stéréotypées ainsi qu'en combats, brefs et peu fréquents. Les mâles ne se sont jamais éloignés des femelles. On a constaté une corrélation positive entre la fréquence des interactions agressives entre mâles et le nombre de femelles en oestrus.

Dans la zone centrale de reproduction, 2,8 femelles en moyenne sont associées avec des mâles pendant la période de plus grande activité; certains mâles sont associés à 8 à 16 femelles pendant des périodes relativement brèves (quelques heures seulement).

Chez les mâles qui ont tenu un territoire pendant au moins 5 jours, 94% ont réussi un ou plusieurs accouplements. On n'a pas observé d'accouplements hors du territoire, dans la zone central de reproduction. Il existe une corrélation positive entre le nombre d'accouplements réussis et la durée d'occupation du territoire. Les mâles arrivés les premiers ont occupé leurs territoires le plus longtemps, et ont réussi le plus grand nombre d'accouplements. L'occupation du territoire a duré en moyenne 24 jours (variation: 15 à 57 jours). Le nombre moyen d'accouplements réussis, par mâle adulte marqué, a été de $3,87 \pm 3,31$. Parmi les mâles reproducteurs, il n'y avait pas de variation importante du nombre d'accouplements; le plus grand nombre d'accouplements réussis par un seul mâle n'a correspondu qu'à 7% de tous les accouplements observés.

Les femelles ont mis bas en moyenne 3,3 jours après leur arrivée; elles se sont accouplées une fois, six jours plus tard, et sont parties pour se nourrir en mer, en moyen 7,6 jours après la parturition. Ensuite, elles ont alterné des périodes de 2,8 jours passés à se nourrir en mer et de 2,3 jours passés à allaiter leurs jeunes.

Les mâles séquestrent les femelles pré-oestrales. Cette stratégie entraîne des différences entre le comportement reproducteur des mâles d'*Otaria byronia* et celui des mâles d'autres espèces d'*Otaries*. Ces différences se manifestent dans la taille des harems, la durée du temps passé loin des femelles (temps qui est occupé par des combats brefs et peu fréquents), le pourcentage élevé de mâles qui s'accouplent, et le peu de variation dans le nombre d'accouplements réussis par les mâles reproducteurs.
