Equal investment in male and female offspring in southern elephant seals

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(With 1 figure in the text)

Sex ratio theory predictions concerning differential parental investment in offspring by sex were tested on southern elephant seals, *Mirounga leonina*, breeding at Península Valdés, Argentina. Females invested equally in sons and daughters, as reflected by the similar mass at birth (mean $\pm$ 1 S.D.) of 14 males ($44 \cdot 1 \pm 6 \cdot 5$ kg) and 14 females ($43 \cdot 4 \pm 3 \cdot 8$ kg), and similar mass at weaning of 52 males ($131 \cdot 5 \pm 22 \cdot 4$ kg) and 38 females ($131 \cdot 4 \pm 18 \cdot 3$ kg). There were also no sex differences in the rate of mass gain during nursing (males $= 4 \cdot 0 \pm 0 \cdot 9$ kg/day; females $= 3 \cdot 9 \pm 0 \cdot 8$ kg/day), rate of mass loss during the first month of post-weaning fast (males $= 0 \cdot 85 \pm 0 \cdot 19$ kg/day; females $= 0 \cdot 92 \pm 0 \cdot 15$ kg/day), mean age at weaning (males $= 22 \cdot 3 \pm 1 \cdot 6$ days; females $= 22 \cdot 7 \pm 1 \cdot 7$ days), and female nursing behaviour. Mother's size accounted for most of the variation in mass of pups at weaning. Mothers ranked as small, medium and large, weaned pups with a mean mass of 102, 130 and 145 kg, respectively. The sex ratio of weanlings did not differ from unity. These data are consistent with Fisher's (1930) sex ratio theory.

Contents

Introduction

According to Fisher's primary sex ratio theory (Fisher, 1930) parents should divide total investment in their offspring symmetrically between sons and daughters by producing as many equally costly individuals of one sex as the other, or less individuals of the more costly sex. Maynard-Smith (1980) challenges Fisher's assumption that the cost of offspring is fixed and the sex ratio variable. He argues that it is evolutionarily stable for parents to invest more in one of the

sexes, even when the primary sex ratio is unity if, by doing so, parents differentially increase the fitness of that sex.

Polygynous and sexually dimorphic seals are attractive models for testing hypotheses on parental investment by sex and after birth (Trivers, 1972), for methodological and theoretical reasons. In phocids, maternal energy transferred as milk is the largest component of parental effort and represents an index of parental investment (Fedak & Anderson, 1982; Ortiz, Le Boeuf & Costa, 1984; Costa *et al.*, 1986; Kovacs & Lavigne, 1986*a*). Lactation is brief and ends abruptly (Bonner, 1984; Kovacs & Lavigne, 1986*a*; Oftedal, Boness & Tedman, 1987), enabling the end of the period of maternal investment to be accurately determined. Variance in lifetime reproductive success (LRS) is expected to be larger in males than in females, and this has been documented in one species (Le Boeuf & Reiter, 1988). If LRS is affected by maternal investment (Trivers, 1972), mothers might be selected to invest more in sons than in daughters if this increases the fitness of sons relatively more than that of daughters (Maynard-Smith, 1980). Differential fitness by sex due to a bias in maternal investment has been shown for a few mammals, such as red deer, *Cervus elaphus* (Clutton-Brock, Albon & Guinness, 1981, 1984; Clutton-Brock, Guinness & Albon, 1982), but it has not been documented in phocids. However, in northern elephant seals, *Mirounga angustirostris*, survival rate to one year of age tends to increase with mass at weaning, and weanling mass is positively and significantly correlated with mass at one year of age for males (Morris, Le Boeuf & Ortiz, 1989, pers. comm.). This suggests that mothers may gain a reproductive advantage by weaning heavy pups, and that the benefit may be larger for male offspring.

Studies of parental investment in polygynous pinnipeds have yielded conflicting results regarding differential parental investment by sex of offspring after birth. In sea lions, fur seals and grey seals, *Halichoerus grypus*, females invest more in male offspring in populations with an equal sex ratio at birth, supporting Maynard-Smith's (1980) theory (Costa & Gentry, 1986; Kovacs & Lavigne, 1986*b*; Trillmich, 1986; Anderson & Fedak, 1987). Other studies on phocids suggest an equal maternal investment in the sexes and support Fisher's (1930) theory (Stewart & Lavigne, 1980; Stewart 1986; Le Boeuf, Condit & Reiter, 1989; McCann, Fedak & Harwood, 1989; Kretzmann, 1990). Here, we examine the extent to which parental investment in southern elephant seals, *M. leonina*, matches the theoretical predictions of differential investment in offspring by sex in a polygynous mammal.

Male southern elephant seal neonates at South Georgia Island, and male northern elephant seal weanlings at Año Nuevo, California, are significantly heavier than females (McCann *et al.*, 1989; Le Boeuf *et al.*, 1989). Male weanlings of the southern species and neonates of the northern congener may also be heavier than females but the difference is based on too small a sample size to be significant (Reiter, Stinson & Le Boeuf, 1978; Le Boeuf *et al.*, 1989; McCann *et al.*, 1989). In both species, variance in pup body mass is better correlated with mother's size, which increases with age (Reiter, Panken & Le Boeuf, 1981), than with pup's sex (Reiter *et al.*, 1981; McCann *et al.*, 1989).

In this paper, we study the effect of pup sex and estimated mother's size class on maternal investment in southern elephant seals breeding at Península Valdés, Argentina. We provide data on body mass at birth and at weaning, growth rate during nursing, duration of lactation, maternal behaviour, and mass loss by both sexes during the post-weaning fast. We also present data on sex ratio at weaning.

The Península Valdés population of elephant seals has distinctive ecological, demographic and geographical features that differentiate it from other colonies of the same species and from those of its northern counterpart (Le Boeuf & Petrinovich, 1974). It is one of the northernmost elephant

seal colonies in the southern hemisphere. It is located in temperate rather than Antarctic or sub-Antarctic waters, and is 550 km away from deep water where elephant seals usually forage (Le Boeuf *et al.*, 1988; Hindell, Slip & Burton, 1989). The colony is growing slowly, harems are unusually small relative to other populations, and density-dependent pup mortality is low (Le Boeuf & Petrinovich, 1974; Honigman, 1988; Lewis, 1989). If investment in the offspring in elephant seals is affected by social and ecological variables, as it is in another polygynous, sexually dimorphic mammal such as the red deer (Clutton-Brock *et al.*, 1982, 1984), we will document such an effect by comparing our results with those obtained in circumpolar islands such as South Georgia. We will show that, despite the social and ecological differences at Península Valdés, results on maternal investment are similar to those from South Georgia and other colonies, augmenting the empirical support for Fisher's (1930) theory concerning the allocation of investment by sex.

Methods

During the 1981 and 1982 breeding seasons, we weighed and obtained the standard length of 28 pups (14 males and 14 females) on the day of their birth at Península Valdés, Argentina. Neonatal mass provides a measure of investment during gestation. Pups were studied during the first half of the breeding season in both years. Mothers were categorized as medium size (see below for an explanation of size categories). As body mass and standard length did not differ between years (Lewis, 1989), we combined the data for each sex. Nineteen of the 28 pups weighed at birth were weighed again within 2 days of weaning to estimate mass gain during the nursing period.

During the 1988 breeding season (August 20–November 2) at La Armonia, we studied maternal behaviour and weighed pups at weaning and again at weekly intervals for 3–5 weeks after weaning. We weighed pups after weaning because differential mass loss might indicate sex differences in metabolism that could affect mass at weaning independently of maternal effort (Costa & Gentry, 1986). To minimize disruption caused by human interference, we did not weigh pups at birth during this breeding season. We marked 82 adult females with dye or bleach (Le Boeuf & Peterson, 1969) as they arrived on the breeding area. Identification cards were kept to record the presence and key reproductive events of marked seals, such as date of parturition, copulation and departure from the rookery. Differential maternal investment in the offspring by sex could affect the length of the interval between these events.

Within one day after parturition, marked females were categorized according to body size as large, medium or small by 3 observers acting independently. These categories were assumed to reflect age (Reiter *et al.*, 1981). Only those females that were assigned to the same size category by all observers were considered in the analysis. This method yields a crude estimate of female size. To test the accuracy of our categorization of females we obtained, during a different study, indirect measures of female length from photographs as described in Reiter *et al.* (1981). Results were consistent with our *a priori* categorization of the size of the photographed females. Females categorized as small, medium and large had a mean length of 180 cm (± 29; $n = 46$), 246 cm (± 17 cm; $n = 39$), and 295 cm (± 21; $n = 46$), respectively.

After marked females gave birth, we attached plastic, serially numbered tags to the interdigital webbing of one or both hind flippers of their pups (Le Boeuf & Peterson, 1969). These pups were not retrieved from the mother because they were not weighed or measured at or near birth. We tagged 76 pups of marked females born throughout the breeding season. Tagged pups were observed throughout daylight hours to determine if they were suckling from other females in addition to their mothers. We weighed 71 of the 76 tagged pups at weaning, 42 males and 29 females. None of them had been seen stealing milk from foster females. All pups were weighed within 1–12 hours of weaning. Two pups, that were adopted by a second female after being weaned by their mothers, were weighed after each weaning episode. Only the first observation was included to estimate mass at weaning. As mean body mass of weanlings by sex was similar for the 1980–81 and 1988 seasons, the data were combined.

We weighed weaned pups by placing them in a cone-shaped canvas sock held fast by straps (Reiter *et al.*, 1978). A calibrated scale (Chatillon WT-12), with a capacity of 500 kg, accurate to 0·5 kg, was hung from a tripod constructed of aluminum pipes. The scale was attached to eyelets on the canvas sock and the pup was lifted using a hand winch. The entire process took about 15 min. The procedure for weighing pups was similar in all years. The scale was calibrated again at the end of the study to give evidence of any potential inaccuracies in the measurements.

Ad libitum observations of behaviour were conducted during daylight hours (09:00–19:00 h) for 75 days from sand dunes or cliffs overlooking the breeding area, 15–25 m from the animals. The duration of suckling sessions, on-teat periods during suckling sessions, and interval between consecutive suckling sessions were determined by focal animal samples (FAS) (Altmann, 1974). Suckling sessions consisted of both on-teat periods and short (less than a minute) breaks between them (Oftedal *et al.*, 1987). We recorded 189 FAS for a total of 484 hours of marked female-pup pairs. We included data only from suckling sessions during which the animal was in full sight all the time. Scan samples (Altmann, 1974) were used to calculate the percentage of time that a female spent suckling. Every 20 min, the activity of up to 76 marked mothers was observed. It took about 5 min to complete one scan of all females. A total of 14,247 records were collected from which only data on nursing are presented in this paper.

Weanling sex ratios (males:females) were estimated by recording the sex of individuals during on-foot surveys of breeding sites along 30 km of coast conducted during the last week of October 1984, 1988 and 1989. The sex of a pup was determined by noting the presence or absence of a penile opening, located posterior to the umbilicus or umbilical scar. As pup mortality is low (3% of 745 pups born at Punta Norte and La Armonia in 1988; see also Honigman, 1988; Lewis, 1989 for similar results from other five years), and it is not significantly sex-biased (Lewis, 1989), weaning sex ratio closely approximates sex ratio at birth.

Variation around the mean is expressed as one standard deviation. Tests are 2-tailed unless otherwise specified.

Results

Body mass and length at birth

The mean mass and standard length of new-born males was similar to that of new-born females (Table I).

Body mass at weaning

The mean mass of male weanlings was similar to that of female weanlings (Table I). The two heaviest pups were males who had been adopted and nursed by other females after being weaned

TABLE I

Mean (± 1 S.D.) body mass (kg), length (cm), rate of mass gain and loss (kg/day), and age at weaning (days) as a function of pup sex. Sample size is in parentheses. The differences are not statistically significant

	Males	Females	Statistics
Mass at birth	44·1 ± 6·5 (14)	43·4 ± 3·8 (14)	Mann-Whitney U = 106; $P > 0·20$
Length at birth	134·1 ± 6·2 (14)	133·3 ± 5·8 (14)	$t = 0·38; P \geqslant 0·71$
Mass at weaning	131·5 ± 22·4 (52)	131·4 ± 18·3 (38)	$t = 0·02; P \geqslant 0·93$
Rate of mass gain	4·0 ± 0·9 (10)	3·9 ± 0·8 (9)	$t = 0·22; P \geqslant 0·83$
Age at weaning	22·3 ± 1·6 (45)	22·7 ± 1·7 (29)	$t = -1·20; P \geqslant 0·23$
Mass loss of weanlings	0·9 ± 0·2 (15)	0·9 ± 0·2 (9)	$t = -1·50; P \geqslant 0·15$

TABLE II

Mean mass of weaned pups in kg (± 1 S.D.) as a function of mother's relative size. Sample size is in parentheses

	Relative size of mother		
	Large	Medium	Small
Males	150·3 ± 21·5 (12)	130·0 ± 11·2 (22)	100·0 ± 9·1 (8)
Females	139·2 ± 13·4 (11)	130·8 ± 14·2 (11)	105·2 ± 25·6 (4)
Both sexes	145·0 ± 18·5 (23)	130·3 ± 12·1 (33)	101·8 ± 15·4 (12)

by their mothers. They weighed 191 and 227·5 kg after nursing 38 and 42 days, respectively. The heaviest weanling that had not been nursed by a stepmother was a male of 180 kg.

Small mothers weaned significantly lighter pups than medium-sized mothers and the latter weaned lighter pups than large mothers (Table II; ANOVA F [of log-transformed data] = 36·76; $d.f. = 2$, 65, $P < 0.05$; Tukey test between means, $P < 0.05$). There was no statistically significant interaction between mother size and pup sex (two-way ANOVA with unequal and disproportional replication; F = 1·69, $P \geqslant 0.38$).

Age at weaning

Seventy four pups were weaned at a mean age of 22·4 ± 1·7 days. Age at weaning varied from 19–26 days. The mean age at weaning of males was similar to that of females (Table I).

Mass at weaning was not correlated with age at weaning for 42 males (Kendall's tau = 0·06, $P \geqslant 0.58$) or for 28 females (Kendall's tau = −0·13, $P \geqslant 0.32$).

Age at weaning did not vary with mother's size. Ten small females weaned pups at a mean age of 23·0 ± 1·6 days, 21 medium-sized females weaned pups at 22·1 ± 1·4 days, and 17 large females weaned pups at 22·8 ± 1·7 days (Kruskal-Wallis test, $\chi^2 = 2.47$, $d.f. = 2$, $P \geqslant 0.29$).

Mass gain during the nursing period

Throughout nursing, male and female pups increased their mass at similar rates. The mean rate of mass gain for male pups was similar to that for female pups (Table I).

Nursing behaviour

Females spent about 15% of their time nursing their pups. The duration of suckling sessions, on-teat time during a session, and the interval between consecutive sessions was not related to the sex of the pup. The mean duration of a suckling session was 14 ± 9 min for 272 male episodes and 13 ± 9 min for 89 female episodes ($t = 1.2$, $P \geqslant 0.23$). Mean on-teat time during the above suckling sessions was 11 ± 8 min for males and 9 ± 6 min for females ($t = 1.7$, $P \geqslant 0.09$). Mean interval between consecutive suckling sessions was 34 ± 24 min for 161 male episodes and 34 ± 26 min for 44 female episodes ($t = 0.07$, $P \geqslant 0.90$).

TABLE III

Suckling behaviour of pups as a function of mother's size (mean ± S.D.; in minutes). Sample size is in parentheses. The differences are not statistically significant (ANOVA $F_{suckling\ session} = 1·1$, $F_{on-teat} = 1·7$, $F_{interval} = 0·04$, $P \geqslant 0·68$, 0·36, 0·99)

	Female size		
	Large	Medium	Small
Suckling session	13·4 ± 6·7 (128)	14·7 ± 10·6 (164)	13·1 ± 8·0 (53)
On-teat period	9·8 ± 5·3 (131)	11·2 ± 8·0 (165)	10·0 ± 5·8 (52)
Interval between nursing sessions	33·8 ± 23·5 (87)	33·6 ± 24·3 (85)	35·0 ± 24·7 (34)

The size of the mother did not have an effect on the length of suckling sessions, on-teat time, or interval between suckling sessions (Table III).

Time spent by females ashore

The sex of the pup did not affect the total time females spent on land reproducing, nor the length of time between arrival at the breeding area, parturition, copulation and departure (Table IV).

Mass loss after weaning

The mean rate of mass loss of males weighed at weaning and at one month of age was similar to that of females (Table I). The rate of mass loss was also similar for both sexes when expressed as a function of weeks after weaning (Table V).

The rate of post-weaning mass loss was positively and significantly correlated with pup body mass at weaning ($r = 0·71$; Fig. 1).

TABLE IV

Mean (± 1 S.D.) duration of female main reproductive events (in days) as a function of the sex of the offspring. Sample size is in parentheses. The differences are not statistically significant ($t_{arrival-departure} = 0·93$, $t_{parturition-copulation} = 1·4$, $t_{copulation-departure} = 1·2$, $P \geqslant 0·68$, 0·34, 0·48)

	Arrival to departure	Parturition to 1st copulation	1st copulation to departure
Male pups	28·5 ± 2·7 (25)	20·0 ± 2·0 (30)	1·8 ± 1·0 (29)
Female pups	27·7 ± 2·0 (13)	20·8 ± 2·2 (21)	1·8 ± 1·4 (18)

TABLE V

Rate of mass loss (kg/day) of male and female weanlings for each interval of time after weaning. The differences are not statistically significant (Mann-Whitney $U_1 = 255$, $U_2 = 272$, $U_3 = 148.5$, $U_4 = 91$; $P > 0.05$). Sample size is in parentheses

	Week intervals after weaning			
	0–1	1–2	2–3	3–4
Males	0·91 ± 0·27 (25)	0·89 ± 0·24 (29)	0·86 ± 0·22 (22)	0·78 ± 0·11 (18)
Females	1·02 ± 0·20 (16)	0·93 ± 0·36 (18)	0·79 ± 0·12 (12)	0·82 ± 0·06 (8)

Sex ratio

Weanling sex ratio was not different from unity in 1984 (1·0:0·9, $n = 687$), 1988 (1·0:0·9, $n = 202$), and 1989 (1·0:1·1, $n = 862$) (G = 0·77, 0·32, 1·04, respectively, $d.f. = 1$, $P \geqslant 0.38$, 0·58, 0·31).

Discussion

Female southern elephant seals at Península Valdés appear to invest equally in sons and daughters, when investment is measured in terms of mass at birth and at the end of lactation, mass gain during nursing, age at weaning, and nursing behaviour. Our results are consistent with those of McCann *et al.* (1989) who found that male and female pups born at South Georgia Island are suckled for the same amount of time, grow at a similar rate, and have a similar body mass at
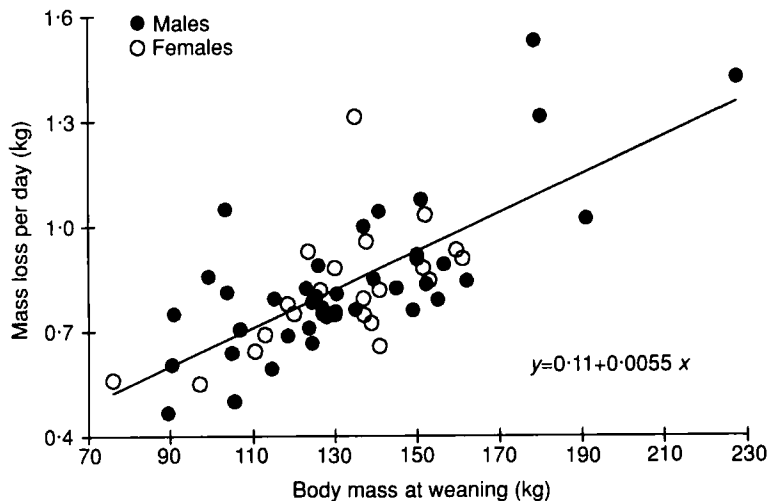

FIG. 1. Rate of mass loss (kg/day) as a function of body mass at weaning. There is no difference in regression lines (slopes and intercept) for males and females (ANCOVA, F for slopes = 0·25; F for intercepts = 0·19; $P > 0.05$).

weaning. Male new-borns at South Georgia are heavier than females but the size difference does not persist at weaning (McCann *et al.*, 1989).

In the northern elephant seal, male weanlings weigh about 8% more than females, and are weaned in equal numbers (Le Boeuf *et al.*, 1989). However, in the studied sample, the difference in mass between the sexes did not decrease the mother's probability of surviving or reproducing again, thus it may not represent a difference in parental investment as defined by Trivers (1972) (Le Boeuf *et al.*, 1989). Moreover, total milk intake, rate of mass gain and field metabolic rate of northern elephant seal pups over the nursing period do not differ between the sexes, nor does body composition at birth and at weaning (Kretzmann, 1990). Our data on weight loss after weaning for the southern elephant seal is in accordance with these results, supporting the point that metabolic rate is similar for male and female pups and weanlings. Thus, data on energetics, body mass and length, behaviour and secondary sex ratio for both species of elephant seals provide support for Fisher's (1930) theory on the ratio of investment by sex.

Our results support the hypothesis that weanling mass is more a function of mother's size than pup sex. The mean mass of weanlings is virtually identical for males and females in the present sample (Table I), but it varies greatly with mother's mass, a difference of 43 kg between small and large mothers (Table II). Larger females have greater fat reserves, and could thus produce heavier offspring. These results are consistent with those on the northern elephant seals (Reiter *et al.*, 1981; Le Boeuf *et al.*, 1989) and southern elephant seals in South Georgia (McCann *et al.*, 1989; Fedak *et al.*, 1989) which also show a positive relation between maternal size and pup size at weaning.

Elephant seals differ from other polygynous and sexually dimorphic pinnipeds in the pattern of investment in the offspring by sex, at weaning time. Male grey seal pups are larger at birth, gain mass at a faster rate, and are weaned heavier than females (Boyd & Campbell, 1971; Kovacs & Lavigne, 1986*b*; Anderson & Fedak, 1987). The energetic cost to grey seal mothers of producing males is 10% higher than the costs of raising daughters (Anderson & Fedak, 1987). Behaviourally, female grey seals spend significantly more time defending and feeding male than female pups (Kovacs, 1987). Similarly, in several species of otariids, males grow faster or are heavier than females at birth, weaning or both (Payne, 1979; Doidge, Croxall & Ricketts, 1984; Kerley, 1985; Costa & Gentry, 1986; Trillmich, 1986; Costa, Trillmich & Croxall, 1988; Boyd & McCann, 1989). In these species, males are larger than females at birth and in adulthood. Conversely, in the monomorphic harp seals, *Phoca groenlandica*, pup mass at birth and at weaning, and pup growth rate do not differ between the sexes (Stewart & Lavigne, 1980; Kovacs & Lavigne, 1985, 1986*a*; Stewart, 1986). Elephant seals, being the most sexually size dimorphic of the pinnipeds at adulthood, show no differential investment and sexual dimorphism early in life, a pattern similar to that of sexually monomorphic species.

The large size of elephant seal mothers may partially explain why the species does not fit predictions based on Maynard-Smith's (1980) theory. If large females may meet the energetic cost of reproduction without depleting their body stores to a dangerously low level, negatively affecting their future fitness (Costa *et al.*, 1986; Le Boeuf *et al.*, 1989; Fedak *et al.*, 1989), they may not be selected to withhold resources from female offspring compared to male offspring. For several taxa studied, females of larger species invest less energy in the offspring relative to their body mass than smaller species (Reiss, 1989). After weaning their pups, large southern elephant seal females have energy reserves similar to those of smaller mothers after parturition (Fedak *et al.*, 1989). The largest females might even have enough energy reserves after weaning a pup to invest in a second offspring (Fedak *et al.*, 1989). In summary, larger mothers have more to give at a lower fitness cost and thus may not have to withhold investment from female pups. But investment is certainly not

trivial for the smaller females. Small and young northern elephant seal females that start investing in reproduction early in life decrease their life expectancies relative to those females that delay maturity for one year longer (Reiter, 1984). Likewise, in harp seals, lactation represents a greater reproductive effort for young females than for older females (Stewart, 1986). At the time of weaning a pup, young harp seal mothers have depleted their fat layer to a dangerously low level, almost to the point of compromising their thermoregulation. Conversely, old females could still fast for about 23 days before risking their survival (Stewart, 1986). Therefore, if the cost of producing an offspring is higher for smaller individuals, one would expect that small mothers in a polygynous species would be selected to allocate extra resources only on male pups, as expected on theoretical grounds (Maynard-Smith, 1980). Consistent with this view, small mothers in South Georgia tend to wean larger male pups than expected for their size (McCann *et al.*, 1989).

Another possible explanation of unbiased investment by sex in elephant seals hinges on the effect of maternal investment on a pup's lifetime fitness. According to Maynard-Smith (1980), females should invest more in male offspring if the latter's fitness would increase proportionately more than if a similar greater-than-average investment were put into female pups. If differential maternal effort does not make a significant contribution to a male's lifetime fitness, Maynard-Smith's (1980) predictions would not even apply to elephant seals. The available information on both elephant seal species is not conclusive about the long-term effects of maternal investment on the fitness of the offspring. Mass at weaning is significantly correlated with mass at one year of age for male pups ($r = 0.50$; $P < 0.001$), but it only accounts for 25% of the variation (Morris *et al.*, 1989), suggesting that other factors in combination are important. Moreover, recent work on northern elephant seals suggests that large size may not be as important as it was thought for male mating success (Clinton, 1990; Haley, 1990). Among adult males of the same age, mating success is not correlated with standard length (Clinton, 1990). Conversely, in red deer, mothers invest more in male than in female offspring (Clutton-Brock *et al.*, 1981, 1982), and maternal investment early in life is related to adult male body size, fighting ability and lifetime reproductive success (Clutton-Brock *et al.*, 1981, 1982, 1984). The fact that maternal investment in red deer may have a more important effect on male fitness than in elephant seals may provide a partial explanation for the different pattern of parental investment in the two species, and their match to sex allocation theory.

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