

Parental investment and the secondary sex ratio in northern elephant seals

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Summary. Data on northern elephant seals, *Mirounga angustirostris*, bearing on sex ratio theory were collected at Año Nuevo, California, and other Californian and Mexican Islands, during the period 1967 to 1988. The mass of males exceeded that of females by 7–8% at birth and at weaning. The sex ratio was biased to males at birth (51.2%) and was near unity at weaning (49.6% males). The sex ratio did not vary as a function of maternal age or maternal mass except in 6-year-old females, who produced significantly more males. Although sons cost more to rear in energetic terms than daughters, and mothers were more successful weaning the latter, the sex of the pup reared exerted no significant effect on the mother's reproductive performance the following year or on her subsequent survival. These data suggest that parents invest equally in sons and daughters when investment is measured in terms of future reproduction (Fisher 1930) and provide no support for the theory of adaptive shifts in sex ratio (Trivers and Willard 1973). The small sex difference in mass due to maternal effort reflects the fact that females fast during lactation and all energy transferred is from limited body stores. Because of these circumstances, selection for superior condition at the end of the period of parental investment may act more strongly on pups, who have the opportunity to steal milk, than on their mothers.

Introduction

There are substantial discrepancies between observed sex ratios of large mammals and predictions from sex ratio theory (Clutton-Brock and Iason 1986). For example, Fisher (1930) and others

(Leigh 1970; Charnov 1982) predict that if one sex is more costly to raise than the other, the sex ratio at the end of the period of parental investment should be biased to the cheaper sex. However, in many mammals, males are larger at birth and at weaning, suggesting that they cost more to the mother, and males and females are equally numerous at weaning (Clutton-Brock et al. 1981; Clutton-Brock and Albon 1982; Trillmich 1986). A second theoretical prediction is that parents of certain species should enhance their fitness by varying the sex ratio of offspring in accordance with their condition and ability to invest (Trivers and Willard 1973). Although this hypothesis has stimulated a great deal of research, the results are conflicting (Myers 1978; Williams 1979; Clutton-Brock and Iason 1986).

In a survey of parental investment patterns in mammals, Clutton-Brock and Albon (1982) concluded that, owing in large part to sparse data, it was not possible to give conclusive answers to the following questions: 1) Do mothers allocate a greater proportion of their resources to offspring of one sex? 2) Is the sex ratio produced 50:50, or if not, is the sex ratio skewed to compensate for more energy allocated to one sex? 3) Does the sex ratio of progeny vary with the parent's ability to invest? The aim of this paper is to address these questions and to test predictions from sex ratio theory using data collected during the course of a long term study of northern elephant seals, *Mirounga angustirostris*.

Elephant seals have several traits that make them useful for testing sex ratio theory in mammals. Sex ratio adjustment is expected to be most likely in highly polygynous, sexually dimorphic species where body size is important in winning fights (Le Beuf 1974; Clutton-Brock et al. 1981; Clutton-Brock and Iason 1986; Armitage 1987);

adult male elephant seals are on average six times heavier than adult females (Costa et al. 1986; B. Le Bœuf, unpublished data). Estimation of parental investment patterns in elephant seals is simplified for several reasons: 1) as in other sexually dimorphic, polygynous pinnipeds (Trillmich 1986; Kovacs and Lavigne 1986), male elephant seals do not invest in offspring; 2) females breed on island beaches and are observable throughout the course of maternal investment, a 24–28 day period during which the lactating mother fasts; 3) pups get all nourishment from mother's milk, therefore, mass at weaning should provide a relative indicator of the energetic component of parental investment (Ortiz et al. 1984; Costa et al. 1986); 4) it is unlikely that post-weaning investment occurs, as has been observed in some primates (Clark 1978) and deer (Clutton-Brock et al. 1981), since female elephant seals go to sea after weaning their pups and mother-pup contact is terminated.

Since variance in lifetime reproductive success is approximately four times greater among males than females (Le Bœuf and Reiter 1988), high quality males are expected to have greater reproductive success than any individual female (Trivers and Willard 1973). Females producing high quality offspring should leave more grand-offspring if they produce males, while low-quality offspring should be female because females have no difficulty obtaining mates.

Previous research on northern elephant seals has revealed several observations pertinent to sex ratio theory. Mothers invest more heavily in male than female offspring since male pups are heavier at birth and at weaning than female pups, and male pups nurse one full day longer than female pups (Le Bœuf and Briggs 1977; Reiter et al. 1978, 1981). Contrary to Fisher's prediction, the sex ratio is not biased toward females but is 1:1 at the end of parental investment (Le Bœuf and Briggs 1977). Contrary to the predictions of Trivers and Willard (1973), there is no evidence that older, larger females, who appear to be in top physical condition, or females giving birth early in the season (cf. Coulson and Hickling 1961; Stirling 1971), bias the sex of their offspring toward males (Reiter et al. 1981).

In this paper, we augment the existing database on the sex ratio at birth and at weaning in this species, present data on pup mass at birth and weaning, describe the sex ratio of offspring produced as a function of mother's age, and show the effect of raising pups of either sex on the subsequent survival, reproductive performance, and reproductive success of the mother.

We test the following predictions derived from sex ratio theory: 1) if a given increment in parental investment has a greater effect on the fitness of males than on females, mothers might be expected to invest more heavily in individual sons than in individual daughters (Willson and Pianka 1963; Reiter et al. 1978; Maynard Smith 1980); 2) since males appear to cost more to produce, judging from sex differences in mass, there should be fewer of them at weaning (Fisher 1930; Leigh 1970; Charnov 1982); 3) mothers should bias investment according to their ability to invest, i.e., young females that are small and still growing should produce females, and large, prime age or old females should produce males (Trivers and Willard 1973); 4) because of an apparently greater energetic investment in males compared to females, which may represent an increased risk to a female's residual reproductive value (Pianka 1974), mothers that raise sons should show a reduction in subsequent survival or reproductive performance relative to those that raise daughters (see also Clutton-Brock and Iason 1986).

Methods

Data on sex ratio were collected at Año Nuevo, California, from 1967 to 1988. For sex ratio at birth and sex ratio at weaning, we combined data collected between 1967 and 1980, that has been previously reported (Le Bœuf et al. 1972; Le Bœuf and Briggs 1977; Reiter et al. 1978; Reiter et al. 1981), with data collected from 1981 to 1988. Sex of pups was determined during the nursing period, at death prior to weaning, or at weaning when they were marked individually with cattle ear tags (Le Bœuf and Peterson 1969). In addition, the sex of 4075 weaned pups was obtained from the following elephant seal rookeries in southern California and Mexico during the years, 1968–1971: San Nicolas, San Miguel, Guadalupe, San Benito and Cedros. Since the results of these samples were similar statistically, the data were pooled.

All other data reported here were obtained at Año Nuevo, California. All measures of pup mass were from offspring of known-age mothers obtained during the period 1978 to 1988. Pups were weighed within two days after weaning by restraining them in a canvas sock and then lifting them by hand winch to a scale (Chatillon, capacity 1000 ± 5 lbs) attached to a tripod (Reiter et al. 1978; Ortiz et al. 1978). A sample of 40 pups was weighed again after 30–80 days of fasting to determine mass lost per day during the fast.

Data relating sex ratio to mother's age were obtained from females tagged as pups (Le Bœuf and Peterson 1969). At the beginning of each breeding season, 225–300 known-age females were marked as they arrived on the rookery pregnant. Pup sex was determined during the course of nursing.

The survival rate and reproductive success of 625 individually marked females that bred at Año Nuevo was determined for breeding seasons following the successful or unsuccessful rearing of pups of either sex. Females and their pups were monitored by daily searches during the breeding season (December to mid-March) and weekly searches during the rest of the year. We recorded the sex of offspring of marked females,

whether their pups died on the rookery prior to weaning, whether they were separated and likely to have died, and whether they survived to weaning in a healthy condition. Females that bred at Año Nuevo sometimes appeared at Southeast Farallon Island, near San Francisco, or at San Miguel Island in southern California; the appearance and reproductive performance of these immigrants were reported to us by colleagues conducting seal research at these sites. We assume that some females that did not reappear following reproduction were not dead but simply lost their tags or were present but not seen (Le Boeuf and Reiter 1988); we expected no differences in these variables as a function of pups sex. We assume that observation of females on the rookery during the breeding season reflects reproductive success because 97% or more of the females that visited the rookery were pregnant.

For some analyses, we separated young primiparous females (age 2–5) and young multiparous females (age 4) from older multiparous females in their prime or old age (Reiter et al. 1981), reasoning that the former, who are still developing, might be more stressed by the reproductive process.

Results

Mass at birth and weaning

Males weighed more than females at birth and at weaning but the difference is significant only at weaning (Table 1). The mass difference between the sexes was similar at both ages; males weighed 7.7% more at birth and 8.2% more at weaning than females. This suggests that if the sample size at birth were as large as that at weaning, the sex difference in mass at birth would be statistically significant. This inference is made stronger by the report that male pups are 7% heavier than female pups at birth in the southern congener, *M. leonina* (Little et al. 1987).

Mass change

Evidence for differences in mass gain of pups, and the cost to their mothers, was also obtained from a sample of mother-pup pairs weighed twice during the nursing period. The mean mass gain of six males was 4.18 ± 0.59 kg/d while that of ten females was 3.96 ± 0.53 kg/d. The mean mass loss of the mothers of the males was 7.34 ± 1.15 kg/d, while that of mothers of the females was 7.21 ± 0.90 kg/d. These small sex differences are probably underestimates because of a bias in ages of the mothers; the mothers of males in this sample had a mean age of 4.67 ± 1.03 years while the mothers of females were 6.4 ± 2.95 years old. Weanling mass increases sharply with mother's age up to age 6 or 7 (Reiter et al. 1981).

No sex differences were evident in mass lost during the 2 1/2 month post-weaning fast of pups. Mean mass loss was 0.65 ± 0.10 kg/d for 16 males and 0.65 ± 0.13 kg/d for 24 females.

Table 1. Mass at birth and weaning (mean \pm 1 standard deviation in kilograms), and mass gain during nursing, in northern elephant seal pups. All data were collected at Año Nuevo, California, during the years, 1978 to 1988. The data for weanlings includes all data previously published by Reiter et al. (1981); Mean nursing days is from Reiter et al. (1978). N is in parentheses

	Males	Females	All animals
Newborns	41.62 ± 5.79 (14)	38.66 ± 5.73 (21)	39.85 ± 5.85 (35)
Weanlings*	136.53 ± 28.44 (412)	126.18 ± 23.62 (424)	131.00 ± 26.96 (836)
Total mass gain (kg)	94.91	87.52	91.15
Mass gain/day (kg)	3.41	3.29	3.38
Mean nursing days	27.8	26.6	27

* The difference in mass of weanlings is statistically significant ($t = 5.74$, $df = 834$, $P < 0.05$); the difference in mass of newborns is not statistically significant ($t = 1.49$, $df = 33$, $P > 0.05$)

Sex ratio at birth and weaning

To determine the sex ratio at birth and at weaning, we combined all data collected from the years 1967 to 1988 on Año Nuevo, on rookeries in southern California and on Mexican Islands (Le Boeuf et al. 1972; Le Boeuf and Briggs 1977; Reiter et al. 1978, 1981). In a sample of 3350 animals, more males (51.8%) were born than females (Chi-square = 4.44, $df = 1$, $P < 0.05$). The sex ratio of pup deaths prior to weaning in 958 animals was skewed to males (51.2% males) but the difference was not significant (Chi-square = 0.60, $df = 1$, $P > 0.05$). The sex ratio at weaning of 11073 animals was 49.6% males, not significantly different from unity (Chi-square = 0.84, $df = 1$, $P > 0.05$).

Sex ratio as a function of mother's age and mass

Female mass at parturition and at the end of lactation changes with age, increasing by about 50% from age 3 to age 6 and then reaching an asymptote (Le Boeuf et al. 1988). Insofar as mass reflects condition and the ability to invest, Trivers and Willard (1973) would predict that the heavier females would bias their offspring sex to males. We summarized all data from 1970 to 1988 on pup sex as a function of mother's age, disregarding whether the pups were raised successfully or not. Females produced more males at nearly every age but the difference is significant only at age six and for the entire sample combined (Table 2). Young females, age 2–5, produced 54.4% males while prime age and older females, age 6–16, produced 56.6%

Table 2. The sex ratio in relation to mother's age in a sample of northern elephant seal pups collected during the years 1970 to 1988 at Año Nuevo, California. The age of females was known from serial tags placed in the hindflippers at one month of age (Le Bœuf and Peterson 1969)

Mother's age	Number of pups born		
	Males	Females	% males
2	0	1	0
3	36	36	50.0
4	121	98	55.2
5	89	71	55.6
6	87	57	60.4*
7	55	51	51.9
8	49	34	59.0
9	27	24	52.9
10	20	17	54.0
11+	24	19	55.8
Totals	508	407	55.5**

* Chi-square=6.25, $df=1$, $P<0.05$. ** Chi-square=11.15, $df=1$, $P<0.05$. All other comparisons are not statistically significant

males. This difference is not significant (Chi-square=0.43, $df=1$, $P>0.05$). Note that the overall sample bias to male pups corresponds to the bias in sex ratio determined in a different way in Table 1.

Weaning success and offspring sex

If sons are more costly to raise, the weaning success of mothers raising sons should be lower than that of mothers raising daughters. This may be more likely among young females for whom reproduction is likely to be more stressful. Table 3 shows that young and primiparous females, age 2 to 5, had a significantly lower success rate raising male offspring compared to raising female offspring. When the data for females of all ages are grouped, mothers were more successful raising daughters than they were raising sons; success rates were 91.7% and 87.8%, respectively. The difference appears to be due principally to the failure of young mothers raising sons.

Survival of females following successful or unsuccessful rearing of pups of either sex

Table 4 shows that for all females combined, the return rate the year after producing sons was significantly higher (61.4%) than after producing daughters (54.2%). This lower return rate of mothers raising female pups was not due to excess mortality, as shown by the data in Table 5. When

Table 3. The weaning success of females as a function of their offspring's sex. The unknown age category refers to females tagged as adults

Female age category	Offspring sex			
	Males		Females	
	% weaned	N	% weaned	N
Age 2 and 3 primiparous	75.0	28	79.4	33
Age 4 primiparous	78.4	74	89.8	59
Age 4 multiparous	84.6	26	100.0	22
Age 5 primiparous	78.9	19	83.3	12
Age 5-16 multiparous	91.6	250	91.6	193
Unknown age	91.1	101	96.8	93
Totals	87.8	498	91.7*	412

* Chi-square=3.85, $df=1$, $P<0.05$. All other individual comparisons of the percentage of pups weaned as a function of offspring sex were not significant (Chi-square= <3.84, $df=1$, $P>0.05$).

** When the top four groups of young females are combined, females weaned significantly more female than male offspring (Chi-square=4.08, $df=1$, $P<0.05$)

we add future sightings of females, beyond the first year after reproduction, the difference in return rate between mothers of sons and mothers of daughters is reduced to an insignificant value. Table 4 also shows that the return rate of primiparous females who raised males did not differ significantly from those that raised females. When all primiparous females are combined, 59.6% of those that raised sons returned the following year compared to a return rate of 56.2% for females that raised daughters (Chi-square=0.79, $df=1$, $P>0.05$).

The above survival analysis was conducted on females that initially raised pups of either sex, our rationale being that the major cost to a female occurred during lactation rather than during gestation. What is the difference in survival rate, as reflected by resighting, between females that successfully reared a pup and females that gave birth to a pup of either sex but failed to wean it? Females that lose their pups on the rookery through separation or death remain on the rookery for as long or longer than females that nurse and wean their pups (Reiter et al. 1981). Their response to pups is variable; they may fail to nurse, nurse orphans occasionally, nurse all orphans that attempt to nurse, or adopt an orphan and nurse it as they

Table 4. Survival, fecundity, offspring sex and weaning success of females the year after successfully rearing male and female pups

Female age cat.	Pup sex in year 1	N	Female status and performance in year 2									
			Observed		Not pregnant		Pup sex		Raised pup		Lost pup	
			Freq.	%	Freq.	%	M/F	% M	Freq.	%	Freq.	%
Age 2 and 3 primiparous	M	21	10	47.6	1	10	3/5	38	7	77.8	2	22.2
	F	26	15	57.7	1	12.5	3/4	43	5	71.4	2	28.6
Age 4 primiparous	M	58	39	67.2	0	0	17/6	74	27	77.1	8	22.9
	F	53	33	62.3	0	0	8/9	47	21	77.8	6	22.2
Age 4 multiparous	M	22	15	68.2	0	0	4/2	67	8	88.9	1	11.1
	F	22	15	68.2	1	9.1	3/4	43	8	80.0	2	20.0
Age 5 primiparous	M	15	7	46.7	0	0	2/2	50	5	83.3	1	16.7
	F	10	2	20.0	0	0	1/0	100	1	100.0	0	0
Age 5-16 multiparous	M	220	128	58.2	0	0	41/42	49	94	91.3	9	8.7
	F	165	86	52.1	1	1.5	31/28	53	57	86.4	9	13.6
Unknown age	M	91	63	69.2*	1	2.4	21/13	62***	32	80.0	8	20.0
	F	89	47	52.8	0	0	9/18	33	32	84.2	6	15.8
All females	M	427	262	61.4**	2	1.0	88/70	56	173	85.6	29	14.4
	F	365	198	54.2	3	2.0	55/63	47	124	83.2	25	16.8

* Chi-square = 5.11, $df=1$, $P<0.05$

** Chi-square = 4.09, $df=1$, $P<0.05$

*** Chi-square = 4.87, $df=1$, $P<0.05$

Chi-square values for all other comparisons between mothers of males and mothers of females were not significant ($df=1$, $P>0.05$)

Table 5. Percent survival of females after rearing male and female pups. Sample sizes are in parentheses. Differences in the not seen and never seen categories are not significant

Pup sex in year 1	Percent of females		
	Seen in year 2	Not seen in year 2 but seen later	Never seen again
Male	61.4 (427)	9.5 (374)	29.1 (374)
Female	54.2 (365)	13.5 (316)	32.3 (316)

Note: The sample sizes for the second and third columns are smaller than those of the first column because sightings in 1986 were excluded because there was only one year to observe females from this cohort

would their own pup (Reiter et al. 1978; Reiter et al. 1981; Riedman and Le Bœuf 1982).

The resight rate of females that reared a pup successfully was significantly higher to the subsequent year than that of females that lost their pups; of 1076 females that reared a pup of either sex, 56.3% were seen the next breeding season in contrast to 47.5% of 408 females that lost their pups (Chi-square = 9.16, $df=1$, $P<0.05$). This significant difference is maintained if we consider all subsequent resights in the years after reproduction

(69.0% of 953 for females that raised a pup vs 62.4% of 391 for females that did not). This discrepancy may not reflect a mortality difference so much as the tendency of females to disperse to a new breeding place the year after losing pups (Reiter et al. 1981). However, this interpretation is unlikely since customary sites to which animals dispersed were under observation.

Reproductive performance following successful or unsuccessful rearing of pups of either sex

Table 4 shows that the sex of the pup raised the previous year had no effect on the mother's pregnancy rate; virtually all returning females were pregnant. Pup sex the second year (slightly biased to males) or success in raising pups were also unaffected. The performance of primiparous females was no different in this regard than that of older multiparous females.

We found no evidence that females that gave birth to a pup but failed to rear it had a different pregnancy rate or sex ratio the following year than females that successfully reared a pup. The subsequent pregnancy rate was 99% for 606 females that weaned their pups and 97.4% for 194 females that failed to wean their pups (Chi-square = 2.73, $df=1$,

$P > 0.05$). The subsequent sex ratio was 52.3% males in 350 females that weaned their pups and 57.5% males in 87 females that did not wean their pups (Chi-square = 0.75, $df = 1$, $P > 0.05$). However, females that failed to wean a pup in one year were less likely to rear a pup the next year than females that were successful in the first year (68.8% of 138 females for females that failed vs 84.9% of 458 females that succeeded; Chi-square = 18.0, $df = 1$, $P < 0.05$).

Discussion

Our data suggest that the greater mass of male pups over female pups at the end of the period of parental investment, although statistically significant, is trivial to the mother because maternal investment in males did not decrease the mother's subsequent reproductive success. Instead, raising a male was associated with a higher probability of a female surviving to the next year and had no effect on the probability of her surviving beyond that time. We do not know exactly how to interpret this apparent contradiction, but the results are clear on one point – survival was no worse after raising a male pup. We conclude that in northern elephant seals, sons are not more costly to produce than daughters, when cost is measured in units of future reproduction, and Fisher (1930) would predict a 1:1 sex ratio at the end of the period of parental investment, exactly as observed. This explanation may hold for some other large mammals in which sons outweigh daughters during parental investment. For example, Trillmich (1986) argued that the sex ratio in Galapagos fur seals, *Arctocephalus galapagoensis*, is at odds with Fisher's theory, yet his own data are consistent with our view since he found that the "higher cost" of raising male pups did not translate into reduction in fertility or survival of the mothers.

In this respect, elephant seals differ from red deer. Hinds that reared male calves were less likely to produce a calf the following year than those that reared females and, if they calved, it was later in the year (Clutton-Brock et al. 1981). This suggests that red deer have more difficulty obtaining food during the overwintering period following reproduction than elephant seals. As soon as female elephant seals wean their pups, they go to sea to feed. During a mean of 73 days at sea, females gain 1.05 ± 0.18 kg/day, or increase their departure mass by $24.1 \pm 4.6\%$ (Le Bœuf et al. 1988). In this short time, post-parturient females recover $79.2 \pm 3.2\%$ of the mass they lost during lactation. Females appear to have no difficulty recovering

mass lost during the previous reproductive effort. After one month on land, the pregnant females return to sea again to forage for eight months prior to giving birth again.

Indeed, females that reared pups were as likely to survive and reproduce again as females that failed to wean their pups. Although females in the latter group are not a rigorous control for reproductive effort, since some of them nurse orphans or adopt them, they clearly invest less energy in nursing pups as a group than females that raise their own pups. From this, we conclude that for females of all ages grouped together, rearing a pup does not reduce the female's subsequent survival or reproductive success.

We address two possible explanations for why rearing sons had no effect on the future survival of mothers. First, the observed sex difference in mass at weaning may not be due entirely to maternal energy transferred. Male pups may have a lower energetic expenditure than female pups resulting in more efficient conversion of milk to body tissue. This is the case in northern fur seals, *Callorhinus ursinus* (Costa and Gentry 1986). However, this explanation seems unlikely for elephant seals; preliminary studies at Año Nuevo indicate that the average daily metabolic rate of suckling males and females is similar (L. Rea, personal communication). Second, the additional energy given to raising sons compared to daughters is so small as to be trivial. Despite great sexual dimorphism in size in adulthood, mass differences between the sexes at birth and at weaning is small compared to fur seals (Costa and Gentry 1986) and the difference is even smaller than in Grey seals, *Haliophurus grypus*, a species that is only moderately sexual dimorphic in adulthood (Anderson and Fedak 1987).

One aspect of the elephant seal's natural history helps to explain this negligible difference in nutrient transfer by mothers to sons and daughters. Pregnant females do all feeding for the production, synthesis and transfer of milk in advance of lactation (Costa et al. 1986). Because females fast during lactation, energy transfer to pups is limited by body stores. Size at weaning in both sexes is a function of mother's size which increases with age (Reiter et al. 1981); this is more important in determining the mass of a pup than its sex. Moreover, since females recover energy lost during lactation rapidly (Le Bœuf et al. 1988), the best maternal strategy is to feed the pup, whatever its sex, as much as possible. These circumstances contrast with those in sea lions and fur seals. In the latter, the mother alternates brief foraging trips to sea

with brief nursing bouts on shore; this enables her to compensate quickly for increased milk transfer to sons.

Given the limits put on elephant seal mothers by body size, selection for superior mass and physical condition of pups may act more strongly on the pups themselves than on the mother and the degree of her maternal investment. Fitness of pups may depend more on additional nursing *after* weaning than on the nourishment received from the mother, given that the mother provides a certain level of nutrients and protection. Two preconditions of the Trivers and Willard hypothesis are that parental investment determines a significant component of offspring quality and that offspring quality at the end of the period of parental investment correlates positively with quality or reproductive success in adulthood. After weaning, most elephant seal pups fast for 2 1/2 months before going to sea to begin feeding on their own. However, some pups of both sexes attempt to prolong nursing by stealing milk from unrelated females or by getting adopted by females that lost their pups (Reiter et al. 1978). In this way, they extend the period of feeding on milk but not at the expense of the genetic parent. Meanwhile, other members of the cohort are fasting. More males than females practice this strategy and males are significantly more successful at it than females. The energetic gain from being a successful milk thief or suckling two "mothers" is reflected in the fact that these "superweaners" may weigh twice as much as normal weanlings. Thus, pups can do much to improve their condition at the end of the period of parental investment. If size at this time is correlated positively with size in adulthood and, in turn, with reproductive success, male pups should be subjected to strong selection pressure to become milk thieves relative to females. One thing is certain, most of the sex difference in mass of adult elephant seals is due to a growth spurt in males that begins at puberty (Laws 1959).

Although it is reasonable to expect that in species like northern elephant seals, where a few males monopolize breeding, females would invest in males only if they can do a good job of it (Clutton-Brock et al. 1981), it is not clear that selection operates in this way. This logic assumes a direct relationship between parental investment and reproductive success of the offspring, knowledge of which is lacking in this species and most other mammals studied. This is one reason why it is difficult to apply our data to the stringent requirements of Maynard Smith's (1980) model. This model predicts that if the primary sex ratio is fixed at 1:1

and the fitness of sons and daughters depends on parental investment, selection will favor greater investment in males than females if: 1) for a given investment, the probability of survival is greater for female pups than for male pups, or 2) survival of the sexes is equal but males have a "frequency-dependent component of fitness" such that those that receive more investment are fitter, or 3) the parent recognizes the sex of the offspring. The sex ratio at birth in our sample was not unity but biased toward males, making it highly probable that the sex ratio at conception was also biased (Trivers 1985). Given the similar probabilities of survival of the two sexes to age two (Reiter et al. 1978), and the lack of data on the relationship between parental effort and future reproductive success of offspring, it is far from clear that there is a frequency-dependent component of fitness. Lastly, we do not know if mothers can recognize the sex of their offspring and we have no reason to conclude that they can.

In contrast to several supportive studies (e.g., Clutton-Brock et al. 1984; Austad and Sunquist 1986; Gosling 1986; Rutberg 1986), our study joins others (e.g., Verme 1969; Mech 1975; Guinness et al. 1978; Armitage 1987; Costa et al. 1988) in not finding clear support for the prediction of Trivers and Willard (1973) that parents adjust the sex ratio of offspring produced according to parental ability to invest. This is telling because elephant seals would appear to be a good test for this prediction. Young females are in a rapid phase of growth and thus, have limited amounts of energy "to spare". Moreover, since energy transfer to the pup is limited by fat reserves of the mother, young females wean smaller pups than older, larger females (Reiter et al. 1981) and young females are less successful rearing male pups. Nevertheless, our data show that the sex ratio does not vary with maternal age or mass; young females did not show a bias in sex ratio to females, as expected, and prime-age females did not produce significantly more sons than daughters.

We conclude that our data on elephant seals cannot be used as evidence against Fisher's theory of the sex ratio. There is no evidence that parental investment in elephant seal mothers is greater for sons than daughters when investment is measured in terms of the future reproductive success of females. In several other pinniped species, mothers produce heavier sons than daughters (grey seals: Boyd and Campbell 1971; Kovacs and Lavigne 1986; Anderson and Fedak 1987; Southern elephant seals, *M. leonina*: Carrick et al. 1962; Little et al. 1987; the subfamily *Arctocephalinae*: Payne

1979; Trillmich 1986; Costa et al. 1988; see review in Croxall and Gentry 1987), but it is not clear in all cases to what extent these differences are due to differences in pup metabolism or to differences in energy transfer from the mother. In the sea lions and fur seals, it is difficult to determine when the period of parental investment has ended and what the sex ratio is at this time because weaning is gradual and its termination is confounded by pups dispersing or beginning to feed on their own. This makes them poor subjects for testing Fisher's theory. In no pinniped has it been shown that higher energetic costs of producing sons translates to higher reproductive costs for the mother. This is important because selection acts on the reproductive costs of breeding (Pianka 1976, 1978), the effects on future reproductive performance. Maternal energetic costs associated with reproductive effort (Clutton-Brock 1984) are only significant if they correlate with reproductive costs, and in elephant seals the association is tenuous.

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