

Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*

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Received June 24, 1985 / Accepted March 22, 1986

Summary. Maternal investment and sex-allocation were measured in a large, sexually dimorphic mammal, the Galapagos fur seal (*Arctocephalus galapagoensis*). The sex ratio at birth was 1.06. Males were always heavier than females and, at least initially, grew faster. Growth was variable from year to year suggesting energetic constraints on maternal investment. Sucking time correlated with milk intake. Mothers suckled yearling and 2-year-old sons more than daughters of the same age. Age at weaning appeared to be the same in both sexes or even slightly greater in males. No sex differences was found in mortality prior to weaning or in post-weaning dispersal. Birth rates of females with yearlings or 2-year-olds were significantly lower than those of females with no dependent young. Mothers invested more in sons than in daughters until weaning. It is unlikely that higher post-weaning investment in daughters balances the higher pre-weaning investment in sons. Data on sex ratio at birth, different growth rates, and weaning age of the sexes are typical of otariid seals as a group. The results of this study fit Maynard Smith's (1980) model of the evolution of sex allocation better than Fisher's (1930).

Introduction

Parental investment is defined as any investment by the parent in an individual offspring that increases the young's chance of survival (and later reproduction) at the cost of reduced survival and/or fertility of the parent (Trivers 1972). Drent and Daan (1980) have argued convincingly for a close correlation between parental energetic effort (as defined by Hirschfeld and Tinkle 1975) and paren-

tal investment in free-living animals. This has been demonstrated for a few bird and mammal species (e.g. Altmann et al. 1978; Bryant 1979; Dittus 1979; Drent and Daan 1980; Clutton-Brock et al. 1983; Reyer 1984). Therefore, estimates of energetic effort are used as indicators of parental investment (Ortiz et al. 1984). However, few quantitative data on parental investment or effort and few data on sex-specific investment have been published (Clark 1978; Clutton-Brock et al. 1981; Dittus 1979; Ortiz et al. 1984; Reiter et al. 1978).

In polygynous mammals adult size of the sexes is often widely different (Alexander et al. 1979). Large adult size is likely to increase fitness (breeding success and/or survival) more in males than in females. The theory of sex allocation (Charnov 1982) predicts that in such a system parents should invest more in individual offspring of the sex with the greater variance in reproductive success if the amount of parental investment partly determines a young's subsequent adult body size. Two ways have been suggested in which allocation of resources in sons and daughters could be made to differ: (1) Fisher (1930) assumed that the amount of parental investment needed to raise one offspring of a given sex to independence was fixed. To invest equal amounts in sons and daughters over a parent's lifetime, the sex ratio should evolve so that it becomes the inverse of the ratio of the costs of rearing sons vs. daughters. (2) As there is little evidence of deviations from a fixed 1:1 (=1.0) sex ratio in mammals (Clutton-Brock and Albon 1982), Maynard Smith (1980) made another model in which he assumed that the sex ratio is fixed while parental investment in sons versus daughters is variable. He showed that greater investment in one sex can be evolutionary stable even at a sex ratio of 1:1.

Fur seals (*Arctocephalus* spp., *Callorhinus ur-*

sinus) are suitable for studying parental investment and sex allocation as they are highly polygynous animals (Bartholomew 1970) with a marked sexual size dimorphism (Alexander et al. 1979). Male reproductive success is more variable than that of females; this is best documented for another pinniped species, the elephant seal, which has a similar polygynous mating system (Le Boeuf 1974). One would therefore predict that in fur seals size is more important for male than for female reproductive success and that additional maternal investment in male young should enhance a son's later reproductive success more than a daughter's.

In this study of the Galapagos fur seal I consider: (1) whether maternal investment in sons and daughters is different; (2) whether the effort expended in raising young fits the criteria of investment as defined by Trivers (1972); and (3) I compare the data with the predictions of Fisher's and Maynard Smith's models of sex-allocation.

Methods

Data were collected at Cabo Hammond, Fernandina, between 1977 and 1984. With the exception of 1978 and 1982, I spent the reproductive season (end of August to beginning of November) at the study site described in Trillmich and Mohren (1981).

Sex ratios were determined in 1977 and 1979–1984. In 1979, 1980, 1983 and 1984 the entire study area (about 530 m of coastline) was checked almost every day for newborn pups. In 1977, 1981 and 1982 only pups on subsections of this coastline were sexed (Table 1) (for 1982 D. Limberger kindly provided her data). Sexed pups were marked to avoid recounts. More than 90% of the reproductive season was covered.

Birth weights were measured within minutes of birth or at least before first suckling. Newborns and older pups were weighed either with a spring balance to the nearest 50 g or with an electronic balance to the nearest 5 g. Yearlings and 2-year-olds were captured with a hoop-net or by hand. They were either kept in the net or placed in a bag and weighed to the nearest 100 g with a spring balance.

Yearlings were weighed when captured for tagging. Capture dates were distributed unevenly over the 2-month field seasons and yearlings can gain weight during this period. Therefore, male and female weights within years were compared by calculating adjusted means from an analysis of covariance (Sokal and Rohlf 1981). Differences between years were tested by analysis of covariance. Animals aged 1 year or over were tagged with Allflex plastic tags on the rear end of the front flipper.

Animals up to 1 year old were always observed to meet regularly with their mothers and if consistently absent were assumed to have died. Mortality and dispersal could not be separated for fur seals more than 1 year old. Minimum survival and site fidelity were calculated from resightings of tagged individuals. Fertility of adult females was calculated from records of tagged individuals in consecutive years.

Time budget data were gathered as described in Trillmich (in press a). Briefly, mother-young pairs were observed for 6–12 h continuously and their behavior recorded every minute on the minute (Altmann 1974). Conclusions are based on 509 h

of time budget observation on 13 pups (≤ 60 days old; 8 males, 5 females), 106.5 h on 8 yearlings (4 males, 4 females), and 118 h on nine 2-year-olds (4 males, 5 females). The mother's attendance time was calculated from 5–10 daily visual checks of the colony area. The data base is presented in Table 3.

Data on milk intake during suckling were obtained by weighing pups shortly before and after a suckling bout. Suckling bouts were timed to the nearest second with a stop watch.

Results

Environmental stochasticity

The Galapagos fur seal lives in a highly variable environment where food shortages occur often but at unpredictable intervals, due to the oceanographic changes associated with "El Niño" (EN) events (Cane 1983; Barber and Chavez 1983). During EN local upwelling diminishes or ceases altogether, water temperatures increase and primary productivity in the fur seals' foraging areas decreases (Feldman et al. 1984); but there is no direct measure of food availability. The years of this study are called *good*, *ordinary* or *poor* using the following criteria: (1) mortality of fur seals was high in poor EN years (Trillmich and Limberger 1985); (2) yearling weight decreased from good to poor years (Table 2); (3) maternal absences increased in duration from good to poor years (Trillmich in press a; Trillmich and Limberger 1985); (4) weaning age increased from good to poor years (see below). According to these criteria 1981 and 1984 were good and 1977, 1979 and 1980 ordinary years. The poor EN years 1982/83 need some special comment. EN started in August/September 1982 and lasted until July 1983. Therefore early in 1982, before the fur seal's reproductive season, conditions were still ordinary and rapidly deteriorated to poor during the reproductive season. In early 1983 primary production in the western part of the Galapagos was drastically reduced (Feldman et al. 1984) but recovered rapidly towards the fur seals' reproductive season. Because of this high environmental variability, data from the different year types will be presented separately.

The sex ratio at birth

Sex ratios (males/females) at birth varied from 0.56 to 1.72 between 1977 and 1984 (Table 1). Differences in sex ratio between seasons were not significant (Chi-square 11.9, $df=6$, $P<0.1$). Males were predominant in 3 out of the 5 largest samples but this trend was only significant in the 1977 data. Few pups were born in 1983 in the reproductive season immediately after the EN event (Trillmich

Table 1. Sex ratio (male:female) in newborn Galapagos fur seals. *P*: significance of difference from a 1:1 sex ratio (Chi-square test)

Year	Males	Females	Sex ratio	<i>P</i>
1977	50	29	1.72	<0.02
1979	87	73	1.19	NS
1980	123	106	1.16	NS
1981	33	34	0.97	NS
1982	21	19	1.11	NS
1983	14	25	0.56	0.1 > <i>P</i> > 0.05
1984	120	138	0.87	NS
Total	448	424	1.06	NS

and Limberger 1985) and the sex ratio was biased towards females (Table 1). For the total 872 newborns sexed between 1977 and 1984 the sex ratio was slightly biased towards males, but did not differ significantly from 1.0.

Weight development of young

Pups. Maternal effort for the embryonal development of a male pup was higher than for that of a female since males were always heavier at birth (Table 2). Birth weights of the few pups born immediately after the strong EN in 1982/83 were significantly lower than in good and ordinary years (Table 2; Trillmich and Limberger 1985). Newborn males born after the poor year were on average 14.5% and females 10% lighter than in other years. The difference in weight reduction between male and female newborns was not significant.

Male pups grew faster than females during the first 60 days after birth (Fig. 1). Growth of pups in the good year 1984 was not significantly differ-

ent from that in 1977 and 1979–1980 shown in Fig. 1 [male pups 1984: $w = 61.2x - 3642$ (g) ($n = 30$); female pups in 1984: $w = 47.5x + 3,958$ (g) ($n = 36$)].

Six-month-old pups were weighed only in early 1981. Males were about 700 g heavier than females (Table 2).

Yearlings. Yearling males were significantly heavier than females in all years (Table 2). The mean weight difference between the sexes was 1.8 kg. Male growth rates (i.e. the slopes of the regressions over the period September–October were always higher than female growth rates (1979, 1980, 1981, 1984), but the differences were not significant.

Growth up to 1 year of age was strongly influenced by differences between years. Yearlings in the good years 1981 and 1984 were significantly heavier than yearlings in the ordinary years 1979 and 1980 ($P < 0.01$, analysis of covariance). In good years males weighed 3.0 kg more than in ordinary years, while female yearlings were 2.6 kg heavier (Table 2). In good vs ordinary years growth rates of yearlings (as estimated from the regression slopes) were not significantly different.

Two-year-olds. Two-year-old males were always heavier than equivalent females. Both sexes were heavier in the good year 1981 than in the ordinary years 1979 and 1980 (Table 2). The growth rates of 2-year-olds again appeared to be higher in males than in females.

Nursing

Fur seal mothers alternate between periods ashore at the site where their pups are (= attendance peri-

Table 2. Mean weights in kg (± 1 SD) of young fur seals of various ages (n = number of different individuals). Age is given in months; age zero = newborn. For yearlings and 2-year-olds, adjusted means (from analysis of covariance) are given with their comparison intervals as determined by the Gabriel approximation (Sokal and Rohlf 1981). *P* determined by Mann-Whitney *U* test; in the case of yearlings from analysis of covariance

Age (mo)	Year of sampling	Type of year	Males (n)	Females (n)	<i>P</i>
0	(1981/84)	good	3.9 \pm 0.3 (23)	3.4 \pm 0.3 (23)	<0.01
0	(1977/79/80)	ordin.	3.8 \pm 0.2 (7)	3.4 \pm 0.2 (3)	<0.02
0	(1983)	poor	3.3 \pm 0.2 (4)	3.1 \pm 0.3 (10)	<0.1
6	(1981)	good	9.3 \pm 1.4 (69)	8.6 \pm 1.2 (62)	<0.01
12	(1979/80)	ordin.	11.1 \pm 0.7 (37)	9.5 \pm 0.7 (42)	<0.01
12	(1981/84)	good	14.1 \pm 0.9 (20)	12.1 \pm 0.8 (29)	<0.01
24	(1979/80)	ordin.	15.0 \pm 1.3 (10)	14.1 \pm 1.1 (14)	<0.05
24	(1981)	good	18.1 \pm 2.4 (3)	15.5 \pm 0.7 (6)	<0.025

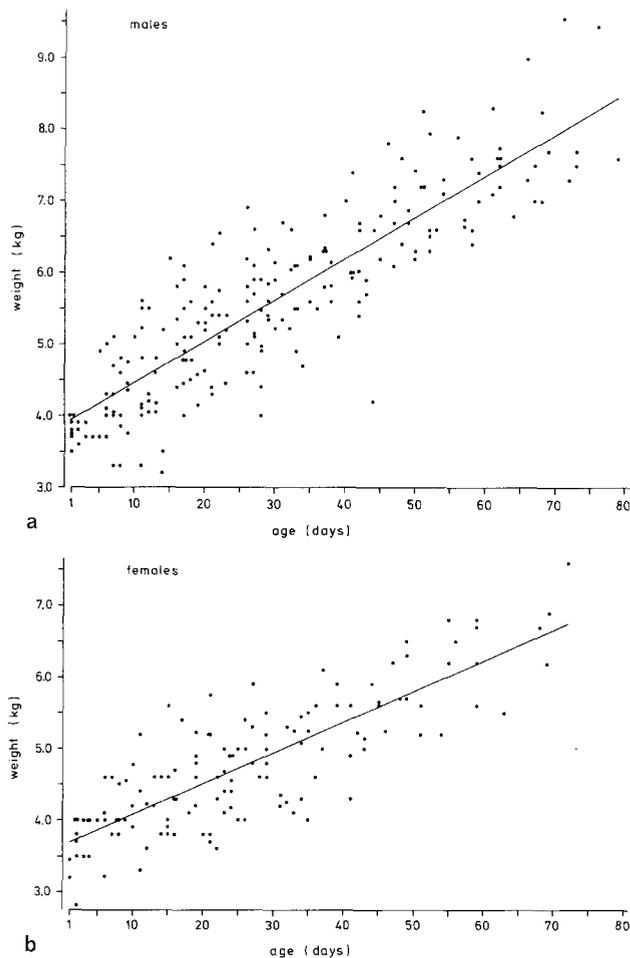


Fig. 1 a, b. Regression of weight (w) on pups' age for the first 70–80 days of life. Data from 1977 and 1979–1980. **a** Regression for males: $w = 57.9x + 3,879$ (g) ($n = 214$); **b** regression for females: $w = 42.7x + 3,661$ (g) ($n = 134$). Slopes are significantly different from zero and from each other ($t = 4.2$, $P < 0.001$)

ods) and periods at sea or ashore elsewhere (= absence periods) (Trillmich in press a). No differences in attendance times were found between mothers of male and of female young of the same age (Table 3; $p > 0.1$ in all cases, Mann-Whitney U test). This result was stable although females spent significantly more time attending their young in good years (1981 and 1984) than in ordinary years (1979 and 1980) (Table 3, and Trillmich in press a).

While attending their young females spent a large percentage of the time nursing. Nursing is a female fur seal's most important energetic effort for her offspring after its birth; pups have almost no chance to get milk from other females (Trillmich 1981). Nursing time can be considered a valid correlate of the amount of milk transferred to a young since milk intake of pups (7–40 days old) correlated significantly with sucking bout length ($r = 0.49$, $P < 0.01$; $n = 73$) but not with the pups' age ($r = 0.16$, NS; $n = 73$).

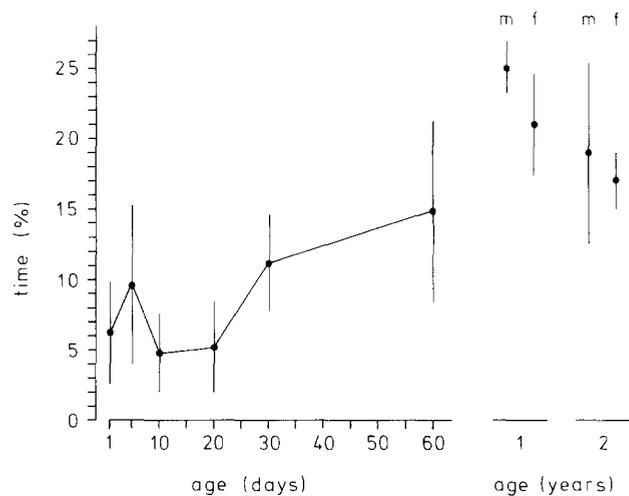


Fig. 2. Changes in sucking per unit time observed (t) with the age (d) of fur seal young. Yearlings place the highest demands on their mothers. Pup data from 1979–1981 (regression: $t = 5.7 + 0.14d$; $P < 0.001$; data base for the different ages: day 1, $n = 7$; day 3, $n = 3$; day 5, $n = 6$; day 10, $n = 8$; day 20, $n = 3$; day 30, $n = 9$; day 60, $n = 6$). Yearling data from 1979 and data for 2-year-olds from 1979 and 1980 (see Methods)

Table 3. Percentage (mean \pm SD) of the total observation time that mothers spent attending their young. Total observation time in female days (no. of individual females observed \times days observed), given separately for mothers with male/female young. In brackets: number of mother-young pairs observed. Only data from mothers of pups ≥ 10 days old are included

		Male	Female	Female days
Pups	1979/80	36.7 \pm 4.3 (6)	36.7 \pm 5.8 (3)	324/125
	1981	48.0 (2)	54.0 \pm 6.8 (4)	66/155
Yearlings	1979	30.0 \pm 5.6 (4)	30.0 \pm 9.6 (4)	168/116
	1984	57.7 (2)	54.5 (1)	36/ 9
2-year-olds	1979/80	34.3 \pm 9.1 (3)	32.3 \pm 5.0 (3)	108/153

Analysis of covariance showed no significant differences in nursing time between male and female pups up to 30 days old. However the adjusted mean and slope for males were slightly higher than those for females as expected from the data on weight development. The increase of nursing time over the first 30 days of a pup's life is shown for both sexes combined in Fig. 2. An additional value for 60-day-old male pups is also given. A comparable value for females could not be obtained as they were born too late (on the study site) in the season in which time budgets were measured. Yearling and 2-year-old dependent young sucked significantly longer than even 60-day-old male pups (Mann-Whitney U tests; for yearlings $P < 0.01$, for 2-year-olds $P < 0.05$). The difference in nursing

time between male and female yearlings and 2-year-olds was significant ($P < 0.025$, combined probabilities from Mann-Whitney U tests). Some yearlings and all 2-year-olds foraged independently of the mother, thus contributing varying amounts to their own metabolic requirements. Nevertheless, males sucked for longer than females (Fig. 2) and therefore should have received more milk.

Age at weaning

Age at weaning varied across cohorts and weaning occurred at some time between the end of the first and the third year (Trillmich in press a). None of the 1977–1984 yearlings were already weaned, but the unusually large ones in 1984 were less frequently with their mothers than yearlings in previous years. Most of the 1981 2-year-olds, which were heavier than those of previous years (Table 2), were already weaned, whereas those from other years were not. Weaned young are less likely to be observed than sucking young. Therefore, the difference in weaning age between years was not determined directly by counting weaned and dependent young but in a different way. In all years the probability of parturition was about the same for females accompanied by 2-year-olds or by yearlings (see below). Consequently the ratio of cases of parturient females with yearlings to those with 2-year-olds in the different years was taken as a good measure of differences in weaning age between cohorts. The ratio was 1.26 in the ordinary years 1977 and 1979/1980 (34 cases with yearling and 27 with 2-year-olds). It was 9.0 in the good year 1981 (18 cases with yearlings and 2 with 2-year-olds) (Chi-square = 7.8; $P < 0.01$).

There was no indication of a difference in weaning age between the sexes from observations on 2-year-olds: 10 out of 24 2-year-old males were weaned and 8 out of 22 females. Observations on 3-year-olds in 1980/1981 indicated that sons were weaned slightly later than daughters: 3 out of 7 male young were seen sucking occasionally but none out of 19 females ($P = 0.026$, Fisher exact probability, two-tailed).

Mortality of dependent young

There seemed to be no sex difference in mortality during the period of maternal investment although a difference would be predicted from the general pattern in mammals (Ralls et al. 1980) and from the males' greater susceptibility to food stress (Widdowson 1976).

The only suggestion that male young were

more susceptible to starvation came from the sex ratio at birth in 1983. This reproductive season began immediately after the EN. Females gave birth to young of below average weight (Table 2) and most of the few pups born in this season were females (Table 1). This may indicate that male embryos were less able to develop to full term under nutritional stress. Comparable data for sex differences in mortality of yearlings and 2-year-olds are not available as all of these animals died during the EN (Trillmich and Limberger 1985). In all other years the sex ratio of dependent young did not differ significantly from that of newborn pups and was always slightly but not significantly biased in favor of males (Chi-square 0.51, $P > 0.1$). In newly weaned 3-year-old young this male bias was stronger, but again not significant (sex ratio: 1.6, $n = 13$).

The probability of resighting was never significantly different for marked male and female young: between 6 and 12 months of age (1981) 57% of 70 marked males and 63% of 62 marked females were resighted; between the ages of 12 and 24 months (1979/1980–1980/1981) 55% of 40 marked males and 40% of 63 marked females were resighted and between the ages of 2 and 3 years, when most young are weaned, 41% of 29 marked males and 56% of 46 marked females were resighted. These values cannot be interpreted as pure mortality, as they include tag-loss, dispersal (for 3-year-olds) and temporary movements of mother-young pairs away from the main study colony. There was, however, no reason to believe that tag loss or movements of mother-pup pairs showed any sex-specific differences.

Dispersal

There was no clear evidence for sex-specific dispersal of young Galapagos fur seals. As just stated, resightings of tagged animals between the ages of 2 and 3 years (i.e. when most were weaned) were slightly, though not significantly higher for females. Of fur seals tagged as 1- or 2-year-olds and resighted as 5- to 7-year-olds almost twice as many were females as males (13% of 79 females and 7% of 59 males); this difference, although suggestive of greater male dispersal, did not reach significance as the number of resighted animals was small due to the high mortality during the 1982/83 EN.

Fertility costs to the female

Birth rates of females varied according to their maternal status. Observations were made on adult fe-

males marked at least 1 year prior to data collection. Of 22 marked females unaccompanied by previous young, 91% gave birth in the years 1980, 1981, 1982 and 1984 (no significant differences between years). The same value was obtained for 11 females that had weaned or lost an offspring in its second year. Only 11% of all females unaccompanied by young pupped in late 1983 after the period of severe food stress (Trillmich and Limberger 1985).

Birth rate was also lower amongst females still caring for young. Those with yearlings experienced the greatest fertility reduction. Of 84 mothers with yearlings (observed in 1979, 1980–1982, 1984; no significant differences between years) 33% pupped, while of 11 mothers with 2-year-olds (1979–1981; 1982) 45% pupped. This is a significant reduction in birth rate compared to lone females (Chi-square test, $P < 0.01$). Birth rates for mothers with male and female young were not significantly different.

Survival costs of mothers cannot be calculated reliably at present since the probability of resighting differs for females of different maternal status making comparisons impossible.

Discussion

Maternal investment

Food is a limiting resource for Galapagos fur seals: during EN starvation mortality of adults and dependent young was high, pup birth weights were low (Table 2) and pregnancy rates greatly reduced (Trillmich and Limberger 1985). These effects, although unusual in extent, are not exceptional: weaker EN events occur every few years (Cane 1983) and somewhat similar conditions exist during the local "warm" season from January to May when the upwelling of cold, nutrient-rich waters around the islands is reduced (Maxwell 1974). The difference in the weight of yearlings between years (Table 2) demonstrates that their growth (which cannot be accurately measured over a 2 month period) is limited by the availability of food. Weaning age increases from good to poor years showing that a female's current efficiency in transferring energy to her offspring determines when she will successfully reproduce again. Similarly, the lowered birth rate of females with young is evidence that resources spent on one offspring limit the possibility of further reproduction. When mothers with a yearling or 2-year-old give birth again they are usually unable to feed their two dependent young simultaneously (Trillmich in press a). The

strongest evidence for this interpretation is that in ordinary years newborns with yearling siblings actually suck longer than those without, but still gain less or no weight and usually die of starvation within a month after birth (unpublished data). Resource transfer from a mother to her offspring thus reduces her chances of future reproduction and provides a measure of maternal investment.

Differential costs of sons and daughters?

Galapagos fur seal females expend more effort on sons than on daughters prior to weaning: at a sex ratio of 1:1 (Table 1) sons are born heavier and grow faster than daughters (Table 2, Fig. 1). As pups initially depend totally on their mothers' milk the higher growth rates of males reflect higher intake and greater effort of their mothers. Yearling sons suck more per unit time than daughters (Fig. 2), even though at this age both sexes contribute part of their food by independent hunting. There is no indication of sex-differential mortality of dependent young and even a suggestion that males may be weaned later than females.

There are three weak points in the evidence for greater investment in sons: (1) The data on weaning age are indirect. (2) Differential dispersal of male and female young cannot be excluded as the samples are small. Furthermore, even if male and female dispersal were equal, daughters may still compete more with their mothers than sons thus compensating the lower pre-weaning cost with a higher post-weaning cost. (3) The higher cost of raising a male pup has not been shown to translate into a correspondingly higher reduction in fertility or survival of the mother.

To (1): I recognize the imprecision of the data on weaning age caused by the great variation between cohorts. However, daughters would have to be weaned substantially later than sons to make up for the greater maternal effort expended on sons and the evidence presented here rather suggests later weaning of male young. The only published information on another pinniped species (Reiter et al 1978) also demonstrates later weaning of male pups. While more data are obviously needed, I will assume equal weaning age of sons and daughters for the present discussion.

To (2): It has been argued that post-weaning investment in daughters – due to their subsequent competition with the mother – may compensate for the higher pre-weaning cost of a son (Clark 1978; Clutton-Brock et al. 1981). In red deer a reduction in fertility caused by food competition within large female kinship groups has been shown

(Clutton-Brock et al. 1983). Such an effect must be very small or equal for sons and daughters in Galapagos fur seals because all members of a colony forage individually over a wide range of the adjacent ocean (Kooyman and Trillmich in press). Post-weaning competition between mother and daughter for suitable pupping habitat on land also seems unlikely. The few females that I followed from birth to first reproduction (at an age of 4–6 years) bred sufficiently far away from their own birth site to make close-kin interaction unlikely. I therefore believe post-weaning investment in both sexes to be negligible.

To (3): The problem that the greater maternal effort for raising a son cannot yet be shown to translate into greater maternal investment has to be kept in mind when I attempt (below) to compare the data with the models of sex allocation.

The results of this study on the Galapagos fur seal seem typical in many respects for the polygynous eared seals (Otariidae). In this family males are born heavier, grow faster and are heavier than females at weaning (reviews on fur seals in: Croxall and Gentry in press; for the Galapagos sea lion, Trillmich in press b). Sex ratios at birth or shortly after birth are even or biased in favor of males (Payne 1979 for *Arctocephalus gazella*; Gentry pers. comm. for *Callorhinus ursinus*; Shaughnessy in press for *Arctocephalus pusillus*; own unpubl. data for *Zalophus californianus wollebaeki*) and no indications of sex-differential mortality and weaning age have been found. It seems possible that competition between female kin in species that breed in high density colonies (sub-polar fur seals) may create a small post-weaning cost for having a daughter since females tend to give birth where they have been born. However, this possible cost cannot be substantiated with presently available data.

Comparison with the models of sex allocation

Higher maternal effort for raising sons at a sex ratio of about 1.06 from birth to weaning contradicts Fisher's (1930) prediction of equal investment in both sexes. This contradiction hinges on the validity of the result that weaning age is the same for both sexes or even slightly older for males. Accepting the arguments made for equal weaning age, the data on the Galapagos fur seal and on otariid seals in general seem to fit Maynard Smith's (1980) theory of a fixed sex ratio but different investment in the sexes much better.

An exception may be found in the South African fur seal (*A. pusillus*). Shaughnessy (in press)

reports a significant male bias with a sex ratio of 1.32 in a very large sample of 27,946 ca. 6-week-old pups. There is no indication that female pups are more likely to die within the first 6 weeks after birth. These data fit neither theory as males of this species are heavier than females both at birth and weaning (David in press; Rand 1956), thus contradicting Fisher's model. In addition, the data deviate from Maynard Smith's (1980) assumption of an invariable 1:1 sex ratio at birth. It would seem that at least in this case one would have to consider both investment and sex ratio as variable parameters.

Although within a given year the energetic cost of raising a son is higher than that for raising a daughter, environmental variability makes the prediction of absolute costs impossible: raising a big son in a good year may be less costly energetically than raising a small daughter in a poor year. Females presumably have a higher foraging efficiency in a good than in a poor year, i.e. higher hunting success for an equal or lower effort expended on foraging. This could explain why females with light yearlings in the ordinary year 1980 had a lower mean weight (27.3 kg; Trillmich 1984) than females with much heavier yearlings (Table 2) in the good year 1984 (when females weighed 32.5 kg, $n=10$; unpubl. data). While the energetic effort of the mother clearly represents maternal investment, this variability in the absolute costs may account for the absence of measurably different effects of raising a son or a daughter on the mothers' fertility. The lack of a differential fertility effect may also imply that mothers limit their maternal effort to a maximal value which they do not surpass no matter what further needs the pup may express. Once this upper threshold is passed pups are left to die as observed during El Niño or, in less severe food stress, growth of young is retarded.

It could also be argued that, in the Galapagos fur seal, time to weaning influences a mother's fertility most strongly. In ordinary years females raise one young every 3 years (unpubl. data). As a rule of thumb the cost of raising an offspring may therefore be measured in years until the next young can be raised. Due to the environmentally determined variation of weaning age across cohorts, this time cost is largely phenotypic and little dependent on the sex of the offspring. If so, selection acting on the mother's fertility will find sons and daughters about equally costly, although within a given year sons need more maternal effort than daughters. Such an interpretation could partly resolve the contradiction between the data presented here and Fisher's theory. However, I prefer to interpret

the data along the lines of Maynard Smith's (1980) theory.

Acknowledgements. I thank W. Arnold, T. Dellinger, C. Drews, C. Kasche, D. Limberger, P. Thorson and K. Trillmich for their invaluable help during the field work, G.L. Kooyman for introducing me to the methods of handling adult fur seals and numerous thoughtful comments, W. Arnold, B.J. Le Boeuf, P. Hammerstein, H. Markl, H.-U. Reyer, M. Taborsky and P. Ward for numerous suggestions that improved the manuscript. W. Wickler unflinchingly supported the study throughout many years. I gratefully acknowledge the support of the Charles Darwin Research Station through its directors C. MacFarland, H.N. Hoeck, F. Koester and G. Reck, and offer my sincere thanks to the Galapagos National Park through its Intendents M. Cifuentes and F. Cepeda. B. Knauer expertly prepared the figures and L. Gardiner kindly corrected the English. This is contribution no. 386 of the Charles Darwin Foundation.

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