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Offspring sex ratio in relation to female size in southern elephant seals, *Mirounga leonina*

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Abstract Southern elephant seals *Mirounga leonina* display extreme sexual dimorphism. In addition females show great variation in size and stored resources at parturition. Therefore they present an excellent opportunity for examination of responses of sex ratio to resource availability. We studied the relationships between the size of southern elephant seal females at parturition and the size and sex of their pups at South Georgia over four breeding seasons. We found a large individual variation in maternal post-partum mass (range 296–977 kg, n=151). Larger mothers gave birth to larger pups, irrespective of the sex of their pup. Male pups were on average 14% larger than females at birth and consequently more costly to bring to parturition. Our results suggest that female southern elephant seals must weigh more than 300 kg if they are to breed at all, and more than 380 kg if they are to give birth to a male pup. Above this threshold the proportion of males among offspring rapidly increases with maternal mass, and stabilizes at a level not significantly different from parity. These results show that smaller females of southern elephant seals vary offspring sex ratio in a way that is consistent with theories on adaptive offspring sex ratio. A smaller mother with a male foetus may benefit from terminating her pregnancy and allocating the resources she saves to her own growth. She could then give birth to and raise a larger pup in the subsequent season.

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Introduction

Trivers and Willard (1973) suggested that in species for which the reproductive success of offspring is related to the size and/or condition of those offspring and where this relationship differs between sexes, mothers should vary the sex of offspring in relation to their own body condition, prematurely terminating investment in offspring that have little chance of reproducing (Trivers and Willard 1973; Clutton-Brock 1991). This has rarely been demonstrated (Clutton-Brock and Iasom 1986). However, variation in sex ratio has been shown to occur in mammals both in natural and experimental situations because of nutritional stress, increasing age, body condition, changes in resource availability, litter size and social rank of mothers (Clutton-Brock and Iason 1986; Clutton-Brock 1991). It is not clear if these changes in sex ratio are a result of the active manipulation of the mother or of the differing susceptibility of male and female foetuses to environmental stress. Alteration of the sex ratio at birth could be the result of factors acting either before (Johnson 1994) or after (Clutton-Brock 1991) conception. In either case, the most likely proximate cause of sex ratio changes after conception is differential mortality. Clutton-Brock (1991) suggested that one way of discriminating between active manipulation by the mother and differences in susceptibility of the offspring is by considering the timing of the sex ratio shift. He argued that if the differential mortality is a result of active parental manipulation, it should occur as early as possible during pregnancy to minimize wastage of resources.

Southern elephant seals (*Mirounga leonina*) provide an opportunity to test these ideas: they are the most

polygynous of seals (Laws 1953, 1956), males may be an order of magnitude larger than the females with which they mate and only the heaviest 2–3% of males have access to females for breeding (McCann 1981). In addition, there is a threefold difference in mass of breeding females (T. Arnbom, M.A Fedak, J.L. Boyd, unpublished work). Females give birth to one pup which is weaned an average of 23 days post-partum (McCann 1980). During lactation, mothers fast and energy is taken solely from stored reserves (Matthews 1929). Mass at parturition is strongly related to total body energy reserves, and is therefore an indication of the quantity of resources the individual female brings ashore (M.A. Fedak, T. Arnbom, J.L. Boyd, unpublished work). In this study we examine the size and sex ratio of pups born to southern elephant seal mothers over a wide range of maternal sizes, and consider the results in terms of the sex allocation theories, and discuss the implications that a shift in sex ratio may have for population dynamics.

Methods

We studied southern elephant seals at Husvik, South Georgia (54°10′S, 36°43′W) during the 1986 and 1988–1990 breeding seasons. A total of 154 adult females were tranquilized using a mixture of tiletamine hydrochloride and zolazepam (Baker et al. 1990), hot-iron branded (Ingham 1967), individually marked with plastic rototags (Dalton Supplies Ltd., Nettlebed, UK), measured (nose-tail length) and weighed (± 1 kg) following McCann et al. (1989) and Arnbom et al. (1993). Of the 154 mothers marked 3 raised two pups each. These females and their six pups were not included in this study. Females were weighed on average 1.5 days (range 0–10 days) after giving birth. Of the 151 females, 140 (including all of the females < 400 kg) were weighed within 3 days of parturition. For females not weighed within 24 h of giving birth, post-partum mass was estimated by linear extrapolation of the average daily mass loss for that female (measured during a period of at least 14 days during the remainder of lactation) back to the day of birth.

The sex of the pup was determined and each pup was weighed (± 0.5 kg) within 3 days after birth using a spring-scale (100 kg, Salter Industrial Measurements Ltd., West Bromwich, UK). The spring-scale was calibrated regularly against a known mass. Seventy pups were weighed on day of birth and the average number of days all pups were weighed after birth was 0.88 ± 0.09 days (n=144). The mass of pups not weighed on the day of birth was estimated by using data from McCann et al. (1989) who weighed individually identified pups for several consecutive days and calculated the average mass gain for pups during the first days after birth. The day of birth was determined by the pup not having been observed during the previous afternoon, so a pup born during the evening was recorded as being born the following day. All pups and mothers, marked at the day of birth, survived until the day of weighing showing that the observed offspring sex ratio was not an effect of postnatal mortality. The mortality of other pups on the study beaches during the lactation period was 1.5% (7/464) in 1988 and 2.2% (7/322) in 1989 (T. Arnbom, M.A. Fedak, J.L. Boyd, unpublished work). When selecting females we made an effort to choose females in extreme size classes and therefore the sample of breeding females is not random. While the mean values are probably not very different from population means, very large and small females are over-represented in the sample and therefore, the distributions about the means for some of the variables of interest are probably not representative of the population. Rather, the sample emphasizes the potential range of values the variables can take and relationships possible over the size range of females in the population.

Of the total sample of females, 108 were aged by counting cementum layers in extracted incisors (Arnbom et al. 1992). During daily beach counts of females, we recorded presence of individual females which were marked and weighed in 1988 and 1989 that returned to the study site in 1989 or 1990.

We used two approaches to look for a change of sex ratio with maternal mass. In the first approach maternal mass was regarded as the response variable and the mass distributions for mothers of male and female offspring were compared with a two-sample randomization test (Manly 1991). In the second approach we used the sex of the offspring as the response variable. To test for an effect of maternal size and age on sex ratio we used logistic regression (Cox 1970; Hosmer and Lemeshow 1989; Trexler and Travis 1993) with sex of the pup as the binary response variable, scored as 0 for females or 1 for males. In this model the probability of a male (P) is related to maternal mass (M) by:

$$P = \frac{1}{1+e^{(a+bM)}}$$

This model provides a flexible empirical framework for testing and describing relationships between binary responses and one or more explanatory variables. A test of the null hypothesis, that a specified parameter value is zero, uses the difference in deviances between two models, one with, and the other without the parameter (where the deviance equals minus twice the log likelihood ratio). The difference in deviance, on the null hypothesis, is approximately distributed as χ^2 with 1 df.

To analyse the form of the detected increase in more detail, we fitted an augmented logistic model in which the upper asymptote was free to take values between 0–1. Models were fitted using the statistical package Genstat 5 (Payne and Lane 1987). Values are given as mean ± SE, except where otherwise indicated.

Results

We found a large individual variation in maternal partum mass [mean=529±120 (SD) kg, n=151, range 296–977 kg]. Females continued to increase in mass and length in the years after first breeding (Fig. 1). Larger mothers gave birth to larger pups irrespective of the sex of the pup (Fig. 2). Male pups were on average 4.8±0.8 kg (range 9.5–16.7%) heavier at birth than female pups, regardless of their mother's size. The relative difference between male and female pups was larger for smaller mothers than for larger mothers.

Mothers of male pups weighed on average 554 kg (SD 14 kg, n=71) compared with mothers of female pups 506 kg (SD 13 kg, n=80). The difference of 48 kg was statistically significant (Monte Carlo randomization test, P=0.010, based on 5000 randomizations, Manly 1991). The top part of Fig. 3 shows the number of pups of each sex born over the range of maternal sizes. There are few males born in the lower size classes. No females below 296 kg were observed to reproduce, and the 9 pups born to mothers in the mass range 296–380 kg were all female pups.

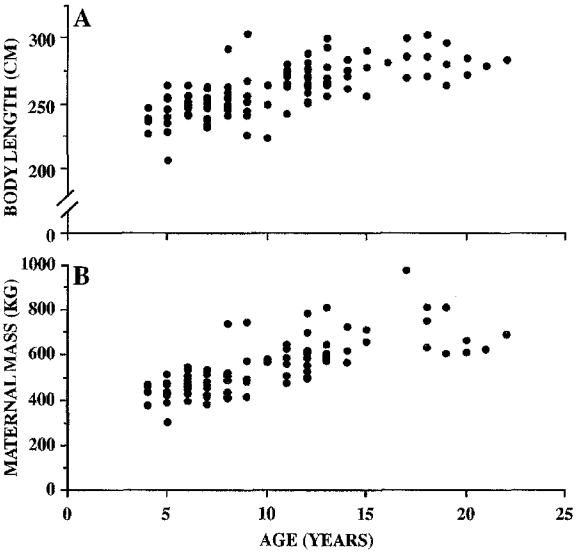

Fig. 1 **A** Body length of lactating females plotted against age (x) determined from incisor growth layers (y=3.0x+230, r^2=0.49, $F_{[1, 106]}$=104, $P < 0.001$) and **B**, maternal mass plotted against age (x) (y=20.2x+346, r^2=0.55, $F_{[1, 88]}$=108, $P < 0.001$).

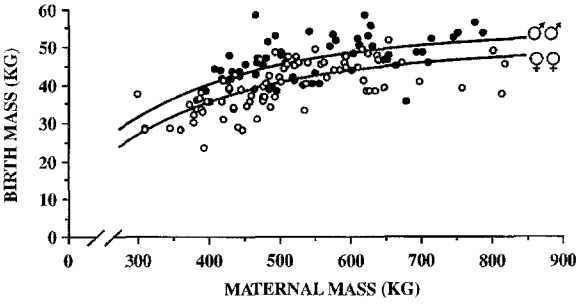

Fig. 2 Birth mass plotted in relation to maternal mass for male pups (*solid circles*) (r^2=0.30, $P < 0.001$) and female pups (open circles) (r^2=0.37, $P < 0.001$). The *fitted lines* are parallel asymptotic exponential curves; males y=52.6−107exp(−0.0055x), females y=47.8–107exp(−0.0055x). The deviation from parallelism was not statistically significant ($F_{[1, 138]}$=0.2, $P > 0.5$)

The increase in sex ratio with maternal mass is statistically significant (logistic regression using binary responses, χ^2_1=6.40, $P < 0.025$) even after allowance was made for age (χ^2_1=6.27, $P < 0.025$) or year effects (χ^2_1=5.50, $P < 0.025$). Sex ratio also increased with maternal length (χ^2_1=6.29, $P < 0.025$) in a similar way to maternal mass. When we treated age as an independent variable together with maternal mass, only mass was statistically significant. The sex ratio appeared to increase rapidly in mothers weighing 300–425 kg, with no detectable increase in larger females. The lower part of Fig. 3 illustrates this as a logistic curve with upper asymptote estimated from the data as close to 50%. This produces a better fit than the logistic with fixed upper asymptote of 100% (χ^2_1=4.70, $P < 0.05$). It is important to note that in this figure the curve results from the individual binary

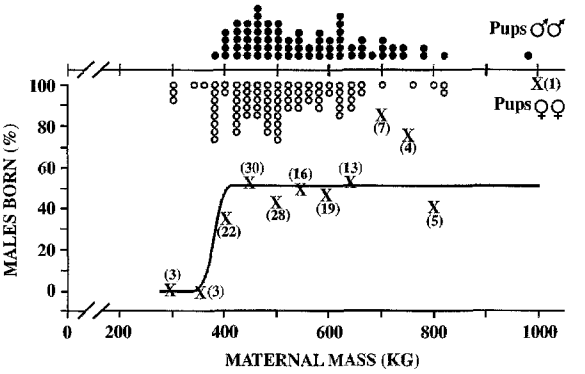

Fig. 3 The top part of the figure shows the number of pups born of each sex (*solid circles* male pups, *open circles* female pups) over the range of maternal sizes divided into 20-kg size classes (291–310 kg, 311–331 kg, and so on). The *lower part* shows sex ratio (% males) in relation to maternal partum mass (n=151). The *fitted line* is the logistic curve P=51/[1+exp(70.9–0.184M)] (SE of estimated asymptote=5%) where P is the proportion of males born and M is maternal partum mass. Note that many other logistic curves, as steep or steeper than that shown, fit the data almost equally well. The curve was fitted to individual responses (see text) and not to the grouped data which is shown as an X for each 50 kg size class (276–325 kg, 326–375 kg, and so on) to facilitate a comparison of the data with the fitted model. Sample size for the each 50 kg size class is shown within *parentheses*

responses; it is not a line fitted to the grouped data or the points shown.

Females which were absent in the study area in the breeding season subsequent to the one observed were significantly smaller (t=2.4, $P < 0.05$, df=99) than females which returned to breed (absent females 514 ±17 kg, n=65; returning females 575±18 kg, n=36). Also included in the group of absent females were four of the five largest females (> 800 kg).

Discussion

For all sizes of mothers, male pups are born proportionately heavier than female pups, reflecting higher nutrient and energy requirements during gestation. We could find no breeding females smaller than 296 kg on the study beach during the 4 years of the study. Only female pups were born to mothers weighing less than 380 kg (n=9). Thereafter the sex ratio increased rapidly to a value not significantly different from parity at a female mass of about 425 kg. Thus, the sex ratio in smaller southern elephant seal females varies in a way that is consistent with the predictions of Trivers and Willard (1973) and Clutton-Brock and Albon (1982). However, the offspring sex ratio did not change with increasing female size in a linear fashion, but rather in a stepwise manner (Fig. 3). We suggest that it is possible that two different thresholds may be operating in female southern elephant seals; a minimum post-partum threshold mass of about 300 kg for female pups, and threshold mass of around 380 kg for male pups.

More data are needed to confirm and refine these estimates.

In southern elephant seals, the female-biased sex ratio at parturition is related to body condition (measured as maternal mass), not age. When both age and mass were considered as independent variables, only mass was significant. No relationship was found between maternal age and sex ratio in northern elephant seals (*Mirounga angustirostris*)(Le Boeuf et al. 1989).

Responses of sex ratio to age and mass seem to vary between and within species. In sheep (*Ovis aries*) and sea otters (*Enhydra lutris*), younger females produce more female offspring than older animals (Kent 1992; Bodkin et al. 1993). The picture is less clear for different populations of bison (*Bison bison*) (Rutberg 1986; Wolff 1988; Green and Rothstein 1991), reindeer (*Rangifer tarandus*) (Skogland 1986; Kojola and Eloranta 1989; Thomas et al. 1989) and white-tailed deer (*Odocoileus virginianus*)(Verme 1969, 1983; Caley and Nudds 1987). In red deer (*Cervus elaphus*), dominance was related to an increased proportion of male offspring, and dominance and body mass were positively related (Clutton-Brock et al. 1982, 1984, 1986). However, it is not clear which of the variables was of primary importance in explaining changes in sex ratio.

During El Niño years, lactating female California sea lions (*Zalophus californianus*) exerience a food shortage and as a consequence, the milk and energy intakes of pups are reduced (Iverson et al. 1991). Ono and Boness (1991) predicted a higher abortion rate of male pups of California sea lions during El Niño years, because male pups are larger at birth and therefore presumably require more energy during the gestation period. A female-biased sex ratio in 2-month-old California sea lions during an El Niño year was observed by Francis and Heath (1991). However, they were unable to determine if it was a product of differential postnatal or prenatal mortality, or a reflection of sex ratios at conception (Francis and Heath 1991). In Galapagos fur seals (*Arctocephalus galapagoensis*) male pups are larger than females at birth, and the sex ratio is biased towards female pups after El Niño events (Trillmich 1986).

It is possible that the observed size difference between mothers of male and female pups could be brought about in another way unrelated to sexual selection. Mothers with male foetuses might forage more effectively and to gain more mass during pregnancy through some influence of the male foetus, as suggested by Anderson and Fedak (1987). If this was true, mothers of male pups would be likely to weigh more in relation to their length than mothers of female pups. Figure 4 shows that this is not the case. Allowing for length, there was no statistically significant difference between the mass of mothers of male pups and female pups. We also checked for any shift in length measurements resulting from changes in mass (Lunn and Boyd 1993) using repeated length measurements of the same animals over the range of mass observed during the course of lactation. The measured length did increase significantly with the mass in the same animal, but the rate of change (0.043 cm/kg) accounted for only a 1% change in length for a 10% change in mass. This is not enough to produce the observed overlapping distributions of masses of mothers. Furthermore, it could be argued that if food was available, all females should gain weight if they are capable of doing so, not just those with male pups.

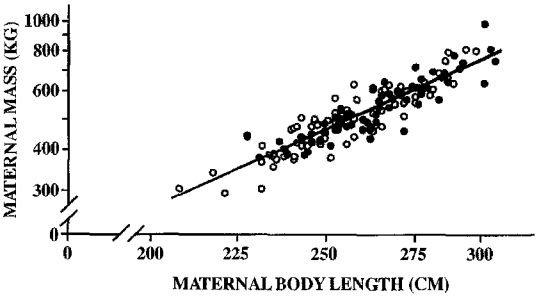

Fig. 4 Log maternal mass plotted in relation to log body length (nose to tail) of mothers having either male pups (*solid circles*, $y=2.61x-8.24$, $r^2=0.82$, $F_{[1,67]}=288$, $P < 0.001$) or female pups (open circles, $y=2.62x-8.30$, $r^2=0.81$, $F_{[1,78]}=324$, $P < 0.001$). Both *regression lines* are drawn in the figure, but because of the overlap, they appear as one

Females which were absent from beaches the year following breeding were significantly smaller than females which returned to breed in consecutive years, despite the fact that four of the five largest (> 800 kg) females were also among the absent females. This pattern is consistent with the idea that breeding is proportionately more costly for small females. In both northern elephant seals and southern elephant seals, the relative investment in pups, during both pregnancy and lactation, decreases as females grow larger (Reiter and Le Boeuf 1991; Fedak et al. 1994). Female northern elephant seals which breed for the first time at 3 years of age exhibit lower survivorship to their next breeding efforts than females that are primiparous at 4 years of age (Huber 1987; Reiter and Le Boeuf 1991) and have lower lifetime reproductive success (Sydeman et al.1991). Male pups born to young mothers have a lower chance of being weaned than female pups (Le Boeuf et al. 1989).

Why should small southern elephant seal females not give birth to males? Mothers giving birth have a limited energy reserve, stored as blubber and protein, which supplies energy and nutrients to the mother, and is used to produce milk for the pup (McCann et al. 1989; M.A. Fedak, T. Arnbom, J.L. Boyd, unpublished work). Mothers fast during the 23-day nursing period, when they lose on average 35% of their post-partum mass (McCann et al. 1989; T. Arnbom, M.A. Fedak,

J.L. Boyd, unpublished work). Smaller and younger females use up to 85% of their total body fat during the nursing period while larger females may use as little as 45% (Fedak et al. 1994). During lactation larger pups (independent of sex) draw more resources from mothers than smaller pups (T. Arnbom, M.A. Fedak, J.L. Boyd, unpublished work). Male pups are on average 14% larger at birth (Fig. 2), and may draw more resources from their mothers than female pups, both during pregnancy and lactation. In addition, the relative difference between male and female pup mass at birth is larger for smaller mothers than for larger mothers. Smaller females may not be able to produce male pups which will survive to reproductive age and successfully reproduce. Resources expended on male pups would therefore be wasted. This may not be true for smaller female pups and may explain why mothers weighing less than 380 kg do not give birth to male pups.

However, we found no evidence which suggests that larger southern elephant seal mothers produce a male-biased sex ratio, such as one might expect on the basis of the prediction of Trivers and Willard (1973). The mechanism which might produce the biased sex ratio in females of any size is unknown. Either pre- (Simpson and Simpson 1982) or post-conception (Clutton-Brock and Albon 1982; Gosling 1986) mechanisms (or both) could be involved. The choice could have consequences for the shape of the relationship between sex ratio and the mother's size. Prior to conception, the mechanism could act on gametes of either sex and could presumably produce biases favouring either with no loss of reproductive potential, given an ample supply of sperm or eggs. After conception, selection must involve some form of differential mortality (such as reduced survival of males in utero, selective abortion or resorption or even higher mortality of smaller mothers with male foetuses) and consequently at least the loss of a reproductive season. If the mechanism for producing a male-biased sex ratio at birth acts after conception, then producing a male bias in large females would involve eliminating a female foetus and the females would miss a season (if an exceptional conception did not occur through copulation occurring outside of the normal breeding season). It seems unlikely that larger and most likely older females would give up a breeding opportunity, especially given that they are likely to have more than ample reserves for producing and feeding a pup.

The question of whether the sex ratio bias towards female pups in small mothers is the result of active intervention by the mother or differential mortality of male offspring remains open. The results presented here are consistent with either active intervention or incidental mortality. However, the fact of the bias occurring prior to birth, before energy demands on the mother reach their peak during lactation, supports the notion that action by the mother may be involved.

The preponderance of female pups among small mothers could have important consequences for the population dynamics of any species in which it occurs, in that it would effectively increase fecundity of the smaller, probably younger animals. Thomas et al. (1989), have pointed out that a young growing population could have a higher intrinsic rate of increase than expected, if younger females have a female-biased sex ratio at birth.

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