

Intraspecific allometry of neonatal size in the Antarctic fur seal (*Arctocephalus galapagoensis*)

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Summary. Intraspecific allometry of pup mass as a function of maternal mass was analysed in Antarctic fur seals (*Arctocephalus gazella*), a highly dimorphic species. The allometric exponent was 0.6, much lower than in interspecific comparisons. Slopes were the same for mother-son pairs as for mother-daughter pairs, but adjusted means were significantly higher for the former, indicating higher reproductive effort of mothers of sons. The correlation of maternal mass with pup mass explained 59% of the variance in female pup mass but only 18% of that in male pup mass. Females appeared to produce sons which were as big as possible. Relative pup mass decreased with increasing maternal mass indicating a lower reproductive effort of bigger and presumably older mothers, contrary to expectations from life history theory. Sex ratio of pups showed no relation to maternal mass.

Introduction

Among homeotherms larger animals as a rule produce larger offspring. The relation is allometric and is usually described as a power function of maternal body mass. For mammals, exponents of maternal mass for the prediction of neonate mass range from 0.71 to 0.94 (Millar 1977, 1981; Blueweiss et al. 1978; Robbins and Robbins 1979; Peters 1983). For precocial mammals the exponent was found to be 0.91 (Martin and MacLarnon 1985). As a consequence of this allometry, relative mass of offspring – e.g. as a percentage of maternal body mass – falls with maternal size in these interspecific comparisons.

Leutenegger (1977) noted a lower exponent value for intrageneric allometry in macaques indi-

cating a different relationship at lower taxonomic levels, an observation often made in other comparisons as well (Clutton-Brock and Harvey 1984; Harvey and Mace 1982; Smith 1980). Apparently the intraspecific scaling of neonatal mass has not been determined for undomesticated mammals, nor has it been asked whether male and female offspring scale similarly. Equal scaling of male and female offspring is not necessarily to be expected where sexual selection is important. Where reproductive success varies more widely among males than females (Trivers 1972; Clutton-Brock et al. 1982) and this variation among adults is influenced by early parental investment, a parent may benefit from expending greater parental effort on sons than on daughters (Maynard Smith 1980).

We explored intraspecific scaling, using a data set collected by one of us (DPC) on Antarctic fur seals (*Arctocephalus gazella*). This species provides an excellent test case for intraspecific scaling since growth in fur seals is indeterminate (Payne 1979) and the body mass of reproductively active females ranges, according to age, between about 25 and 55 kg body mass. Furthermore, this species is highly dimorphic, with full-grown males weighing about 5 times as much as females (Payne 1979). Mothers produce a single, large, precocial young and males are born significantly heavier than females and usually grow faster until weaning (Payne 1979; Croxall et al. 1988). Therefore, theoretical considerations suggest that large females should predominantly produce sons and small females daughters (Trivers and Willard 1973).

We tested specifically: (i) whether the intraspecific relationship between maternal body mass and neonatal mass differs from the interspecific one, (ii) whether sons and daughters scale differently to maternal body mass, and (iii) whether maternal body mass influences the sex ratio of offspring.

Table 1. Regressions of pup mass as the dependent variable against maternal mass of Antarctic fur seals. Body mass was measured within 24 h of parturition for 22 mother-son pairs and 25 mother-daughter pairs. Regression equations for mass in kg. PM=pup mass; MM=maternal mass; RPM=relative pup mass=(PM/MM) * 100; m=male; f=female; S.E.=standard error of slope; r =Pearson's correlation coefficient; P =two-tailed probability; N =sample size

Regression of	Intercept	Slope	S.E.	r	P	N
log PM – MM	-0.247	0.598	0.135	0.551	<0.001	47
log fPM – MM	-0.269	0.594	0.103	0.770	<0.001	25
log mPM – MM	-0.067	0.507	0.241	0.426	<0.05	22
PM – MM	2.32	0.071	0.018	0.503	<0.001	47
fPM – MM	2.07	0.068	0.013	0.734	<0.001	25
mPM – MM	2.88	0.068	0.032	0.423	=0.05	22
log RPM – MM	1.75	-0.401	0.135	-0.405	<0.01	47
log fRPM – MM	1.73	-0.406	0.103	-0.636	<0.001	25
log mRPM – MM	1.93	-0.492	0.241	-0.415	<0.1	22

Methods

Antarctic fur seals were studied during the austral summers of 1983–84 and 1984–85 at Bird Island, South Georgia (54°00'S, 38°02'W). The animals were weighed to the nearest 50 g on a platform balance. Neonatal and maternal mass were measured on the day of birth or the day thereafter. In three newborn Galapagos fur seals (*Arctocephalus galapagoensis*) mass at 24 h after birth was 1% less than at birth. Thus measurements within 24 h of birth reliably estimate neonate mass. Differences between years and sexes were tested by analysis of covariance (COVARAN; Sokal and Rohlf 1981) and by Mann-Whitney U -tests (MWUT). All significances (P -values) given are two-tailed.

Results

Absolute pup mass at birth increased significantly with maternal body mass (Table 1). The logarithmic regression did not give a much better fit than the linear one (Table 1). Slopes for the mass relations of mother-son pairs were not significantly different from those for mother-daughter pairs (Fig. 1 and Table 1; $P > 0.1$, COVARAN). However, the correlation between maternal and male pup mass just reached significance, while that for maternal and female pup mass was highly significant (Table 1). In both years, analysed separately, male pup mass did not significantly correlate with maternal mass, whereas these relations were always highly significant for mothers with daughters. Mean male pup mass was greater than that of female pups (5.57 ± 0.77 kg, $n=22$, versus 4.74 ± 0.58 kg, $n=25$) leading to significantly different intercepts and adjusted means for the regressions ($P < 0.05$, COVARAN; Fig. 1). Neither slopes nor adjusted means differed significantly between years (COVARAN). We also calculated these regressions using female standard length and condition (condition = (maternal mass * 100)/standard length³) as the independent variables. None of these regressions were significant.

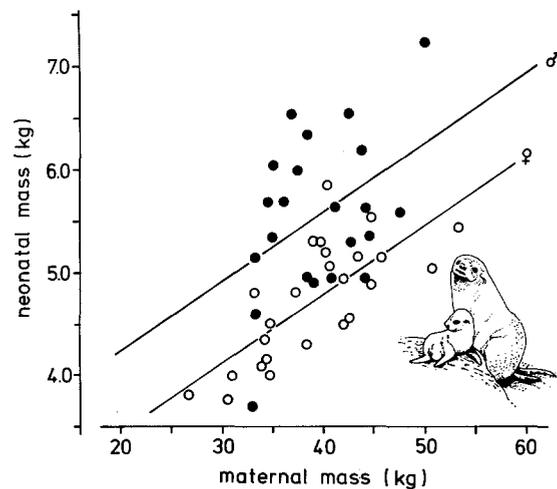


Fig. 1. Neonatal offspring mass as a function of maternal mass at the time of parturition in Antarctic fur seals. \circ = female neonates; \bullet = male neonates. Slopes for male and female neonates are not significantly different, but intercepts are (for levels of significance see text). Regression equations in Table 1

Relative pup mass decreased with increasing maternal mass, indicating a lower reproductive effort of bigger mothers (Table 1; $P = 0.001$; COVARAN). Mothers of all sizes expended relatively more effort on the production of sons ($P < 0.05$; COVARAN). Daughters were on average $12.25\% \pm 1.25\%$ (mean \pm s.d.; $n=25$) of maternal mass while sons were $14.16\% \pm 2.03\%$ ($n=22$).

In the poor krill year 1983–84 (Croxall et al. 1988) female Antarctic fur seals weighed at parturition significantly less (37.2 ± 6.1 kg, $n=15$) than in 1984–85 (40.3 ± 5.1 kg, $n=32$), an apparently normal year (MWUT, $P = 0.05$). Mean pup mass relative to maternal body mass tended to be greater in the food-poor year 1983–84 than in the food-rich year 1984–85. In 1983–84 female pups were $12.6\% \pm 1.2\%$ of maternal mass while in 1984–85 it was $12.1\% \pm 1.3\%$, and for male pups the respec-

tive numbers were $14.5\% \pm 2.0\%$ versus $14.0\% \pm 2.1\%$; but these differences between years were not significant.

Females with male pups had a mean mass of 39.6 ± 4.8 kg ($n=22$) and those with female pups of 39.1 ± 6.2 kg ($n=25$). The difference was not significant within either of the two years or for both years combined (MWUT, $P=0.468$). Median mass of females in our sample was 39.4 kg. Sex ratio of pups of mothers of above median mass was about the same as that of mothers of below median mass (above median 10:13 (males:females) or 0.43; below median 12:11 or 0.52). This is contrary to the theoretical expectation of adaptive sex ratio shift.

Discussion

Intra-versus interspecific scaling of neonatal mass

Over the range of maternal body mass of Antarctic fur seals from 26 to 53 kg linear scaling describes the variation in neonatal mass almost as accurately as logarithmic scaling. Upon recalculation, this also proved to be true for published analyses at a generic (Macaques; Leutenegger 1977) or sub-familial level (Phocid seals; Kovacs and Lavigne 1986). This is not very surprising since small sections of a logarithmic curve can be approximated quite well with a linear fit.

For comparison with published analyses of interspecific scaling the exponential description is more useful since most analyses are reported as logarithmic regressions. For organ mass intraspecific comparisons usually yielded lower exponents than interspecific comparisons (Smith 1980). Our finding suggests the same for birth mass relative to maternal mass. The exponent 0.6 for all neonates or female neonates only (Table 1) is lower than those reported for mammals in general (Peters 1983). As Martin and MacLarnon (1985) pointed out one should, however, distinguish between mammals with altricial and precocial young. Their exponent for a sample of 130 species with precocial young was 0.91, considerably higher than the intraspecific exponent we found. Kovacs and Lavigne (1986) report an exponent of 0.82 for phocid seals which lies closer to our value. However, their value is based on inaccurate data for the body mass of elephant seal females and their pups (they used 900 kg for northern and 790 kg for southern elephant seal females). Reanalysis of their regression using recently obtained data on both species collected within 3 days of parturition (Northern elephant seal females: 480 ± 96 kg, $n=15$, and their

pups 40 ± 6.5 kg, $n=15$; LeBoeuf and Costa unpubl. data; Southern elephant seal females: 500 ± 111 kg, $n=26$, and their pups 43 ± 6 kg, $n=29$; Fedak and McCann 1987) yields an exponent of 0.930 (± 0.118 , S.E. of the slope), much closer to Martin and MacLarnon's (1985) value for precocial mammals and clearly different from the intraspecific slope found in the Antarctic fur seal.

Intraspecifically neonate size increases less with maternal size than in the comparison of animals of widely differing taxonomic levels (mouse to elephant). If so, our data indicate that size per se may not produce such strong allometry, and other factors connected with different adaptations, e.g. altricial versus precocial (Martin and MacLarnon 1985), also play a major role in size-correlated changes.

Maternal effort on male and female offspring

The most interesting result of our study was that maternal mass was a good predictor of female neonate mass, but was not nearly as good for male neonates. This was not due to greater variance in pup mass. In our data, the coefficient of variation was about the same for female (CV = 12.2%) and male neonates (CV = 13.8%). Doidge et al. (1984) stated that male neonate mass varies less between years than female neonate mass (although, upon testing, this effect is not significant; F -test, $P > 0.1$). Only 18% of the variance in male birth mass is explained by maternal mass while 59% of it is explained in female neonates (Table 1; correlation with log-values). Females appear to produce sons which at birth are as big as possible and factors other than body mass, e.g. condition of the mother, may correlate better with neonatal male mass. However, we found no significant correlation between condition at parturition or female standard length (an indicator of her age) and pup mass. However, maternal condition over the course of the preceding year, when she was carrying the fetus, might still be more influential in determining male neonate mass than condition at parturition.

Fur seal males are under strong intra-sexual selection for large size since in these highly polygynous species body size becomes very important in male-male territorial competition permitting access to females in reproductive condition. Thus male size largely determines the contribution which a male is expected to make to the next generation. The importance of male-male competition has been documented for the Northern elephant seal (LeBoeuf 1974) and in red deer (Clutton-Brock et al. 1982). Females appear to be under less selec-

tion for large size, presumably because the probability of successful reproduction in females is less dependent on size. Nevertheless, the question arises why daughters do not take as much of their mothers' reserves as they can get, i.e. become as big as male pups.

Adaptive sex ratio shift

The relationship between pup sex and maternal size postulated by Trivers and Willard (1973) was not detectable in our data set. Contrary to their hypothesis, mass of mothers of daughters was almost the same as that of mothers of sons and sex-ratio of offspring was not clearly biased according to maternal mass. Of course, mass at parturition may be a poor estimator of maternal condition at the time of conception, a year before, but this seems not to be very likely since maternal mass is largely a function of age, although the variation within each cohort is still substantial (Payne 1979). Since life-history theory (Horn and Rubenstein 1984) predicts that mothers will expend greater maternal effort as their reproductive value drops, production of more sons – the more expensive sex – by bigger mothers would be expected. This does not happen. Furthermore, our finding that relative pup mass decreases with increasing maternal mass (and therefore presumably maternal age) also indicates that the reproductive effort of older mothers may become lower rather than increase.

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