

Kathryn A. Ono · Daryl J. Boness

## Sexual dimorphism in sea lion pups: differential maternal investment, or sex-specific differences in energy allocation?

Received: 28 April 1995/Accepted after revision: 25 July 1995

**Abstract** Proximal mechanisms underlying a faster growth rate in male compared to female California sea lion pups were investigated. Males are significantly larger at birth than females. Specifically, we asked if differential maternal investment contributed to enhanced male growth via: (1) larger mothers having disproportionately more male pups, (2) more time and energy put into foraging by mothers of male pups, and (3) greater milk production in mothers of male pups. We also considered four aspects of differential energy utilization and acquisition by male and female pups: (1) male pups attempting to save energy for growth by changes in behavior, (2) longer suckling bouts with mother and more sneak suckling of non-filial females by male pups, (3) lower maintenance costs in males via a lowered resting metabolic rate, and (4) increased assimilation efficiency in males. Our study showed that there are no differences in the size of females or length of foraging trips for mothers of male and female pups. Male pups received more milk from their mothers, but the difference was no longer significant when the larger body size of males was considered. There were no differences in either the activity budgets or suckling behavior of male and female pups. Male pups, however, did have lower resting metabolic rates than females. We conclude that enhanced male perinatal growth is a consequence of a larger size at birth, proportionally more milk from mothers to support the greater demands of larger body size, and lower maintenance costs due to a lower resting metabolic rate.

**Key words** California sea lion · Maternal investment · Sexual dimorphism · Growth rate · Metabolic rate

### Introduction

In many polygynous species males are larger than females as adults (Alexander et al. 1979). The reasons for this appear to be due to the reproductive advantages accrued by large size in males. Investment theory predicts that for dimorphic species such as these, parents should expend greater resources on male offspring than female offspring (Trivers and Willard 1973; Maynard Smith 1980). Although some empirical studies support these predictions from investment theory, others do not (reviewed in Lee and Moss 1986; Wolff 1988; Green and Berger 1990; Byers and Moodie 1990). Regardless, the proximal mechanisms through which males grow larger than females, especially during early ontogeny, have not been well studied in many animals. The pattern of differential investment may be varied, occurring principally prenatally or postnatally, or both. It may also be in the form of a greater effort over a comparable period or greater effort by extending the period of care for one sex (Reiter et al. 1978; Maynard Smith 1980; Clutton-Brock et al. 1981; Clutton-Brock and Albon 1982; Gosling et al. 1984). Additionally, offspring are not passive recipients of parental resources, so that differences in behavior and energy use by male and female offspring must also be considered (Kretzmann et al. 1993).

Numerous studies of growth in sexually dimorphic otariid pinnipeds have pointed to increased maternal investment in male pups as the primary factor responsible for larger male size at birth and during early ontogeny (Trillmich 1986; Costa et al. 1988; Boyd and McCann 1989; Cappozzo et al. 1991). Studies of sexually dimorphic phocid pinnipeds provide a less clear picture (Reiter et al. 1978; Kovacs and Lavigne

K.A. Ono (✉)<sup>1</sup> · D.J. Boness  
Department of Zoological Research, National Zoological Park,  
Smithsonian Institution, Washington, D.C. 20008, USA

*Present address:*

<sup>1</sup>Department of Life Sciences, University of New England,  
Hills Beach Road, Biddeford, ME 04005, USA

1986a, b; Bowen et al. 1992b; Kretzmann et al. 1993). This disparity may be due to the difference in lactation strategies in these two groups: otariid females alternate oceanic foraging trips with periods on land to nurse their pup, while most phocid females store nutrients during a prolonged prepartum feeding trip, and fast during the entire lactation period. Phocid females, therefore, probably have a lower ability to differentially supply pups of either sex prior to weaning. Most phocid pups also undergo a prolonged post-weaning fast, making maximum maternal expenditure prior to weaning critical for either sex. For either family, there has been little investigation into possible mechanisms by which male pups might behave or use energy differently in order to conserve energy for growth (cf. Reiter et al. 1978; Kretzmann et al. 1993).

Pinnipeds are good subjects for the study of early differential growth and maternal investment since neonates, being born on land, are removed from the primary source of food, and therefore consume only milk. Many pinnipeds also breed in dense aggregations, have limited mobility on land, and are philopatric, making the simultaneous observation of a large number of individuals possible.

Among otariid species, reproductively active females of a wide range in body size are able to produce and successfully rear a pup. In contrast, successful reproduction in males is more dependent on adult body size. The adult sex ratio on breeding areas is highly female biased and males engage in aggressive competition to hold territories within the prime sites where the largest number of females congregate (reviewed in Boness 1991). There are two reasons to suspect that large body size may be important in the ability of males to garner and maintain a territory on breeding areas. Male fights rely heavily on pushing and biting (Peterson and Bartholomew 1967; Gentry 1970), and large body size allows males to fast for long periods, since they do not abandon their territories to feed during their territorial tenure. There is some evidence of the importance of this in Antarctic fur seals (Boyd and Duck 1991). However, the significance of male size has not been clearly demonstrated due to the difficulty of catching and weighing adult male otariids. If early maternal investment is positively correlated with adult body size and large body size gives male otariids an advantage in monopolizing females, then Trivers and Willard (1973) predict that females should invest more in male offspring. Although there have been few studies directly investigating male body size in relation to the ability to obtain or hold territories in otariids, studies of other size dimorphic species indicate that body size is a key ingredient for access to mating (Espmark 1964; Clutton-Brock et al. 1982; Clinton 1990; Haley 1994; Haley et al. 1994).

The California sea lion (*Zalophus californianus*) is a highly dimorphic pinniped, in which adult males

weigh an average of 375 kg and adult females average 94 kg (Lluch Belda 1969), a ratio of 4:1. The weight ratio of male and female pups during their first week postpartum is 1.18:1 (calculated from Table 4, in Ono et al. 1987). After giving birth on the breeding area, female sea lions remain with their pup for about a week, then initiate typical otariid feeding/attendance cycles, where they alternately go to sea to feed for a few days before returning to nurse their pup for a period of several days (Heath et al. 1991). Intermittent feeding throughout the lactation period allows females to adjust their food intake according to the milk demands of their pup.

Differences in the growth of mammalian neonates may reflect differences in energy acquisition and/or utilization. There are two major avenues available to pups for differential energy flux: via differential maternal expenditure, and via differential use of energy by pups through either behavioral or physiological means. The purpose of this paper is to delineate when sexual size differences begin and how they are achieved in the California sea lion. Specifically, we evaluated three possible means of differential maternal expenditure:

1. If larger females produce more milk, or larger pups at birth, then we would expect them to produce disproportionately more male pups, since it should be to their advantage to do so.
2. Mothers with male pups may have to spend more time at sea feeding in order to supply them with more milk; they may also have to spend more time on land to allow their pup to ingest a greater amount of milk, and therefore have longer total cycles than mothers of female pups.
3. Females of any size should produce more milk, or nutritionally richer milk for male pups. If mothers of male pups spend similar amounts of time at sea foraging to mothers of female pups, but were able to forage more efficiently, then we would expect this difference to be manifest in a greater supply of milk to male pups.

It should be noted that these hypotheses are based on the assumption that increased maternal investment ultimately translates into increases in adult size, survival and/or reproductive success of offspring. There is presently no direct evidence to either support or refute this assumption in pinnipeds, or for that matter in other mammals.

We also examined four possible hypotheses regarding differential energy utilization in male and female pups.

1. Male pups may alter their behavior to conserve energy, and thereby have more energy available for growth. They might achieve this by resting more, or participating less often in high energy behaviors such as swimming and playing.

2. Male pups may work to obtain more energy from their mothers by suckling more, or from unrelated females by sneak suckling (i.e., taking milk from a female without her knowledge),

3. Male pups may have a lower resting metabolic rate, and thereby require less total energy for maintenance, leaving more for growth.

4. Male pups may be more efficient at assimilating the energy and nutrients in milk, that is they may have better digestive abilities and extract more from milk prior to excretion.

## Methods

Some of the findings presented in this paper result from reanalyses of previously published work in which data for each sex may have been presented separately, but sex differences were not a focus of the paper (Oftedal et al. 1987a; Ono et al. 1987; Thompson et al. 1987; Boness et al. 1991; Ono and Boness 1991). These papers also provide a more detailed description of materials and methods used. Each year between 1982 and 1985, behavioral observations of females and pups were made at Trailer Cove (area 1A in Peterson and Bartholomew 1967), San Nicolas Island, Channel Islands, California. Observations were made between 0600 and 1800 hours for approximately 10 weeks per year, beginning in mid-May. Females were identified using natural scars, or were remotely marked with paint pellets or dye-filled eggs prior to or shortly after parturition. Pups were rounded-up *en masse*, individually marked with bleach, sexed, weighed and measured just after the peak of births, and rounded-up again for reweighing and measuring at about 2 months of age. Since we knew the parturition dates for our scarred and marked females, the ages of marked pups was also known. The arrival and departure of the females were noted when observed. In the years 1982–1984, individually identifiable (known) pairs were scan sampled once per hour, noting presence or absence of the mother on the study area, behavior of each member of the pair, and location of each member (see Ono et al. 1987 for a more complete description of the study area and methods).

Pup behavior was grouped into four major categories as defined in detail in Ono et al. (1987): low active, active, rest, suckle. “Low active” behaviors involve moving some part of the body, but they probably utilize less energy than “active” behaviors. For instance, grooming and sitting upright were all considered low active, whereas playing and swimming were considered active. The proportion of observations spent on each behavior was calculated for individual pups, from which a mean for each sex was obtained. Sample sizes reflect the number of individual pups for which at least 250 observations were obtained. Observations on pups that died within the observation period are not included in this data set. Non-filial sucking is defined as attempting to extract milk from a female other than the pup’s mother. Data on the non-filial sucking of marked pups include attempts by pups which died within the first 2 months. Most of these pups apparently died of starvation.

Female feeding (attendance) cycles were calculated using the rules outlined in Heath et al. (1991). Females not seen on a given day were considered absent (presumably at sea feeding). Females were considered to be present the entire day if seen at all on a given day. Each period present is the number of consecutive days that a female was seen on the study area. The period ends when the female is not seen for an entire day. Periods of absence are computed in the same manner. For all females combined, there was a mean of

9.53 and minimum of 4 periods present, and mean of 9.60 and minimum of 3 periods absent used to calculate a mean cycle per female. Mean periods present and absent per female were used to compute annual means. Feeding cycles were calculated as the number of days absent plus the following number of days present. Again, an overall mean of the mean cycle duration per female was used to determine annual cycles for mothers of male and female pups. A simultaneous significance procedure was used to adjust for multiple tests (Rice 1989).

Relative female size was determined by observation in the following manner. Whenever two known females were lying or sitting in close proximity with one another (generally within one body length), their relative sizes were estimated as either larger, smaller, or the same. Both females were also ranked as being average, large, or small compared with the female population as a whole. An attempt was made to record as many comparisons between as many different female pairs as often as possible. There was a mean of 4.58 comparisons made for each female ranked in 1983 (SD = 2.45) and 3.34 comparisons in 1984 (SD = 2.72). Females were then ranked according to the number of females they were judged to be larger than, as is done in determining a dominance rank (Brown 1975). Females estimated to be the same size were given the same rank, so that there were fewer ranks than females in both years. In total, 26 females were compared in 1983 and 30 in 1984, using only mothers of pups which were still alive in early August of each year. A  $\chi^2$  test (SPSSPC) was used to analyze the effect of female size on the sex of pups. Females were divided into three categories for this analysis, median rank, smaller than median, and larger than median. For the effect of female rank on initial pup mass or on growth rate, a Spearman correlation coefficient, using individual female ranks, was performed (ten ranks in 1983, eight ranks in 1984).

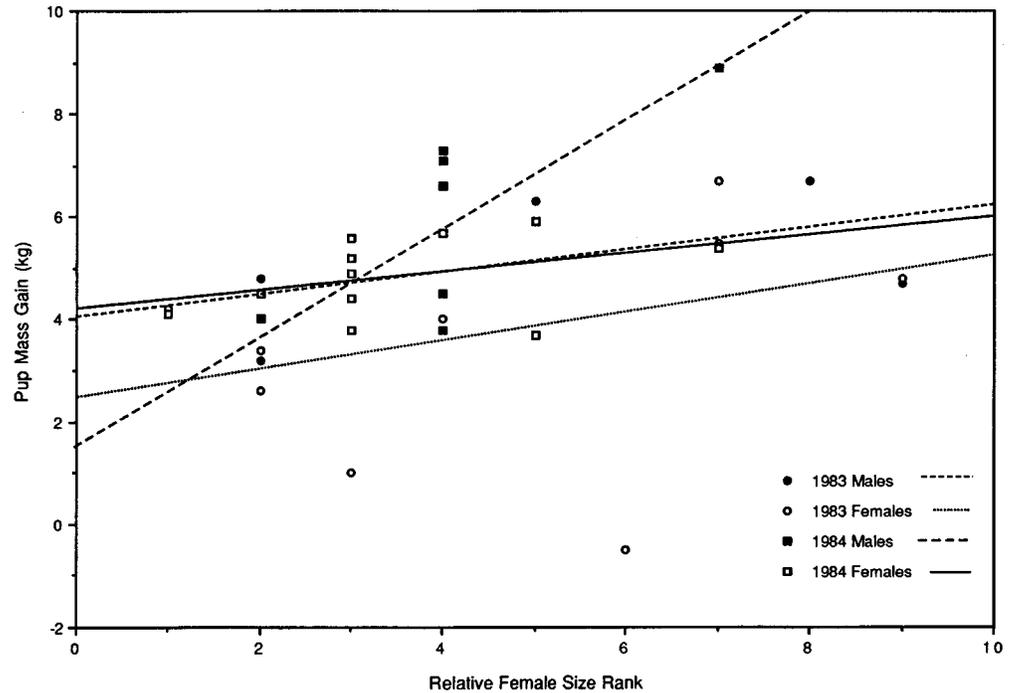
Growth rates used in this paper were previously reported in Ono et al. (1987) and were only from marked pups residing on the behavior study area. Rates were computed by dividing two serial mass measurements of each pup by the number of days between weighings. Sex differences in mass and mass gain were analyzed using an ANCOVA (SPSSPC) with initial pup mass as a covariate to adjust for any growth advantage provided by being larger initially.

Milk intake of pups was measured in 1982, 1983 and 1984 using deuterium oxide ( $D_2O$ ) dilution (reported in Oftedal and Iverson 1987; Oftedal et al. 1987a). Intake was measured on pups outside the behavioral study site to minimize disturbance of behavioral observations.

Metabolic rate was measured on 39 pups in 1985 (20 females, 19 males) approximately 3–5 weeks of age using a Beckman 744 gas oxygen analyzer (Thompson et al. 1987). Pups were always captured between 0730 and 0830 hours, and metabolic measurements were made between 0830 and 2200 hours. To minimize disturbances, pups were caught as a group only once a day. Metabolic measurements were taken up to 14 h after capture because some pups needed to be in the chamber for a prolonged period (they did not always rest immediately), the chamber needed to be calibrated between runs, and some pups were run more than once at different temperatures.

Pups were kept in the chamber until they had remained still for at least 10 min. Pups were always released where they were caught on the same day. Data were analyzed using two different combinations of the data set, with only one record per pup used in each case. In the first analysis, the first period in the metabolic chamber was used for each pup, regardless of chamber temperature, even though temperatures below 19°C may be below the thermoneutral zone for these pups (this analysis was reported in Thompson et al. 1987). In the second analysis, the first measurement period for each pup was used only if the chamber temperature was at least 19°C, otherwise the second period, which was run at a higher temperature, was used (analysis performed for this paper).

**Fig. 1** Pup mass gain as a function of relative female size rank. For both sexes combined, Spearman's  $r$ : 1983  $r = 0.47$ ,  $P = 0.033$ ,  $n = 16$ , 1984  $r = 0.43$ ,  $P = 0.027$ ,  $n = 19$ , consensus  $P$ -value  $P = 0.004$ . There were no significant differences between sexes in either year ( $P > 0.05$ )



## Results

### Evidence for early dimorphism: size and growth rate

Although we took five different measurements as indices of pup size (length of proximal edge of right foreflipper, length of lateral edge of right hindflipper, axillary girth, length from tip of nose to tip of tail, mass), they were all highly correlated ( $P < 0.05$ , Boness et al. 1991), and we use mass as the index of pup size in the remainder of this paper. Mass measurements taken within the 1st week of life for pups caught

throughout the island showed that male pups were significantly larger than female pups for each of the four years that neonates were weighed ( $P < 0.0001$  for each year, see Table 4 in Ono et al. 1987). Similarly, at the behavior study area, measurements at the first roundup when pups were less than 2 weeks old demonstrated that males were significantly larger than females ( $P < 0.001$  for 1982, 1984, 1985;  $P < 0.01$  for 1983, Table 4, Ono et al. 1987). At 2 months of age, males were still larger than females ( $P < 0.001$  1982–1985, Table 4, Ono et al. 1987). Mean growth rates were significantly greater for males than for females in all years ( $P < 0.05$  for 1982–1984,  $P < 0.01$  for 1985).

**Table 1** Mean attendance parameters for mothers of male and female California sea lion pups on San Nicolas Island, California. *Present*, *absent* and *cycle length* are given in days

Year Pup sex	1982		1983		1984		1985	
	Male	Female	Male	Female	Male	Female	Male	Female
<i>n</i>	6	7	7	8	8	12	13	7
Present	1.65	1.99	1.88	1.87	1.75	1.77	1.80	1.60
SD	0.36	0.38	0.52	1.18	0.34	0.58	0.25	0.30
Absent	2.20	2.01	2.63	2.48	2.26	2.30	1.86	1.48 <sup>a</sup>
SD	0.18	0.73	0.74	1.09	0.42	0.57	0.41	0.45
Cycle length	3.83	3.83	4.49	4.26	4.21	4.24	3.65	3.05 <sup>a</sup>
SD	0.38	0.78	1.02	1.24	0.80	0.98	0.45	0.28
Percent present	46.88	54.53	49.12	47.19	52.73	51.94	57.82	62.32
SD	6.68	8.66	5.31	12.69	4.53	6.16	6.78	7.73

<sup>a</sup>Differences between mothers with male and female pups were tested with a Mann-Whitney  $U$ -statistic. The only significant differences were for absences ( $U = 15.0$ ,  $Z = -2.42$ ,  $P_{1\text{-tailed}}$  corrected for simultaneous significance = 0.03), and for cycle length ( $U = 12.5$ ,  $Z = -2.62$ ,  $P_{2\text{-tailed}}$  corrected for simultaneous significance = 0.03) in 1985

## Maternal investment

Larger females were not more likely to produce male pups ( $\chi^2 = 0.32$ ,  $n = 24$ ,  $P = 0.85$  for 1983;  $\chi^2$ ,  $n = 30$ ,  $P > 0.05$  for 1984), nor were they more likely to produce larger pups at birth (Kendall's tau = 0.22,  $n = 24$ ,  $P = 0.08$  for 1983; Kendall's tau =  $-0.06$ ,  $n = 30$ ,  $P = 0.35$  for 1984). However, larger females did have faster growing pups, regardless of pup sex (Fig. 1,  $P < 0.01$  using combined probabilities test).

In each of 4 years studied, there were few significant differences between mothers of male and female pups in the proportion of time a female spent at the study area, the duration of feeding trips (absences), duration of shore visits (periods present) to nurse their pups between foraging trips, and length of feeding cycles (Table 1). The only significant differences were those in 1985 mothers of male pups spent a longer time away from the study area, and had overall longer feeding cycles than mothers of female pups (for both,  $P = 0.03$ ).

A previous study of milk intake performed on the same population as this study showed that in the 3

years studied, daily milk yield, estimated from pup milk intake, was significantly higher in mothers of male pups than those of female pups (see Tables 3 and 4 in Oftedal et al. 1987). However, when milk or energy intake was calculated per unit body weight, there was no longer a significant sex effect. The intake per metabolic body size (mass<sup>0.83</sup>) was also calculated since larger bodies may be more efficient in channeling energy into growth. Energy intake calculated per metabolic body size was also not significantly different between male and female pups (Tables 3 and 4 in Oftedal et al. 1987).

## Pup behavior

There is little evidence of male pups behaving differently than female pups. There were no significant differences between sexes in rest, low active or active behaviors (Table 2). Sucking behavior also showed no consistent differences when analyzed either as the proportion of total observations, or as a proportion of only those observations taken when the pup's mother was present (Table 2). However, male pups spent a larger proportion of their total time sucking in 1984 ( $P = 0.05$ ).

**Table 2** Activity budgets for California sea lion pups in three different years. Data are shown as mean percent of scan samples individual pups spent in four categories (REST, ACTIVE, LOW ACTIVE, SUCK). The percent of scans pups were seen sucking when only considering scans taken when the pup's mother was present are shown below

Year Pup sex	1982		1983		1984	
	Male	Female	Male	Female	Male	Female
<i>n</i>	8	7	7	10	10	13
Rest	39.1	38.5	40.4	41.6	36.2	37.3
SD	4.7	9.1	5.6	9.1	4.8	3.9
ACTIVE	33.5	30.3	25.7	25.2	21.5	22.1
SD	3.7	4.9	5.4	7.5	5.1	6.3
LOW ACTIVE	9.3	10.6	20.1	19.9	27.7	29.8
SD	4.6	2.7	3.3	3.3	3.0	4.3
SUCK	18.1	20.6	13.9	13.3	14.6	10.7
SD	4.3	5.4	4.3	5.4	3.3	3.6 <sup>a</sup>
Mother present only:						
SUCK	29.4	28.6	31.9	29.1	28.4	20.1
SD	7.2	8.4	11.8	9.6	8.0	7.9

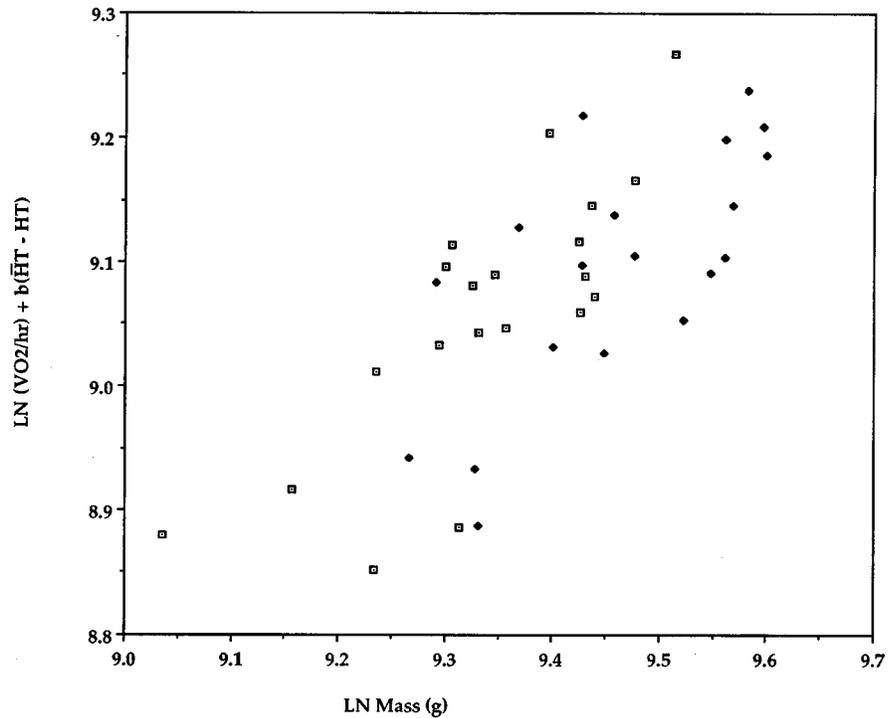
<sup>a</sup>Yearly differences between male and female pups were tested using a Mann-Whitney *U*-statistic. The only significant difference is in the proportion of time pups spent suckling in 1984 ( $P < 0.05$ ) when adjusted for multiple comparisons

**Table 3** Numbers of marked, known sex pups that attempted non-filial sucking at least one time (*attempted*) during the breeding season (June – August) compared with those which were never observed attempting non-filial sucking

Year Pup sex	1982		1983		1984	
	Male	Female	Male	Female	Male	Female
Attempted <sup>a</sup>	3	1	11	14	11	8
Did not attempt	28	30	8	13	10	16
Number of attempts/pup $\pm$ SD	1.67 $\pm 1.15$	1.00	1.82 $\pm 1.33$	2.14 $\pm 1.56$	2.00 $\pm 1.34$	2.00 $\pm 2.14$

<sup>a</sup>Yearly *P*-values obtained from a CBET test (Rice 1988) for those which attempted vs. did not attempt non-filial sucking showed no significant sex differences in any year at  $P < 0.05$ . Mann-Whitney *U*-tests revealed no differences between male and female pups in the number of attempts per pup per year (given as  $x \pm SD$ )

**Fig. 2** Resting metabolism for 39 free-ranging California sea lion pups approximately 3–5 weeks of age. A difference in metabolic rate between sexes with the effects of holding time (HT) removed was significant ( $P = 0.045$ ). *Open squares* denote female pups, *solid diamonds* denote male pups



Male pups were no more likely than female pups to attempt to obtain milk from females other than their mother (non-filial sucking) at least once, nor were they more likely to attempt non-filial sucking more frequently (Table 3). There was also no sex difference in the number or duration of successful non-filial sucking (defined as contacting the female's nipple for at least 1 s, Mann-Whitney  $U$ -test,  $P > 0.05$ ). For all 3 years combined, there were only ten successful attempts, with the mean duration for male pups 47.67 s ( $n = 6$ ,  $SD = 66.54$ ) and the mean duration for females 702.5 s ( $n = 4$ ,  $SD = 998.61$ ). The high mean for female pups was due to a 36-min non-filial sucking episode by one pup.

#### Pup physiology

A previous analysis of the first measurement period of resting metabolic rate (RMR), taken between 15.8 and 26.0°C, indicated no differences between male and female pups when mass was controlled ( $n = 39$ ,  $r = 0.42$ ,  $P_{\text{one-tailed}} = 0.10$ ,  $\bar{x} = 0.780 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ,  $SD = 0.063$ , Thompson et al. 1987). However, when mass was not controlled, there was a significant difference between sexes ( $t = -2.31$ ,  $P_{\text{one-tailed}} = 0.013$ , males:  $\bar{x} = 0.7571 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ,  $SD = 0.060$ , females:  $\bar{x} = 0.8011 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$ ,  $SD = 0.059$ ). Also, for all first measurements the rectal temperatures of male pups taken upon removal from the metabolic chamber was significantly lower than that for female pups (females:  $\bar{x} = 37.945^\circ\text{C}$ ,  $SD = 0.502$ ,  $n = 20$ ; males:  $\bar{x} = 37.623$ ,  $SD = 0.437$ ,  $n = 19$ ;  $t = 2.12$ ,  $P_{\text{one-tailed}} = 0.02$ ).

Pups may have been below their thermoneutral zone at metabolic measurements taken below 19°C (Thompson et al. 1987). At temperatures above 19°C, there is a negative correlation between the amount of time pups were held in pet kennels after capture and prior to measurement (i.e., holding time) and RMR ( $r = -0.26$ ,  $P = 0.05$ ). This may have occurred because pups tended to calm down with increased exposure to humans and handling. An analysis of covariance with the effects of holding time and mass removed gave a significantly lower metabolic rate for male pups (Fig. 2,  $t = 1.75$ ,  $P_{\text{sex}} = 0.045$ ). Males also had a lower rate when the effects of holding time and metabolic body size (mass<sup>0.83</sup>) had been controlled in an analysis of covariance ( $t = 1.75$ ,  $P_{\text{sex}} = 0.044$ ).

#### Discussion

Weights of pups measured within their first week of life indicate that sexual size dimorphism begins prenatally in this species, as it does with many otariids (Costa and Gentry 1986; Trillmich 1986; Costa et al. 1988; Cappozzo et al. 1991). This size advantage of males was present in all 4 years studied, despite a strong El Niño which affected many aspects of maternal behavior in 1983 and 1984 (Ono et al. 1987; Boness et al. 1991; Iverson et al. 1991; Heath et al. 1991). The male:female size ratio in neonates is small (1.2:1) compared to that in adults (4:1).

The male size advantage was maintained to at least 2 months postpartum, and in fact was enhanced over this period. This is evident in that the growth rate of male pups was greater than that of females, regardless of their initial size. Thus, given a male and female pup born at the same size, the male would grow faster. Male pups must, therefore, receive a greater energy input, assimilate the energy more efficiently, or conserve energy for growth through behavioral or physiological means, or some combination of these.

### Maternal effects

There is both a theoretical as well as empirical basis on which to expect that female size may influence maternal investment. Parturient female *Zalophus* vary widely in size and female otariids are thought to grow continuously throughout their reproductive years (Payne 1979; Costa et al. 1988). Thus, larger females are most likely older and more experienced. Larger females also have a greater mass from which to draw nourishment for their pups. Larger size in pinnipeds may be correlated with the ability to dive deeper (Costa 1991). If large size is a measure of condition or ability, then according to Trivers and Willard (1973), we would expect larger females to be in better condition and have more male pups.

We did not find that female size influenced pup sex ratio or estimates of prenatal investment as predicted. However, larger female size was positively correlated with pup growth for both sexes, indicating that larger females did provide more nutrients to their pups (by investing more body stores or by being more efficient foragers), or that fast growth and large size are heritable characteristics. It is possible that body size is not a good indicator of female condition or energy stores. One should ideally have information on body composition since two females of equal mass may differ considerably in their proportion of body fat to lean mass (e.g., Bowen et al. 1992a). Although no direct measurements of female condition were taken during the 1982–1983 El Niño, we do have indirect evidence that female condition may be correlated with pup sex. Given the large scale decline in prey availability and other measures of female performance (Ono et al. 1987; Arntz et al. 1991; Feldkamp et al. 1991; Costa et al. 1991; Heath et al. 1991) we might assume that females were on average in poorer condition than in “normal” years. During the 1982–1983 El Niño, there was a decline in the proportion of male pups born (Ono and Boness 1991) and pup growth rates were depressed, although birthweights were not (Boness et al. 1991), indicating that female condition may affect pup sex ratio and growth. It should be noted that the 2 years for which we have data on relative female size were years affected by this severe El Niño (1983 and 1984; Ono et al. 1987).

The fact that relative female size was not significantly related to the initial size of pups (assumed to reflect prenatal investment), and that perinatal pup size did not vary significantly between years given the strong El Niño in 1983, may suggest that pup birth mass is somehow relatively tightly controlled, so that pups are at an optimum mass for survival at birth (Ono et al. 1987; Boness et al. 1991). It is possible that pups drained their mothers' nutrient supply more prenatally during the food poor year to get to that optimum size. This is supported by the finding that females departed on their first postpartum feeding trip earlier during the El Niño year, perhaps reflecting a diminished nutritional state at parturition exacerbated by a week of fasting and lactation (Ono et al. 1987). Another explanation is that the added energy drain of pregnancy is not sufficient to tax female resources while they have full time to forage before parturition. Boyd and McCann (1989) estimated that the metabolic costs for fetal growth and maintenance in *Arctocephalus gazella* are small compared to the metabolic costs of the mother during gestation. Finally, between-year differences in the age and size structure of the female population could have negated any interannual difference in the birth mass of pups, i.e. if younger females did not pup during the El Niño year, then the population would have been primarily composed of larger females (I. Boyd, personal communication). However, there was no interannual difference in mass of lactating female *Z. californianus* measured on San Miguel Island during 1983 and 1984 (Costa et al. 1991).

Relative female size was positively correlated to pup mass gain for both sexes, i.e., larger females were able to provide more energy to their pups, even if the pups were not larger at birth. This relationship may reflect differences in female foraging capabilities rather than a larger draw from body stores. We would expect large mothers to invest even more in male pups, so that the slope for males should be greater than that for females. In 1984, the slope for males was higher, but not significantly ( $P = 0.08$ , Fig. 1). In Antarctic fur seals (*Arctocephalus gazella*), maternal mass is positively correlated with pup birth mass, although two studies conducted on the same island, but in different years, contradict each other with respect to the ability of maternal mass to explain the variation in male and female pup mass (Costa et al. 1988; Boyd and McCann 1989). Neither of these studies looked at the effects of maternal mass on pup growth rate.

The second hypothesis we examined concerning differential maternal investment was that females of male pups should spend more time at sea feeding to provide the additional resources required for enhanced growth. Feeding trips for mothers of male pups were significantly longer only in 1985, and therefore cannot explain observed growth differences between male and female pups in other years. Goldsworthy (1992) showed

that the difference between foraging trip length increased during lactation for Antarctic fur seal mothers with male versus female pups, suggesting that the difference is a response to pup energy demand, as male pups grow faster than female pups. The interesting question is whether milk production is based on pup sex or pup size.

We examined whether females produced more milk for male pups than for female pups, and found that they did produce more milk for male pups, but when body size was taken into account, the difference was no longer significant. This seems to indicate that male pups received more milk because they were larger, not because they were male, and further supports the suggestion of Goldsworthy (1992) that females are responding to the greater energy demand of the initially larger male pups. Large female pups received the same amount of milk as males of the same size. This relationship held true when metabolic body size was considered. That is, when the theoretical requirements per body size are taken into account, pups are getting what they need based on size, not sex.

There is little evidence for sex specific increases in intakes in other species. Published data on fur seals (*Callorhinus ursinus*, Costa and Gentry 1986), elephant seals (*Mirounga angustirostris*, Ortiz et al. 1984; Kretzmann et al. 1993), reindeer and caribou (McEwen and Whitehead 1971) have shown no significant differences between male and female young when intake is calculated per metabolic body size ( $\text{mass}^{0.83}$ ). In fact, for elephant seals, female young receive significantly more milk per metabolic body size ( $n = 5$ ,  $t = 3.35$ ,  $P < 0.05$  using data from Ortiz et al. 1984; Kretzmann et al. (1993) found the same relationship for their complete data set, and no difference when only 5-year-old mothers were considered). Although Reiter et al. (1978) found that male northern elephant seal pups nursed 1 day longer than females (the assumption being that they got more milk), a later study by Kretzmann et al. (1993) found no differences in lactation length for mothers of male and female pups.

The small number of milk samples collected from female sea lions during any one stage of lactation precluded the determination of differing composition for male versus female pups. The variance in composition between samples taken from different females was similar to the variance between samples taken sequentially or from different teats of the same female (O.T. Oftedal, S.J. Iverson, D.J. Boness, unpublished work). From this we assume that there is no difference in milk composition between mothers with male and female pups. The possibility that females produce richer milk for male pups is not totally out of the question. We know that some species of pinnipeds produce milk with a higher per volume lipid content than others (Oftedal et al. 1987 a, b). Kretzmann et al. (1991) found high vari-

ability in lipid content of Australian sea lion milk from females with pups of similar ages. They also found successive samples from the same individual to vary more than 26% in lipid content between samples taken within a week of each other. Trillmich (1990) has also shown that variation in milk fat content can occur within a species. Female Galapagos fur seals (*Arctocephalus galapagoensis*) with longer feeding trips had richer milk than those with shorter feeding trips. Riedman and Ortiz (1979) also found variation between females in milk collected from northern elephant seals.

In short, our evidence for enhanced maternal investment toward male pups suggests that this occurs primarily in the form of prenatal investment, so that males are larger at birth than female pups. Females then appear to meet the greater energy demands of the larger male pups by producing more milk than they would for the smaller female pups. Whether this increase in milk production leads to a loss of future fitness by the mother, and thereby constitutes a difference in maternal investment *sensu* Trivers-Willard is unknown. We do not have data on subsequent reproductive success of the females in this study.

#### Pup behavior and physiology

Since male pups do not receive more milk than females per unit mass, but grow faster despite this, it appears that another factor may be contributing to enhanced male growth. Male pups do not seem to allocate more energy to growth by participating less in energetically expensive daily activities, nor do they generally spend more time suckling than female pups. Studies of other otariid species also have found no differences in the amount of time spent suckling by male and female pups (Higgins et al. 1988; Trillmich 1986; Cappozzo et al. 1991; Macy 1982). It remains to be seen if male pups actually use less energy in performing specific behaviors. Costa and Gentry (1986) found a significantly lower overall energy expenditure by male northern fur seal pups.

Our data suggest that male pups may have a lower resting metabolic rate than females. This factor alone could account for a relatively large energetic savings, and a substantial portion of the difference in growth rate given that other necessary nutrients were provided in sufficient quantity.

Another indication that there may be some differences in resting metabolic rate was that females had higher body (rectal) temperatures than male pups. Body temperature and metabolic rate are positively correlated (Schmidt-Nielsen 1975). Differences in body composition could also partially explain lower mass-specific metabolic rates in males. If male pups had a larger proportion of their weight composed of adipose rather than lean mass, their mass-specific metabolic rate should be lower.

It has long been known that digestive and absorptive efficiency can vary with physiological state and age. For instance, pregnant women are capable of greater absorption of some nutrients, and neonates are capable of higher synthesis and storage of ingested proteins than adults (Guyton 1991). Oftedal et al. (1987) found no differences in efficiency of energy assimilation between male and female California sea lion pups. However, there are two confounding factors in their data set that may have obscured any differences: (1) male pups did not grow faster than females in their sample, and (2) the bulk of the data was obtained during a severe El Niño. If pups were not getting enough milk during the El Niño years, then it might be expected that pups of both sexes would be at maximum absorptive efficiency. Kretzmann et al. (1993) did not find a significant difference when testing to determine if male elephant seal pups had a higher efficiency in converting milk into mass gain.

It appears, then, that both differential maternal investment *and* sex differences in pup energy allocation may contribute to larger male pups during their first two months of life. We can only assume that this difference is maintained as pups become older. Male pups start out larger, and as a consequence receive more milk from their mothers. However, the hypothesis that females invest more resources postnatally in males *because* they are male (Trivers and Willard 1973; Maynard Smith 1980) is not substantiated. Females appear to expend more postnatal effort on male pups because male pups are larger. Male pups may also contribute to their faster growth by maintaining a lower metabolic rate. If they do have a slower metabolism and lower body temperature, then the question arises as to whether there is a cost or tradeoff. Why wouldn't female pups also grow as quickly as possible, especially if there is any correlation between pup size and subsequent survival? Possible costs are that males may be more easily chilled during cold weather, since young pups do not thermoregulate well, and males may also be more susceptible to infection due to their lowered body temperature.

Viewing it from the mother's perspective, a female's prenatal and early postnatal investment will be higher if she has a male pup. However, in this species there is some evidence that mothers may tend to nurse their female yearlings for a longer period of time, probably due to the fact that females tend to stay near the natal islands while male yearlings migrate north (Francis and Heath 1991). Given that mothers did not appear to disperse resources differentially according to pup sex, and that in normal years there was reasonable opportunity for them to increase foraging effort (i.e., there were no rigid constraints upon total investment), then the lack of observed differences may indicate that differential maternal investment does not provide enough increased fitness benefits for it to evolve. This would suggest that

pup mediated factors, both during the period of maternal care and postweaning, are more important in determining adult sexual dimorphism and future reproductive success.

**Acknowledgements** This study could not have been accomplished without the dedication of the many research assistants who worked out at San Nicolas Island. Special thanks go to M. Caspers, P. Frumhoff, E. Gimble, J. Griffen, C. Halbert, L. Osborn, W. Price, W. Rice, M. Schenker, J. Whittington, and Y. Yount. L. Dabek and S. Pereira demonstrated unusual perseverance by spending several seasons in the field, L. Dabek also assisted in data analysis. Logistic support was generously supplied by the Pacific Missile Test Center and Naval Air Station at Point Mugu and on San Nicolas Island; we are especially indebted to R. Dow and G. Giffen. O. Oftedal and S. Iverson were also intimately involved in this study and we thank them for their input and companionship in the field. We also thank S. Thompson for his work on the metabolic study. W. Rice provided statistical consultation. The manuscript was improved by helpful comments from I. Boyd, F. Trillmich, M. Kretzmann and B. Holland. Special thanks to F. Trillmich for his ideas on maternal investment theory.

## References

- Alexander RD, Hoogland JL, Howard RD, Noonan KM, Sherman PW (1979) Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates, and humans. In: Chagnon NA, Irons W (eds) *Evolutionary biology and human sexual behavior: an anthropological perspective*. Duxbury, North Scituate, pp 402–435
- Arntz W, Pearcy WG, Trillmich F (1991) Biological consequences of the 1982–83 EL Niño in the Eastern Pacific. In: Trillmich F, Ono KA (eds) *Pinnipeds and El Niño: responses to environmental stress*. Springer, Berlin Heidelberg New York, pp 22–42
- Boness DJ (1991) Determinants of mating systems in the Otariidae (Pinnipedia). In: Renoof D (ed) *Behaviour of pinnipeds*. Chapman and Hall, London, pp 1–44
- Boness DJ, Oftedal OT, Ono KA (1991) The effect of El Niño on pup development in the California sea lion (*Zalophus californianus*). I. Early postnatal growth. In: Trillmich F, Ono KA (eds) *Pinnipeds and El Niño: responses to environmental stress*. Springer, Berlin Heidelberg New York, pp 173–179
- Bowen WD, Oftedal OT, Boness DJ (1992a) Mass and energy transfer during lactation in a small phocid, the Harbor Seal (*Phoca vitulina*). *Physiol Zool* 65:844–866
- Bowen WD, Stobo WT, Smith SJ (1992b) Mass changes of grey seal *Halichoerus grypus* pups on Sable Island: differential maternal investment reconsidered. *J Zool Lond* 227:607–622
- Boyd IL, McCann TS (1989) Pre-natal investment in reproduction by female Antarctic fur seals. *Behav Ecol Sociobiol* 24:377–385
- Boyd IL, Duck CD (1991) Mass changes and metabolism in territorial male Antarctic fur seals (*Arctocephalus gazella*). *Physiol Zool* 64:375–392
- Brown JL (1975) *The evolution of behavior*. Norton, New York
- Byers JA, Moodie JD (1990) Sex-specific maternal investment in pronghorn; the question of a limit on differential provisioning in ungulates. *Behav Ecol Sociobiol* 26:157–164
- Cappozzo HL, Campagna C, Monserrat J (1991) Sexual dimorphism in newborn southern sea lions. *Marine Mamm Sci* 7:385–394
- Clinton W (1990) *Sexual-selection and the life-history of male northern elephant seals*. PhD dissertation, University of California, Santa Cruz
- Clutton-Brock TH, Albon SD (1982) Parental investment in male and female offspring in mammals. In: King's College

- Sociobiology Group (ed) Current problems in sociobiology. Cambridge University Press, Cambridge, pp 223–247
- Clutton-Brock TH, Albon SD, Guinness FE (1981) Parental investment in male and female offspring in polygynous mammals. *Nature* 289:487–489
- Clutton-Brock TH, Guinness FE, Albon SD (1982) Red deer: behavior and ecology of two sexes. University of Chicago Press, Chicago
- Costa DP (1991) Reproductive and foraging energetics of pinnipeds: Implications for life history patterns. In: Renouf D (ed) Behaviour of pinnipeds. Chapman and Hall, London, pp 300–344
- Costa DP, Gentry RL (1986) Free-ranging energetics of northern fur seals. In: Gentry RL, Kooyman GL (eds) Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, pp 79–101
- Costa DP, Trillmich F, Croxall JP (1988) Intraspecific allometry of neonatal size in the Antarctic fur seal (*Arctocephalus gazella*). *Behav Ecol Sociobiol* 22:361–364
- Costa DP, Antonelis GA, De Long RL (1991) Effects of El Niño on the foraging energetics of the California sea lion. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño: responses to environmental stress. Springer, Berlin Heidelberg New York, pp 156–165
- Espmark Y (1964) Studies in dominance-subordination relationship in a group of semi-domestic reindeer (*Rangifer tarandus* L.). *Anim Behav* 12:420–425
- Feldkamp SD, De Long RL, Antonelis GA (1991) Effects of El Niño (1983) on the foraging patterns of California sea lions (*Zalophus californianus*) near San Miguel Island, California. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño: responses to environmental stress. Springer, Berlin Heidelberg New York, pp 146–155
- Francis JM, Heath CB (1991) The effects of El Niño on the frequency and sex ratio of suckling yearlings in the California sea lion. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño: responses to environmental stress. Springer, Berlin Heidelberg New York, pp 193–201
- Gentry RL (1970) Social behavior of the Steller sea lion. PhD dissertation, University of California, Santa Cruz
- Goldsworthy SD (1992) Maternal care in three species of southern fur seal (*Arctocephalus* spp.). PhD dissertation, Monash University, Melbourne
- Gosling LM, Baker SJ, Wright KMH (1984) Differential investment by female coypus (*Myocastor coypus*) during lactation. *Symp Zool Soc Lond* 51:273–300
- Green WCH, Berger J (1990) Maternal investment in sons and daughters: problems of methodology. *Behav Ecol Sociobiol* 27:99–102
- Guyton AC (1991) Textbook of medical physiology, 8th edn. Saunders, Philadelphia
- Haley MP (1994) Resource-holding power asymmetries, the prior residence effect, and reproductive payoffs in male northern elephant seal fights. *Behav Ecol Sociobiol* 34:427–434
- Haley MP, Deutch CJ, LeBoeuf BJ (1994) Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Anim Behav* 48:1249–1260
- Heath CB, Ono KA, Boness DJ, Francis JM (1991) The influence of El Niño on female attendance patterns in the California sea lion. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño: responses to environmental stress. Springer, Berlin Heidelberg New York, pp 138–145
- Higgins LV, Costa DP, Huntley AC, LeBoeuf BJ (1988) Behavioral and physiological measurements of maternal investment in the Steller sea lion, *Eumetopias jubatus*. *Mar Mamm Sci* 4:44–58
- Iverson SJ, Oftedal OT, Boness DJ (1991) The effect of El Niño on pup development in the California sea lion (*Zalophus californianus*). I. Milk intake. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño: responses to environmental stress. Springer, Berlin Heidelberg New York, pp 180–184
- Kovacs KM, Lavigne DM (1986a) Maternal investment and neonatal growth in phocid seals. *J Anim Ecol* 55:1035–1051
- Kovacs KM, Lavigne DM (1986b) Growth of grey seal (*Halichoerus grypus*) neonates: differential maternal investment in the sexes. *Can J Zool* 64:1937–1943
- Kretzmann MB, Costa DP, Higgins LV, Needham DJ (1991) Milk composition of Australian sea lions, *Neophoca cinerea*: variability in lipid content. *Can J Zool* 69:2556–2561
- Kretzmann MB, Costa DP, LeBoeuf BJ (1993) Maternal energy investment in elephant seal pups: evidence for sexual equality? *Am Nat* 141:466–480
- Lee PC, Moss CJ (1986) Early maternal investment in male and female African elephant calves. *Behav Ecol Sociobiol* 18:353–361
- Lluch Belda D (1969) El lobo marino de California *Zalophus californianus californianus* (Lesson 1828) Allen 1880. Observaciones sobre su ecología y explotación. Instituto Mexicano de Recurso Renovables, AC Mexico, DF, pp 69
- Macy SK (1982) Mother-pup interactions in the Northern fur seal. PhD Dissertation, University of Washington
- Maynard Smith J (1980) A new theory of sexual investment. *Behav Ecol Sociobiol* 7:247–251
- McEwan EH, Whitehead PE (1971) Measurement of the milk intake of reindeer and caribou calves using tritiated water. *Can J Zool* 49:443–447
- Oftedal OT, Iverson SJ (1987) Hydrogen isotope methodology for measurement of milk intake and energetics of growth in suckling pinnipeds. In: Huntley AC, Costa DP, Worthy GA, Castellani MA (eds) Approaches to marine mammal energetics (Special publication 1). Society for Marine Mammalogy, Allen Press, Lawrence, KS, pp 67–96
- Oftedal OT, Iverson SJ, Boness DJ (1987a) Milk and energy intakes of suckling California sea lion *Zalophus californianus* pups in relation to sex, growth, and predicted maintenance requirements. *Physiol Zool* 60:560–575
- Oftedal OT, Boness DJ, Tedman RA (1987b) The behavior, physiology, and anatomy of lactation in the pinnipedia. *Current Mamm* 1:175–245
- Ono KA, Boness DJ (1991) The influence of El Niño on mother-pup behavior, pup ontogeny, and sex ratios in the California sea lion. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño: responses to environmental stress. Springer, Berlin Heidelberg New York, pp 185–192
- Ono KA, Boness DJ, Oftedal OT (1987) The effect of a natural environmental disturbance on maternal investment and pup behavior in the California sea lion. *Behav Ecol Sociobiol* 21:109–118
- Ortiz CL, LeBoeuf BJ, Costa D (1984) Milk intake of elephant seal pups: an index of parental investment. *Am Nat* 124:416–422
- Payne MR (1979) Growth in the Antarctic fur seal *Arctocephalus gazella*. *J Zool Lond* 187:1–20
- Peterson RS, Bartholomew GA (1967) The natural history and behavior of the California sea lion (Special Publication 1). American Society of Mammalogists, pp 79
- Reiter J, Stinson NL, LeBoeuf BJ (1978) Northern elephant seal development: the transition from weaning to nutritional independence. *Behav Ecol Sociobiol* 3:337–367
- Rice WR (1988) A new probability model for determining exact *P*-values for  $2 \times 2$  contingency tables when comparing binomial proportions. *Biometrics* 44:1–22
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43:223–225
- Riedman M, Ortiz CL (1979) Changes in milk composition during lactation in the northern elephant seal. *Physiol Zool* 52:240–249
- Schmidt-Nielsen K (1975) Animal physiology: adaptation and environment. Cambridge University Press, New York
- Thompson SD, Ono KA, Oftedal OT, Boness DJ (1987) Thermoregulation and resting metabolic rate of California sea lion (*Zalophus californianus*) pups. *Physiol Zool* 60:730–736

- Trillmich F (1986) Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. Behav Ecol Sociobiol 19:157–164
- Trillmich F (1990) The behavioral ecology of maternal effort in fur seals and sea lions. Behaviour 114:3–20
- Trivers RL, Willard DE (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92
- Wolff JO (1988) Maternal investment and sex ratio adjustment in American bison calves. Behav Ecol Sociobiol 23:127–133

Communicated by F. Trillmich