

Clive R. McMahon · Corey J. A. Bradshaw

Harem choice and breeding experience of female southern elephant seals influence offspring survival

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Abstract Female mammals can increase their lifetime fitness through modification of investment potential and by providing better rearing environments with improved breeding experience. We examined the relationships between reproductive fitness and the behavioural decisions that female southern elephant seals (*Mirounga leonina*) made during the breeding season. We examined whether mother age and breeding experience influenced reproductive success (measured as 1st-year survival probability), and whether there was a change in the choice of harem size with increasing age. Pups produced by young mothers had lower 1st-year survival probability than pups produced by older mothers. A significant increase in mean female mass with age required an analysis of both these effects on offspring survival. There was a significant positive effect of both female age and mass, and the interaction between the two, on 1st-year pup survival. The proportion of young mothers (<5 years old) decreased and the proportion of older mothers (>6 years old) increased with increasing harem size (harems surveyed from 1997 to 2001). Females chose larger harems in which to breed as they aged. Females demonstrated fidelity to breeding areas among successive breeding seasons, with older females displaying greater

breeding-site fidelity than younger females. The mean number of previous breeding attempts per female within a harem (breeding experience) increased significantly with increasing harem size. Breeding females returned to breed later in the breeding season as they aged—we hypothesize that young, subordinate females gain a priority advantage by returning earlier. These results lend support to the hypothesis that there are fitness advantages, in terms of offspring survival, that are conferred to females that breed in successively larger harems with age. Potential mechanisms that select for females to improve their breeding conditions include improved mate selection and the avoidance of conspecific harassment in harems.

Keywords Reproductive success · *Mirounga leonina* · Pup survival · Harem size · Harem density

Introduction

Female mammals can improve their reproductive fitness through a genetic contribution and other means, such as investment trade-offs and behavioural “decisions” (Arnold 1994). Some of the non-genetic determinants found to affect reproductive fitness include parent age and previous breeding experience (Clutton-Brock 1988; Reiter and Le Boeuf 1991; Hepp and Kennamer 1993; Lunn et al. 1994; Forslund and Part 1995; Ellis et al. 2000), body size and body condition (Hastings and Testa 1998; Mellish et al. 1999a; Pomeroy et al. 1999; Bowen et al. 2001a; Hall et al. 2001), and dominance status or rank (Clutton-Brock et al. 1984; Côté and Festa-Bianchet 2001). Increased breeding experience can improve reproductive success via several mechanisms (reviewed by Stearns 1992), including improved resource provisioning prior to birth (pre-partum expenditure) and during the rearing of offspring, selection of more competitive mates leading to increased offspring fitness, and the provision of more suitable rearing environments (e.g. placement with colonies, nest sites, exposure). In the case of polygynous mammals, where the mother provides the majority of care

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C. J. A. Bradshaw (✉)
Antarctic Wildlife Research Unit, School of Zoology,
University of Tasmania,
Private Bag 05, Hobart, Tasmania 7001, Australia
e-mail: corey.bradshaw@utas.edu.au
Tel.: +61-3-62262644
Fax: +61-3-62262745

C. R. McMahon
Australian Antarctic Division,
Channel Highway, Kingston, Tasmania 7050, Australia

Present address:

C. R. McMahon, Antarctic Wildlife Research Unit,
School of Zoology,
University of Tasmania,
Private Bag 05, Hobart, Tasmania 7001, Australia

and resources to the offspring, choices made prior to and during reproductive events can have profound effects on the survival of the offspring (Arnold 1994; Cameron et al. 2000).

Few mammalian breeding systems are more extreme than that of elephant seals (*Mirounga* spp.), and this taxon provides many advantages for studying variation in reproductive success. Social interactions ashore are less complex because they are not influenced by foraging behaviour, and reproductive expenditure through, the transfer of fat to offspring, can be measured easily (Hindell and Slip 1997). Moreover, elephant seals haul out at predictable sites and can be marked easily and thereby individually recognized. Previously, Reiter et al. (1981) found that older northern elephant seal (*Mirounga angustirostris*) females were reproductively more successful than younger conspecifics, presumably because older females were larger, were reproductively more experienced, had higher social rank and were more likely to mate with higher-ranked males. Thus, younger females appear to increase their reproductive success either by moving to smaller harems, establishing new breeding colonies, or by delaying the age at primiparity in situations of high breeding density (Reiter et al. 1981; Reiter and Le Boeuf 1991).

Southern elephant seals (*M. leonina*), like *M. angustirostris*, are capital breeders (Boyd 2000) in which the males do not contribute to the growth or rearing of offspring. Pups are reared and nursed exclusively by females during a short, 24-day lactation period (Laws 1953). Females fast during this time and are reliant on stored resources accumulated during the preceding winter's foraging trip for maintenance and milk production (Fedak et al. 1996). The amount of resources a mother has stored during this time and the success with which she rears her pup determine the probability the pup survives its 1st year (McMahon et al. 2000b), and hence the mother's long-term reproductive output (Arnbom et al. 1997).

However, many factors affect the acquisition, storage and transfer of resources between a mother seal and her pup. These include environmental factors that influence ocean productivity and hence the availability of food, the ability of a mother to gather these resources, and the age- and size-specific physical and physiological processes required to store and deliver these resources (Fedak et al. 1996; Arnbom et al. 1997; Mellish et al. 1999b; Ellis et al. 2000; Bowen et al. 2001a, 2001b). Furthermore, mothers can attempt to minimize the amount of disturbance and conspecific harassment within the nursing environment, thereby reducing the incidence of mother-pup separation and pup death (Christensen and Le Boeuf 1978; McCann 1981, 1982; Riedman and Le Boeuf 1982; Boness et al. 1995; Galimberti et al. 2000b, 2000c). Indeed, where and when a female chooses to rear her pup will influence pup size and safety, and these factors are particularly pertinent to the immediate (from birth to weaning; Boyd and McCann 1989; Lunn et al. 1994; Pistorius et al. 2001) and

longer term (to age one McMahon et al. 2000b; Hall et al. 2001) survival of pups.

Thus, examining how female elephant seals maximize their reproductive output through behavioural choices made prior to weaning is an important precursor to the understanding of variation in lifetime reproductive success (Trivers 1972). Recently, Pistorius et al. (2001) studied the pre- and immediate post-weaning mortality of elephant seals in a small population at Marion Island (46°54'S, 37°45'E), and the possible factors related to this mortality. They found that: (1) early mortality was not related to overall population size, but that mortality was higher in smaller versus larger harems, (2) this mortality was a consequence of small harems being dominated and controlled by young, inexperienced harem masters that crushed and killed pups, (3) there was a higher proportion of primiparous females in smaller harems, and (4) that the primiparous females were not as successful as older mothers in rearing and provisioning pups.

Here we expand on previous behavioural research within the genus *Mirounga* (Reiter et al. 1981; McCann 1982; Reiter and Le Boeuf 1991; Baldi et al. 1996; Galimberti et al. 2000a, 2000b, 2000c; Pistorius et al. 2001) to describe the age structure within breeding harems and to examine the effects of mother age, breeding experience and size relative to 1st-year survival of their offspring. We test the hypotheses that: (1) there is a change in age composition of individuals within a harem relative to harem size, and we predict that the proportion of young mothers decreases with increasing harem size; (2) there is a change in the choice of harem size with female age (and experience), and we predict that individual females haul out in progressively larger harems as they age; (3) that arrival time at the colony is dependent on age; here we predict that younger, inexperienced mothers avoid peak haul-out times during the breeding season to increase the chances of maintaining a position within a large harem, and (4) mother mass and age affect breeding success through the modification of offspring survival; here, we predict that larger, older and more experienced mothers can increase the pre- and post-weaning survival probability of their offspring during the 1st year of life.

Methods

Individual capture and marking

In October and November of each year starting in 1993 and ending in 1999, approximately 2,000 recently weaned southern elephant seal pups were captured on the isthmus of Macquarie Island (54°30'S, 158°50'E). This was done to study the demography of the Macquarie Island population (McMahon et al. 2003). Fifty-millimetre cast-iron cattle brands were used to hot-brand seals on both rear flanks (Chittleborough and Ealey 1951; Carrick and Ingham 1960). A four-character alpha-numeric brand consisting of a letter prefix followed by a three-digit number uniquely identified cohort and individual. In each year, approximately 1,000 of the seals branded were also previously (at birth) tagged with 2 plastic,

4-digit tags (McMahon et al. 1997, 1999). From 1987 to 1992, an additional 659 seals were tagged at weaning.

To assess the effect of mother mass on pup survival, females aged 4–9 were caught immediately post-partum using the techniques described in McMahon et al. (2000a) and Field et al. (2002). Once sedated, individuals were weighed to the nearest kilogramme using a tripod and electronic scales, as described in Hindell and Slip (1997).

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Censuses

Daily censuses of the isthmus were done during the breeding season to determine the presence of branded and tagged female seals, and to count the number of females in each harem (McMahon et al. 1999, 2003). All harems on the isthmus were examined in each year of the study (see Results section for a detailed description of the breeding harems on the isthmus). In a few instances where individuals were unidentifiable by brands alone, we were able to use hind-flipper tags to identify the individual. Flipper tags validated all brand identifications when tags were present. Due to the different number of animals tagged or branded in each year, especially those tagged prior to the commencement of the branding in 1993, the proportions of females seen breeding in 1997, 1998 and 1999 were expressed relative to the number of females in each cohort known to be alive from subsequent resights in years 2000–2002. Here, an animal was known to be alive if it was sighted at least once in that or subsequent years, an approach similar to that used by Crocker et al. (2001).

Harem characteristics

To examine the extent, and to estimate the density (females per unit area) of all harems on the northern isthmus, we plotted the approximate mean extent of the harems surveyed from 1997 to 2001 using ARC/INFO geographic information system (GIS) software. Harem positions were determined with the aid of geographic features identified from topographical, vegetation, substratum and artificial-structures maps provided by the Australian Antarctic Division Data Centre (<http://www.aad.gov.au>).

Analysis

Female age distribution in harems

We hypothesized that the age distribution of females would vary relative to harem size. We chose to analyse three main categories of female age because of insufficient sample sizes for older mother ages (i.e. >8 years). These categories were: (1) females under 5 years of age were termed “young”, (2) 5- and 6-year olds were termed “mid”, and (3) those over 6 years were considered “older” (or “prime” as defined by Reiter et al. 1981). Female southern elephant seals do not begin pupping typically until the age of 4, although there are some records of females pupping as early as age 3 (Hindell 1991; McMahon et al. 2003).

The change in age structure among harems of differing size was examined in two ways. First, a randomized, linear regression (RT V. 2.1; Manly 1997) of the proportion of females in each age class (young, mid, older) was used against the maximum harem size observed during the course of the breeding season from the 5 years studied. To examine variation in harem age structure, harem sizes were split into three separate classes: “small” (<100 females), “medium” (100–300 females) and “large” (>300 females). These categories were chosen because the range of harem sizes over the years of investigation ($n=64$ harem size estimates) demonstrated that only 25% of harems contained >300 females; the mean harem

size was 227.1 females, and the median was 173. Our choice of categories represents a meaningful and simple summary of the range in harem sizes for subsequent frequency analysis (i.e. to reduce the number of cells with no data in contingency tables). A 3×3 G -test of independence (Sokal and Rohlf 1981) was used to test the hypothesis that the number of young and older females was independent of harem size.

We found that pre-partum females arriving at Macquarie Island were often seen in several different harems prior to settling within a particular harem and giving birth. We predicted here that due to aggressive interactions among females within harems, younger, subordinate females would be forced by their older conspecifics to move from a particular harem more often than older, more experienced females. To test this hypothesis, we examined the number of harems in which young and older individuals were resighted during the course of the breeding season for all years studied. All females that were resighted only once within a breeding season were removed from the analysis. Differences among years and age classes were tested using a randomized analysis of variance (Manly 1997).

Longitudinal harem choice

We examined the trends of individual females to choose harems of particular sizes as they aged. We hypothesized that if older females opted for larger harems in which to breed, there should be a tendency for females to choose larger harems in consecutive breeding seasons. All females sighted in 1997 and 1998 were followed through their individual breeding histories to 2001, and harem of choice in each year was noted. If a female chose a larger harem in the year following 1997 or 1998 (i.e. “1st” to “2nd”), then she was deemed to have increased the size of her harem of choice. If the harem of choice in the consecutive breeding season was smaller, she was deemed to have decreased the size of her harem of choice, and if the harem was within ten females (less than the standard error of the maximum number of females ashore during the breeding season, see Results) at maximum size in the consecutive season, she was deemed to have chosen a harem of the “same” size. However, many individuals were not seen in the year following 1997 or 1998, so the harem of choice in the next breeding season for which there was a resight record (i.e. “1st” to “next”) was also noted. We tested departure from the expected proportions if change in harem size was random with respect to the average proportion of harems in each class (i.e. small, medium, large) from 1997 to 2001 using a G -test for goodness of fit. We also tested whether the proportions of females within each class depended on age class (young, mid, older) using a G -test of independence.

Finally, those females for which there were complete resighting records from time of first-known breeding (i.e. 1997 or 1998) to 2001 were examined. For these females that were known to have bred every year, the proportion of harems within the breeding resight record that were identical within the four (1998–2001) or five (1997–2001) breeding seasons in which they had been seen participating were calculated. For example, if a female chose to breed in the same harem in 4 of the 5 breeding seasons she had been seen, the proportion of identical harems was $4/5=0.80$. If an individual changed harems each year, then her proportion was 0.0. We also examined the change in harem size from one season to the next relative to whether or not a female remained in the same harem, and relative to her age.

Female age and breeding experience

In addition to examining age structure within harems of various sizes, data on the observed breeding experience of each female were recorded. For this we examined the females present in the 2001 breeding season, and for these compiled the lifetime number of breeding seasons in which each female was seen breeding (i.e. observed hauled out within a harem on Macquarie Island). The

resulting data were analysed in much the same way as the age-structure data described above. However, we also tested the hypothesis with the 2001 data that breeding experience alone (i.e. the number of observed breeding episodes) was related to harem size. For this, we removed primiparous females with no previous breeding experience because they were necessarily inexperienced, and females older than 8 years, due to lower resight effort in the years prior to 1997. We used a general linear model to test the hypothesis that the breeding experience was not different among harem sizes (small, medium and large), defining harem size as a fixed term in the model.

Female arrival and peak numbers ashore

Daily counts of all females present in the isthmus study area were done from 1997 to 2001. The distribution of these raw counts approximated a Gaussian curve, as described previously by Hindell and Burton (1987). We used the following equation to describe the daily count data (i.e. number of females ashore) for each year:

$$Y = ht \left(e^{\left(\frac{-0.5(x-\mu)}{SD} \right)^2} \right)$$

where ht is the height of the curve (i.e. the maximum number of females counted), μ is the day on which the maximum number of females was counted, and SD is the standard deviation of the number of days that seals were hauled out during the breeding season. The curve of best fit for each year's breeding episode was determined using the least-squares technique described in Hindell and Burton (1987). This curve provided estimates for the day of maximum number of seals present. The derived day was taken to represent the day of maximum numbers ashore. Thus, the number of seals counted in each harem on this day was the number used in our assessment of the relationship between female numbers and harem age-structure.

We hypothesized that inexperienced females would avoid peak haul-out times because of reduced competitive ability. To investigate the time of arrival on shore for both young and old females, the earliest date sighted for each individual female during a particular breeding season was recorded. A general linear model of the form:

$$\text{Julian day} = \text{age} + \text{year} + \text{age} * \text{year} + \text{error}$$

was used to test for the effects of *age* (covariate), year (1997–2001; random term) and the age by year interaction (*age*year*) on the day of arrival (transformed into Julian day to examine trends among years).

We also examined the apparent predictability of maximum harem size based on the observed harem sizes at set time intervals prior to the date of maximum haul out. Using the number of females counted at 1, 2 and 3 weeks prior to the date of maximum harem size per year, we used least-squares linear regression to examine the relative constancy of harem size when most females were hauling out (years combined).

Pup survival relative to female characteristics and harem size

We hypothesized that offspring survival is related to the number of previous breeding events experienced by the mother. Therefore, young (i.e. inexperienced) females should demonstrate lower offspring survival than females with some experience. We examined pre-weaning (i.e. from birth to weaning) relative to mother age, and 1st-year (weaning to age 1) survival relative to mother size and age.

Pre-weaning survival. We examined pre-weaning survival relative to mother age ($n=293$) over all years combined due to a low proportion of pups dying prior to weaning. Here, we designed a randomized contingency analysis analogous to a chi-square good-

ness of fit. Using the age categories defined previously (young, mid and older), we determined the fate of pups over the lactation period and used the overall number of pups surviving in the three classes as an expected survival probability. The probability of rejecting the null hypothesis (no difference in pre-weaning survival among age classes) was estimated by calculating the number of times the sum of the squared difference of the expected versus simulated (10,000 randomizations) distributions was less than or equal to the observed versus expected sum of squared differences. We also repeated the analysis using only the two most-extreme age classes—young and older females. We were unable to test the effect of mother size in combination with age due to small sample sizes.

We also tested whether pre-weaning mortality was related to harem size (i.e. to verify that estimates of post-weaning mortality were not confounded by pre-weaning mortality); we used data from 1998, 1999 and 2000 where the numbers of pups that were tagged as neonates and died prior to weaning were recorded. The number of pups per harem was expressed as a proportion of the number of pups tagged initially per harem. We used a randomized analysis of variance (RT V.2, Manly 1997) to examine whether the proportions varied among years, and then used a randomized linear regression (RT V.2.1, Manly 1997) to test whether the proportions were related to maximum harem size.

Post-weaning survival. To examine 1st-year survival relative to mother characteristics, capture-history matrices were constructed from the resight history of individual seals that had both brands and tags ($n=203$). Multiple resights within a year were treated as a single sighting. These capture matrices were used as input files for the capture-mark-recapture (CMR) program MARK (White and Burnham 1999) to estimate survival and capture probabilities from the resight records of the marked individuals. MARK provides survival (ϕ) and recapture (ρ) estimates under the Cormack-Jolly-Seber (CJS) model (Cormack 1964; Jolly 1965; Seber 1965) and under several models that appear as special cases of the CJS-model (Lebreton et al. 1992).

Individual covariates (mother age) of pup survival were included in the model by expressing the natural logarithm of the probability of survival (i.e. the logit of survival) as a logistic function of the covariates:

$$\text{Logit}(\phi) = \text{intercept} + \beta_{(x)} \left(\frac{x - \bar{x}}{SD_x} \right) - \beta_{(x^2)} - \left(\frac{x^2 - \bar{x}^2}{SD_{x^2}} \right)$$

where $\text{logit}(\phi)$ is the survival estimate of a seal with the covariate x , β is the logit function parameter calculated in MARK for covariate x , and SD is the standard deviation of the covariate x . This model (function) is embedded in the log-likelihood function for survival as in a logistic regression. This model assumes that there is a maximum value for the variable x and that there are some selective penalties associated with the extreme values of x —for example, inexperience of young seals and reproductive senescence in older seals (Schaffer 1974).

Starting from a general model that fits the data, we used the Akaike information criteria (AIC) and ΔAIC scores to select the most parsimonious model(s) (Burnham and Anderson 1998). As a rough guide, Burnham and Anderson (1998) suggested that models with $\Delta\text{AICs} \leq 2$ have substantial support, those with ΔAICs of 4–7 have some support, while those models with $\Delta\text{AICs} > 10$ have no support. The likelihood ratio tests within MARK were used to test specific hypotheses (Lebreton et al. 1992).

Body mass of female southern elephant seals has been reported to increase with age (McLaren 1993; Arnbom et al. 1994); therefore, the changes in post-parturition mass in females from ages 4–9 for which there were mass data were examined. Given that the effect of mother age on offspring survival may be masked by changes in mother mass, the combined effect of mother age and mother mass (post-parturition) was tested on the likelihood of pup survival to 1 year of age. To this end, a simple history for the offspring of known-age females for which mass data were available was constructed, noting whether the pup had survived (1) or was presumed to have died (0) in its 1st year of life. A pup was

presumed to have survived to age 1 if it was sighted at least once in any year after its 1st year of life. Because elephant seals may be alive and not sighted for many years (Hindell 1991), our observations of survival are necessarily conservative and underestimates of the true value. Two measures of female mass were available: (1) direct estimates of body mass from weighing (± 1 kg; $n_{\text{total}}=62$), and (2) relative estimates of female size made at parturition (i.e. large, medium and small, after Campagna et al. 1992; $n_{\text{total}}=292$). Two independent observers assigned females into one of these categories such that a crude, yet functional (Campagna et al. 1992) estimate of size for each individual female was obtained. Because mother mass and age were correlated, we used a logistic regression to partition the variances of the independent variables on pup survival (Freckleton 2002). Here, we tested the effects of maternal mass (mass or size), age (in years) and the interaction between these two terms on the survival of the offspring to age 1 using a model of the form:

$$\text{survival (1) or death (0)} = \text{age} + (\text{mass or size}) \\ + \text{age} * (\text{mass or size})$$

where the independent variables were expressed as covariates. The fit of all five possible models from the saturated model shown above was assessed using AIC weights as described in Lebreton et al. (1992). Significance of model terms was assessed using the Wald statistic, and these were assumed to follow the χ^2 distribution (Milner et al. 1999). For graphical purposes only, the relative ages of mothers were separated into two categories: "inexperienced" (<5 years old) and "experienced" (>5 years old). Also for graphical purposes only, the median mass from those females for which masses were estimated was determined, and the sample was divided into two classes: "small" \leq median mass, and "large" $>$ median mass (see Results).

Results

Description of harems

During the study, approximately 12% ($n=3200$) of the entire Macquarie Island female breeding population ($n=20,300$, Goldsworthy et al. 2001) hauled out to pup and mate on the northern isthmus of the island (Fig. 1; see also Hindell and Burton 1987). The breeding aggregation on the northern isthmus represents the largest aggregation on the entire island; the next largest aggregation occurs at Hurd Point at the southern extreme of the island (approximately 1,600 females). Harems formed on both the eastern (2.5 km long) and western (1.7 km long) beaches of the isthmus, although the average number of harems was higher on the western beach ($n=9$) relative to the eastern beach ($n=7$) during each year of the study (Fig. 1—note that although harems represent discrete aggregations, a few harems coalesce during the peak haul-out periods). This translates to approximately 69% of the isthmus females choosing to breed on the western beach each year. The western beaches are exposed to regular, strong winds and high surf conditions relative to the more sheltered eastern beaches (Carrick et al. 1962; Engelhard et al. 2001). It has been suggested that the western beach provides easier access than the eastern beach because the latter is bound by a rock platform that may hinder access (Carrick et al. 1962).

Harem sizes remained relatively constant from year to year over the course of the study. That is, large harems

tended to remain large, and small harems tended to remain small. Mean harem size (average over 4 years) ranged from 44 females (SD=31) to 748 females (SD=54). Based on approximate estimates of mean harem extent and area, harem density (number of females per unit area) ranged from 3.5 to 21.3 females/100 m²; however, there was no relationship between mean harem density and mean harem size ($P_{20000}=0.467$).

Pooling among years, we found that, on average, young females were resighted in more harems during the course of the breeding season than older females (young: 1.439 ± 0.035 ; older: 1.361 ± 0.036), but the difference was not significant ($P_{20000}=0.118$). There was, however, a significant difference among years for the number of harem resightings (ages pooled; $P_{20000}=0.030$; range: 1.328–1.523 harems). An examination of the means for each year demonstrated that the number of harems in which a young female was seen exceeded that for older females in all years except 1999.

Female age distribution in harems

The possibility that there were inter-annual differences in the proportions of different age cohorts ashore was considered. The proportion of young and older females that bred in years 1997–1999 relative to the number of females known to be alive (from subsequent resighting) was approximately constant over the years examined (G -test of independence: young $G_2=2.48$, $P=0.290$; older $G_2=1.20$, $P=0.549$; Table 1); however, there was a significant dependency between the proportion of mid-age females and year due to a small increase in this proportion in 1999 ($G_2=7.29$, $P=0.026$; Table 1). The total number of females breeding on the isthmus of the island relative to those known to be alive ranged from 0.182 to 0.280 from 1997 to 1999 (Table 1).

Our results on harem age structure confirmed those of Pistorius et al. (2001), but over a much greater range in harem sizes. The proportion of young mothers decreased with increasing harem size (Fig. 2a; randomized linear regression: $P_{20000}=0.025$), albeit the amount of variation described by harem size was low. There was no relationship between harem size and the proportion of mid-age mothers (Fig. 2b; randomized linear regression: $P_{20000}=0.658$); however, the proportion of older mothers increased with increasing harem size (Fig. 2c; randomized linear regression: $P_{20000}=0.011$). Likewise, the G -tests of independence testing for the numbers of young, mid-age and older animals relative to harem size demonstrated similar results. We rejected the null hypotheses of these proportions being independent of harem size for all years except 1997 and 1998 (Table 2), possibly due to low sample sizes of older females in the earlier years of the marking program. The observed increase in the proportion of older females, especially in 2000 and 2001, reflects the aging of the marked component of the population.

Fig. 1 Map of the northern isthmus of Macquarie Island and the approximate average positions of harems on the eastern and western beaches from 1997 to 2001

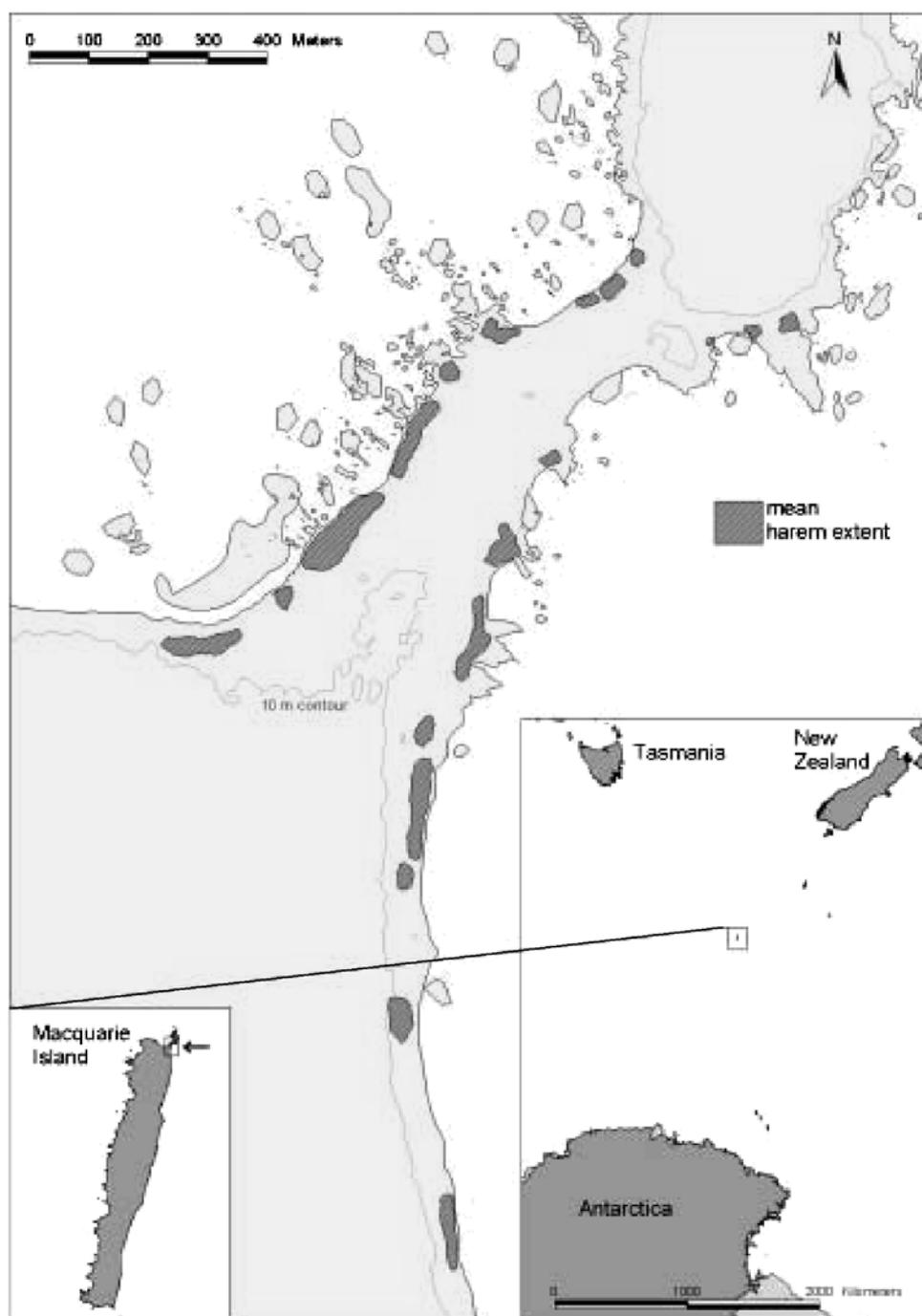


Table 1 Number of marked animals (branded or tagged) seen breeding on the isthmus of Macquarie Island during a particular breeding season and the number known to be alive at that time (from subsequent re-sighting). Only years 1997–1999 are shown due to insufficient time elapsed to assess the numbers alive in 2000 and 2001

Year	Maternal age	Originally marked	Breeding	Known alive	Proportion breeding
1997	Young	1927	42	930	0.045
	Mid	228	4	68	0.059
	Older	431	9	72	0.125
	Total				0.229
1998	Young	967	26	410	0.063
	Mid	1017	20	406	0.049
	Older	602	6	85	0.070
	Total				0.182
1999	Young	977	24	379	0.071
	Mid	1927	64	664	0.096
	Older	659	9	80	0.113
	Total				0.280

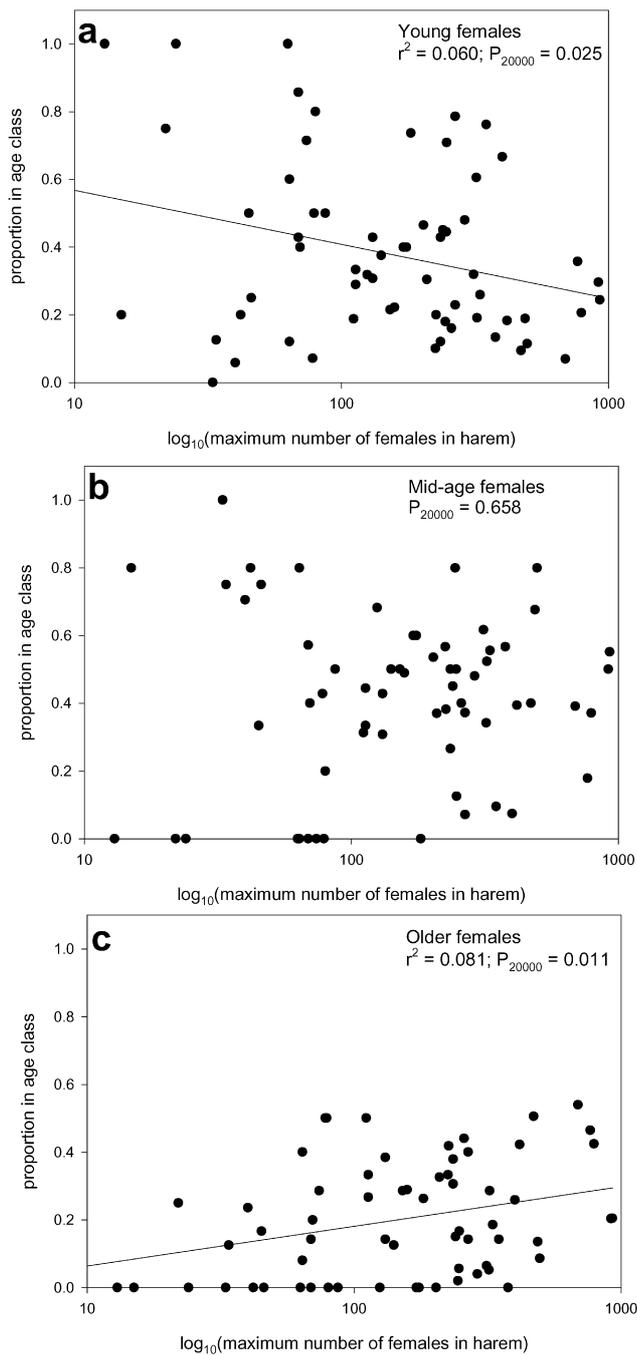


Fig. 2a–c Relationship between the proportion of marked animals termed **a** “young”, **b** “mid”, and **c** “older” relative to harem size (i.e. maximum number of females ashore), combined over all years (1997–2001)

Longitudinal harem choice

Using the data from individual seals seen in the 1997 and 1998 breeding seasons and following these animals through to 2001, there was a dependency of change in consecutive harem size with age (Fig. 3). The number of females increasing, decreasing, or remaining consistent with the size of their harems depended on age for both the

Table 2 Numbers of young and older females within small (<100), medium (100–300) and large (>300) harems. Adjusted G -statistics (G -Test of Independence) and the corresponding rejection probabilities for independence between female age and harem size are given

	Small	Medium	Large	$G_{adj(2)}$	P
1997					
No. (%) harems	8 (53)	4 (27)	3 (20)		
Young	26	44	44		
Mid	3	7	9		
Older	7	11	23	3.98	0.137
1998					
No. (%) harems	2 (18)	6 (55)	3 (27)		
Young	4	43	46		
Mid	5	48	65		
Older	1	12	18	0.98	0.612
1999					
No. (%) harems	4 (31)	5 (38)	4 (31)		
Young	7	38	46		
Mid	13	85	128		
Older	1	7	25	6.51	0.039
2000					
No. (%) harems	5 (38)	4 (31)	4 (31)		
Young	11	16	33		
Mid	38	54	116		
Older	16	41	113	23.13	<0.001
2001					
No. (%) harems	4 (31)	7 (54)	2 (15)		
Young	10	89	44		
Mid	18	128	84		
Older	10	117	94	6.68	0.035
Avg. no. (%) harems	4.6 (34)	5.2 (41)	3.2 (25)		

1st-2nd season comparison (G -test of independence: $G_2=9.30$, $P=0.010$), and for the 1st-Next season comparison (G -test of independence: $G_2=18.06$, $P<0.001$). Using the average proportion of harems of each size class from 1997 to 2001 as the expected values (Table 2), young females chose to breed in larger harems in a consecutive season (G -test of independence: $G_2=10.64$, $P=0.005$), as did older females (G -test of independence: $G_2=9.74$, $P=0.008$). However, mid-aged females demonstrated a random change in harem size in consecutive breeding seasons (G -test of independence: $G_2=0.11$, $P=0.949$).

Females also—though not significantly—chose the same harem in which to breed in consecutive seasons, and this fidelity increased with age, as summarized by the mean proportion of identical harem choice for females with full sighting records from 1997 or 1998. On average, young females opted to breed in the same harem 44% ($\pm 5\%$) of their recorded breeding seasons, whereas mid-age and older females opted for the same harem 62% ($\pm 7\%$) and 66% ($\pm 7\%$) of their recorded breeding seasons, respectively (Fig. 3). A randomized ANOVA indicated a rejection probability (i.e. at least one age class different to the others) of $P_{20000}=0.06$.

Combining data from 1997–2001, we found that when females changed harems in consecutive breeding seasons, they chose to breed in harems that were on average 41

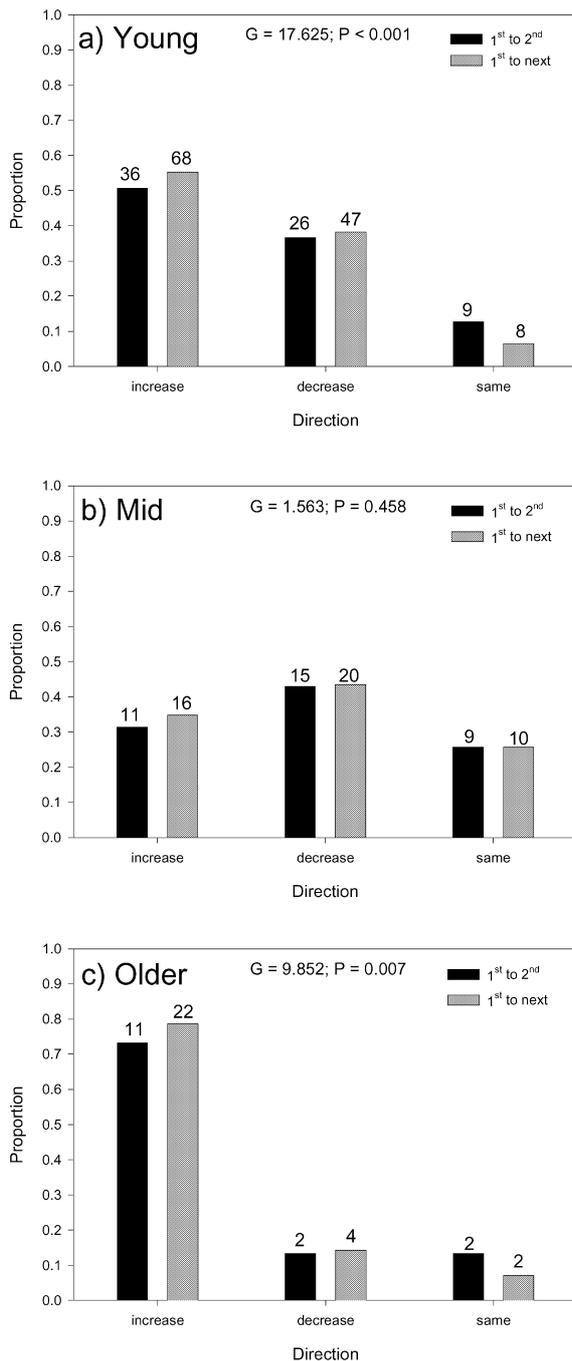


Fig. 3 **a** Change in size of harem of choice in consecutive years (1st-2nd) and for next known breeding season (1st-next) for young females, **b** for mid-age females, and **c** for older females (sample sizes shown)

females larger (average difference between size of breeding harems chosen between consecutive years among all individuals). When the choice of harem was identical, the average difference in harem size was 12 females fewer. These patterns varied according to female age—young females that changed harems increased harem size by 159 on average, with those remaining in the same harem increasing by 70 individuals. Older

females that changed harems increased average harem size by only 27 females; older females remaining in the same harem experienced an average difference in harem size of 22 females fewer.

Female age and breeding experience

Females were more likely to be observed breeding as they aged (Fig. 4a). There was a significant increase in the mean number of observed breeding episodes with increasing harem size (general linear model: $F_{2,416} = 3.517$, $P = 0.031$; residuals homoscedastic; Fig. 4b), with the proportion of primiparous females decreasing and the proportion of multiparous females increasing with increasing harem size (G -test of independence: $G_2 = 7.16$, $P = 0.028$; Fig. 4c). There was no significant difference in the skew to the breeding experience distributions between harem size classes (median=2 observed lifetime breeding experience for each harem size class).

Female arrival and peak numbers ashore

The Gaussian curve fits indicated that the date of maximum number of females ashore during the breeding season varied little during the 5 years of investigation. Here, the day of maximum females ashore was 15 October (1997 and 1998), 16 October (1999), and 14 October (2000 and 2001).

The overall general linear model (GLM) pooling data among years detected a significant effect of age (GLM: $F_{1,1796} = 5.363$, $P = 0.021$), but not of year ($F_{4,1796} = 1.019$, $P = 0.396$) or of the interaction $age \times year$ ($F_{4,1796} = 1.341$, $P = 0.292$) on arrival time. The mean arrival for young females was Julian day 276.8, or 3 October; mean arrival for mid-age females was Julian day 280.4, or 7 October, and the mean arrival for older females was Julian day 281.5, or 8 October (Fig. 5).

The relationship between maximum harem size and observed harem size at 1-, 2- and 3-week intervals prior to the date of maximum harem size demonstrated a strong predictability of maximum harem size at even 3 weeks prior to the dates of maximum haul out. However, the slope of the least-squares relationship (β) and the degree of dispersion around the prediction line (as measured by the R^2 value) increased with increasing time prior to the date of maximum haul out. Individuals arriving only 1 week prior to maximum haul out (i.e. older females) could predict maximum harem size with little error ($R^2_{adj} = 0.978$, $\beta = 1.059$; $F_{1,65} = 2973.7$, $P < 0.001$). Two weeks prior to maximum haul out (i.e., when younger females were arriving), error in predictability increased ($R^2_{adj} = 0.952$, $\beta = 1.490$; $F_{1,65} = 1218.9$, $P < 0.001$). At 3 weeks prior to maximum haul out, predictability decreased even further ($R^2_{adj} = 0.898$, $\beta = 2.737$; $F_{1,65} = 581.6$, $P < 0.001$).

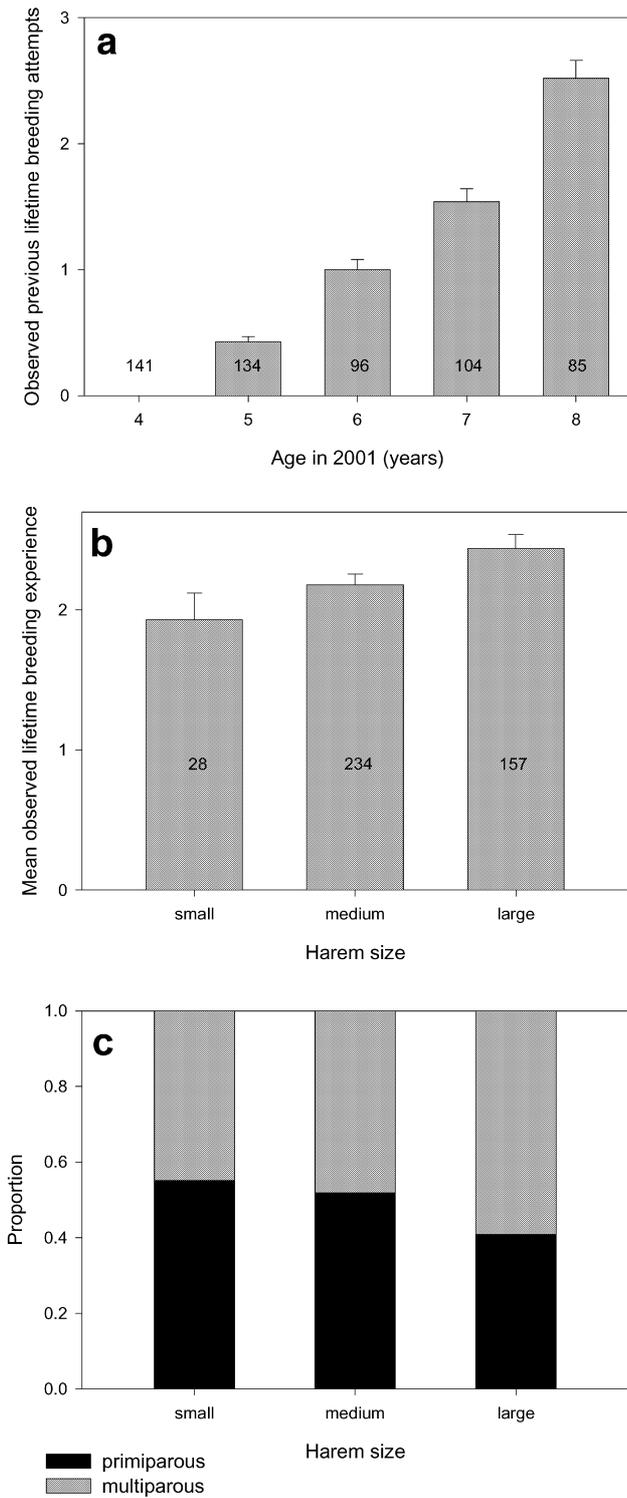


Fig. 4 **a** The relationship between the number of known lifetime breeding attempts and female age for individuals sighted in the 2001 breeding season (sample sizes shown), **b** mean breeding experience of females (breeding seasons where sighted) in small, medium and large harems (sample sizes shown), **c** the proportion of primiparous and multiparous in harems of differing sizes

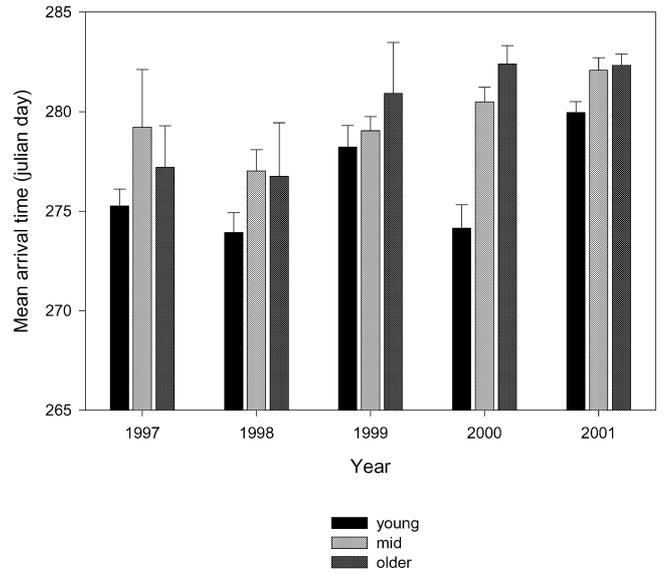


Fig. 5 Mean arrival times (Julian day) for young and older females in the 1997–2001 breeding seasons

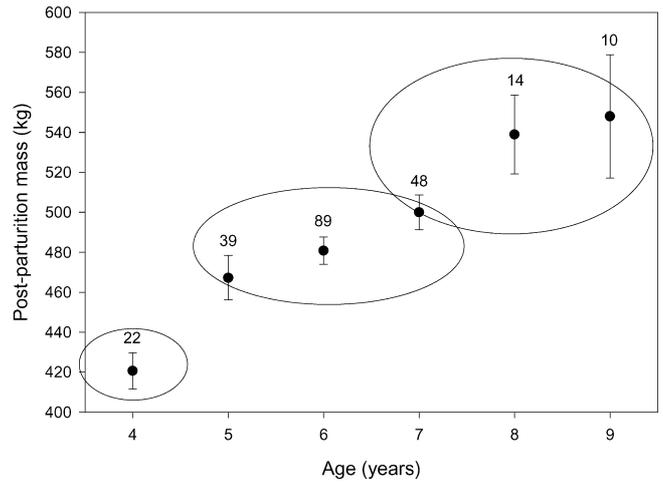


Fig. 6 Change in mean post-partum mass of females from age 4 to 9 years (years pooled; sample sizes shown). Groupings represent the approximate division in mass classes with age (Tukey HSD post-hoc test, see Results)

Change in female mass with age

There was a significant increase in mass with age from age 4 to 9 (GLM: $F_{1,233}=74.56, P<0.001$), after which the measurement error precluded the detection of further trends (Fig. 6). A post-hoc Tukey HSD test revealed mass classes of females relative to age that broadly followed the age classes we identified (i.e. young, mid- and older). Four-year-old females were significantly lighter than older age classes (all $P_s \leq 0.048$), and 5- and 6-year-old females appeared to form a specific mass class ($P_{5-6}=0.852$). Seven-year-old females represented a tran-

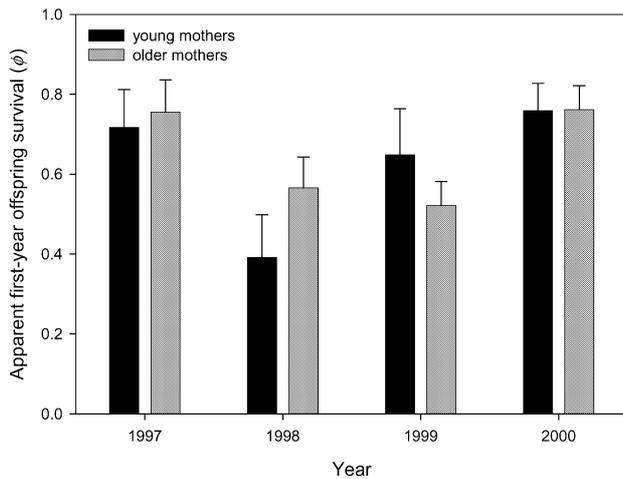


Fig. 7 The mean apparent survival probability ($\phi \pm 1$ SE) of offspring during the 1st year of life relative to year (cohort). Data are presented relative to mother age class

sitional mass class between the 5- to 6-year olds and the >7-year-olds ($P_{6-7}=0.514$; $P_{7-8}=0.421$; $P_{6-8}=0.030$).

Pup survival relative to female characteristics and harem size

Pre-weaning survival

The randomized contingency analysis indicated that there was no evidence to reject the null hypothesis of equal pre-weaning survival among age classes ($P_{20000}=0.287$). Using only the “young” and “older” mother age classes, there was still no evidence for a difference in pre-weaning pup survival ($P_{20000}=0.508$).

There was no evidence for a difference among years (1998–2000) in pre-weaning pup mortality ($P_{20000}=0.940$). Therefore, we pooled the data among years to increase sample size. The randomized linear regression indicated that the proportion of tagged pups dying prior to weaning ranged from 0 to 0.200 ($n=31$ harems, $\bar{x}=0.046$, $SE=0.009$). After 20,000 randomizations, there was no evidence of a relationship with maximum harem size ($P_{20000}=0.885$).

Post-weaning survival

There were no apparent differences in the 1st-year survival estimates for male and female seals (likelihood ratio test: $\chi^2_2=1.017$, $P=0.601$), so these data were pooled and analysed together. Inter-annual (cohort) differences in 1st-year survival were examined and it was found that survival estimates differed among cohorts (likelihood ratio test: $\chi^2_2=6.848$, $P=0.033$; Fig. 7). Pups produced by young mothers had lower 1st-year survival probabilities than pups produced by older mothers (Fig. 8). This

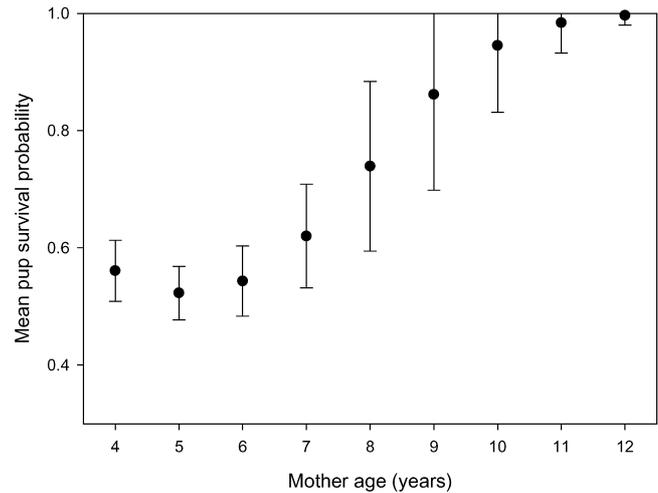


Fig. 8 The relationship between mother age and the probability of 1st-year pup survival determined from the simplified logistic function $\text{logit}(\phi) = \text{intercept} + \beta \text{ mother age} - \beta \text{ mother age}^2$. The error bars represent the standard errors for each mother age-specific estimate of pup ϕ

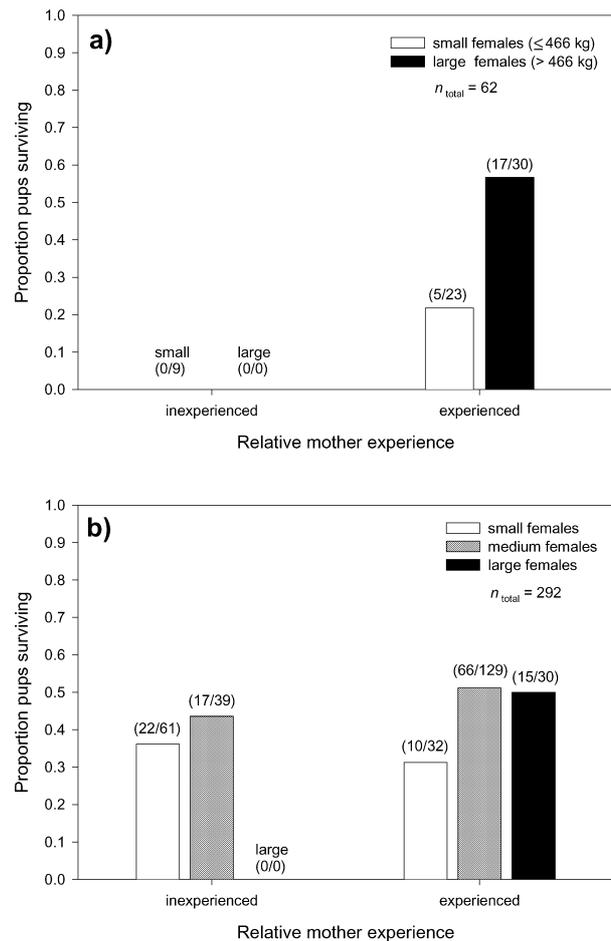


Fig. 9 **a** Contribution of maternal mass and age to the probability of offspring survival to 1 year of age. Here, “small” females ≤ 466 kg, and “large” females > 466 kg. **b** Contribution of relative maternal size (i.e. small, medium, large) and age to the probability of offspring survival to 1 year of age

logistic relationship (likelihood ratio test: $\chi^2_1=3.206$, $P=0.073$) accounted for 92% of the variation in 1st-year survival estimates at Macquarie Island.

The logistic regression models testing for the combined effects of maternal age and mass on offspring survival demonstrated that females for whom mass data were available increased the likelihood of offspring survival with increases in both mass and age. AIC weights showed that the best-fit model (AIC weight=0.542) included both main terms (age: $\chi^2_1=4.92$, $P=0.027$, $\beta=3.39$, $SE_\beta=1.53$; mass: $\chi^2_1=4.70$, $P=0.030$, $\beta=0.04$, $SE_\beta=0.02$) and the interaction ($\chi^2_1=4.39$, $P=0.036$, $\beta=-0.005$, $SE_\beta=0.003$; Fig. 9a). Thus, maternal age contributes to offspring survival in addition to mass (i.e. increased probability of offspring survival with increasing maternal age and mass). The logistic regression results using relative maternal size only were less conclusive. The best-fit model included only the *age* term (AIC weight=0.622, $\chi^2_1=9.29$, $P=0.002$, $\beta=0.23$, $SE_\beta=0.08$; Fig. 9b).

Discussion

Although the effect of maternal age on offspring survival in elephant seals has been investigated previously in the short term (birth to weaning; Reiter et al. 1981; Pistorius et al. 2001), the consequences of maternal age on longer-term offspring survival have not been investigated previously. We have demonstrated that: (1) older females produce pups that are more likely to survive the 1st year of life, and (2) the survival probability of offspring increases with increasing maternal age. Although 1st-year survival does not encapsulate a complete measure of lifetime reproductive success because it does not necessarily relate to the probability that individuals are recruited into the breeding population, it is much stronger evidence than survival probability to weaning alone (Reiter et al. 1981; Pistorius et al. 2001), because the period of highest mortality in southern elephant seals is usually during the 1st year of life (McMahon et al. 2000b).

However, age itself is not the only female characteristic contributing to variation in offspring survival. Although females within the ages considered in this study also increased in mass with age, we found a significant contribution of both maternal age and mass to offspring mass and survival, as in many long-lived animals (e.g. Clutton-Brock 1988; Ellis et al. 2000). In general, this phenomenon is related to age-dependent increases in reproductive competence and foraging ability (e.g. Saether 1997; Bowen et al. 2001b).

Because adult female southern elephant seals hauled out and chose to breed in larger harems as they aged (see also Reiter et al. 1981), we hypothesize that in addition to older females being better mothers (through higher energy expenditure during lactation—Arnbom et al. 1997), they contribute to the success of their pups by providing a

better rearing environment—large harems. This raises the question: what advantages are conferred to breeding females by choosing large harems? Reiter and Le Boeuf (1991) predicted that mothers experiencing intense competition for breeding space should delay breeding attempts until they are able to procure a good position within existing harems. The lack of relationship between harem density and harem size in our data suggests that density may not be a good predictor of female performance because breeding space does not appear to be limited. The abundance of breeding space may be due to a reduction in population density at Macquarie Island by almost 50% since the 1950s (Hindell and Burton 1987). We hypothesize, therefore, that young female southern elephant seals at Macquarie Island increase their fitness through behavioural choices made during breeding rather than delaying primiparity as would be expected in a higher-density population.

Variation in pre-weaning survival may confound the interpretation that large harems are conducive to increased post-weaning survival (Le Boeuf et al. 1994). For example, if large harems provide better rearing environments leading to higher-quality weanlings at the end of lactation, yet pre-weaning survival in these harems is low, there would not necessarily be an advantage to breeding in large harems. In contrast to northern elephant seals (Le Boeuf et al. 1994), pre-weaning survival was relatively high across all age classes, corresponding to a reduced power to detect differences among age classes and harem sizes. Although we found no evidence for a relationship between pre-weaning pup mortality and harem size, Pistorius et al. (2001) found that mortality was highest in small harems at Marion Island. The lack of relationship in our study compared to that of Pistorius et al. (2001) may be due to the log-linear relationship they found between pup mortality and harem size. Given that the largest harems at Marion Island are approximately an order of magnitude smaller than those at Macquarie Island, the log-linear relationship between harem size and pup survival suggests that the effect may not have been detectable among larger harems. However, we also suggest that it may not necessarily be harem size per se that influences pre-weaning survival; rather, beach topography and exposure to waves may be more important factors (Huber et al. 1991; Le Boeuf et al. 1994).

In other elephant-seal colonies, it appears that the centres of large harems are less vulnerable to flooding at high tides, provide more stable space between females, offer refugia from challenging males at the periphery of the harem, and provide less opportunity for milk-thieving from weaned or abandoned pups (Reiter et al. 1981; Galimberti et al. 2000c). Therefore, there appear to be real advantages associated with position within a harem, and it follows that females compete for these advantages. Indeed, the mean age of females on the periphery of *M. angustirostris* harems was lower than of those in the centre (Reiter et al. 1981), and in the Falkland Islands, *M. leonina* “centre” females had a lower likelihood of interacting with secondary males (Galimberti et al.

2000b). There is also evidence that male harassment of harem-breeding phocid seals increases with decreasing breeding sex ratios (adult females:adult males). Galimberti et al. (2000b) found that the individual harassment rate of females decreased as the relative number of females increased in the breeding population, suggesting that larger harems with high breeding sex ratios are conducive to lower harassment rates. They also found that female activity was higher in smaller versus larger harems. Likewise, Boness et al. (1995) demonstrated that the frequency of male grey-seal (*Halichoerus grypus*) harassment increased during the pupping period as the relative number of males increased, thus contributing to reduced female performance later in the season.

We were also able to establish that harem choice by females was not related solely to age; there was strong evidence to suggest that breeding experience itself was an important factor. This suggests that not only does the selection for and residence in large harems provide a better rearing environment due to reduced male harassment, but there may be added benefits given that these harems are almost exclusively controlled by large, dominant males that secure their position prior to maximum haul out. A female may therefore improve the quality of her future offspring by choosing to breed in large harems, thereby increasing the probability of mating with large, socially dominant males (Cox and Le Boeuf 1977; Reiter et al. 1981; Pomeroy et al. 2001).

Given that there are numerous advantageous to breeding in a large harem, what determines which individuals breed in a particular harem? Young females are typically dominated by older, more experienced females, and this hierarchy is established due to age and experience effects rather than simple size relationships (Christensen and Le Boeuf 1978; Reiter et al. 1981; McCann 1982). Young, subordinate *M. angustirostris* females were less successful in rearing pups to weaning when in large harems versus small harems (Reiter et al. 1981), and young primiparous females also had lower survival in the year following the first breeding attempt (Reiter and Le Boeuf 1991). It was hypothesized that older ("prime") females are better at protecting and nurturing their pups due to their greater size, their ability to dominate aggressive encounters (Christensen and Le Boeuf 1978; Reiter et al. 1981; McCann 1982), have earlier arrival times and have greater maternal experience. Additionally, our data suggested that young females may have been forced out of harems more often than their older conspecifics (i.e. seen in more harems during the course of the breeding season), although the results were inconclusive.

Although we found evidence for older and more experienced mothers to choose larger harems, arrival time was opposite to that found in other phocid seals (Reiter et al. 1981; Pomeroy et al. 1999). Reiter et al. (1981) hypothesized that older females return earlier because they are more efficient foragers. However, our results demonstrate that young females return and pup earlier in the season, which is in accordance with earlier observa-

tions of *M. leonina* haul-out behaviour at South Georgia (McCann 1982). Given that younger females are generally subordinate to older, larger females in terms of ideal placement within a harem (Reiter et al. 1981), it follows that younger females may be able to achieve better placement by arriving earlier. It is widely accepted that established territory holders, even when physically or otherwise less dominant, are more likely to retain a territory given prior residence (Rohwer 1982; Tobias 1997). This priority effect can result due to resident awareness of established boundaries with neighbours (Beletsky and Orians 1987), as predicted by the value-asymmetry hypothesis (Beletsky and Orians 1989). However, any advantage accrued by earlier establishment might be offset by the lowered predictability of maximum harem size with early arrival.

In summary, our results emphasize the importance of reproductive competition in shaping individual reproductive success in colonial breeders. We have shown that: (1) both age and breeding experience are important factors influencing the survival probability of pups, and (2) breeding females can improve the rearing environment for their offspring by choosing larger, more stable harems in which to breed. The circumpolar distribution of *M. leonina*, the large number of disparate colonies and the high temporal and spatial variation in marine productivity makes this species an ideal candidate to examine elements of reproductive behaviour in large mammals. Subtle inter-population variation in reproductive behaviour may continue to provide insights into the selective forces shaping female breeding behaviour in this and other long-lived vertebrates.

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References

- Arnbom T, Fedak MA, Rothery P (1994) Offspring sex ratio in relation to female size in southern elephant seals, *Mirounga leonina*. *Behav Ecol Sociobiol* 35:373–378
- Arnbom T, Fedak MA, Boyd IL (1997) Factors affecting maternal expenditure in southern elephant seals during lactation. *Ecology* 78:471–483
- Arnold SJ (1994) Multivariate inheritance and evolution: a review of concepts. In: Boake CRB (ed) *Quantitative genetic studies of behavioral evolution*. University of Chicago Press, Chicago, pp 17–48

- Baldi R, Campagna C, Pedraza S, Le Boeuf BJ (1996) Social effects of space availability on the breeding behaviour of elephant seals in Patagonia. *Anim Behav* 51:717–724
- Beletsky LD, Orians GH (1987) Territoriality among male red-winged blackbirds. II. Removal experiments and site dominance. *Behav Ecol Sociobiol* 20:339–349
- Beletsky LD, Orians GH (1989) Territoriality among male red-winged blackbirds. III. Testing hypotheses of territorial dominance. *Behav Ecol Sociobiol* 24:333–339
- Boness DJ, Bowen WD, Iverson SJ (1995) Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? *Behav Ecol Sociobiol* 36:1–10
- Bowen WD, Ellis SL, Iverson SJ, Boness DJ (2001a) Maternal effects on offspring growth rate and weaning mass in harbour seals. *Can J Zool* 79:1088–1101
- Bowen WD, Iverson SJ, Boness DJ, Oftedal OT (2001b) Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. *Funct Ecol* 15:325–334
- Boyd IL (2000) State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Funct Ecol* 14:623–630
- Boyd IL, McCann TS (1989) Pre-natal investment in reproduction by female Antarctic fur seals. *Behav Ecol Sociobiol* 24:377–385
- Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer, Berlin Heidelberg New York
- Cameron EZ, Linklater WL, Stafford KJ, Minot EO (2000) Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? *Behav Ecol Sociobiol* 47:243–249
- Campagna C, Le Boeuf BJ, Lewis M, Baldi R (1992) Equal investment in male and female offspring in the southern elephant seal. *J Zool Lond* 226:551–561
- Carrick R, Ingham SE (1960) Ecological studies of the southern elephant seal *Mirounga leonina* (L.), at Macquarie Island and at Heard Island. *Mammalia* 24:325–342
- Carrick R, Csordas SE, Ingham SE (1962) Studies on the southern elephant seal, *Mirounga leonina* (L.). IV. Breeding and development. *CSIRO Wildlife Res* 7:161–197
- Chittleborough RG, Ealey EHM (1951) Seal marking at Heard Island, 1949. I. Department of External Affairs, Antarctic Division, Melbourne
- Christensen TE, Le Boeuf BJ (1978) Aggression in the female northern elephant seal, *Mirounga angustirostris*. *Behaviour* 64:158–172
- Clutton-Brock TH (1988) Reproductive success. Studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Ill
- Clutton-Brock TH, Albon SD, Guinness FE (1984) Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* 308:358–360
- Cormack RM (1964) Models for capture-recapture. *Biometrika* 51:429–438
- Côté SD, Festa-Bianchet M (2001) Reproductive success in female mountain goats: the influence of age and social rank. *Anim Behav* 62:173–181
- Cox C, Le Boeuf BJ (1977) Female incitation of male competition: a mechanism in sexual selection. *Am Nat* 111:317–335
- Crocker DE, Williams JD, Costa DP, Le Boeuf BJ (2001) Maternal traits and reproductive effort in northern elephant seals. *Ecology* 82:3541–3555
- Ellis SL, Bowen WD, Boness DJ, Iverson SJ (2000) Maternal effects on offspring mass and stage of development at birth in the harbor seal, *Phoca vitulina*. *J Mammal* 81:1143–1156
- Engelhard GH, Hoff J van den, Broekman M, Baarspul ANJ, Field I, Burton HR, Reijnders PJH (2001) Mass of weaned elephant seal pups in areas of low and high human presence. *Polar Biol* 24:244–251
- Fedak MA, Arnborn T, Boyd IL (1996) The relation between size of southern elephant seal mothers, the growth of their pups and the use of maternal energy, fat and protein during lactation. *Physiol Zool* 69:887–911
- Field IC, Bradshaw CJA, McMahon CR, Harrington J, Burton HR (2002) Effects of age, size and condition of elephant seals (*Mirounga leonina*) on their intravenous anaesthesia with tiletamine and zolazepam. *Vet Rec* 151:235–240
- Forslund P, Part T (1995) Age and reproduction in birds—hypotheses and tests. *Trends Ecol Evol* 10:374–378
- Freckleton RP (2002) On the misuse of residuals in ecology: regression of residuals vs. multiple regression. *J Anim Ecol* 71:542–545
- Galimberti F, Boitani L, Marzetti I (2000a) Female strategies of harassment reduction in southern elephant seals. *Ethol Ecol Evol* 12:367–388
- Galimberti F, Boitani L, Marzetti I (2000b) The frequency and costs of harassment in southern elephant seals. *Ethol Ecol Evol* 12:345–365
- Galimberti F, Boitani L, Marzetti I (2000c) Harassment during arrival on land and departure to sea in southern elephant seals. *Ethol Ecol Evol* 12:389–404
- Goldsworthy SD, He X, Tuck GN, Lewis M, Williams R (2001) Trophic interactions between the Patagonian toothfish, its fishery, and seals and seabirds around Macquarie Island. *Mar Ecol Prog Ser* 218:283–302
- Hall AJ, McConnell BJ, Barker RJ (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. *J Anim Ecol* 70:138–149
- Hastings KK, Testa JW (1998) Maternal and birth colony effects on survival of Weddell seal offspring from McMurdo Sound, Antarctica. *J Anim Ecol* 67:722–740
- Hepp GR, Kennamer RA (1993) Effects of age and experience on reproductive performance of wood ducks. *Ecology* 74:2027–2036
- Hindell MA (1991) Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *J Anim Ecol* 60:119–134
- Hindell MA, Burton HR (1987) Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *J Zool Lond* 213:365–380
- Hindell MA, Slip DJ (1997) The importance of being fat: maternal expenditure in the southern elephant seal *Mirounga leonina*. In: Hindell M, Kemper C (eds) Marine mammal research in the Southern Hemisphere, vol 1. Status, ecology and medicine. Surrey Beatty, Chipping Norton, pp 72–77
- Huber HR, Beckham C, Nisbet J (1991) Effects of the 1982–83 El Niño on northern elephant seals on the South Farallon Islands, California. In: Trillmich F, Ono KA (eds) Pinnipeds and El Niño: responses to environmental stress, vol 88. Springer, Berlin Heidelberg New York, pp 219–233
- Jolly GM (1965) Explicit estimates from mark-recapture data with both death and immigration-stochastic models. *Biometrika* 52:225–247
- Laws RM (1953) The elephant seal (*Mirounga leonina* Linn.). I. Growth and age. *Falkland Isl Depend Surv Sci Rep* 8:1–62
- Le Boeuf BJ, Morris P, Reiter J (1994) Juvenile survivorship of northern elephant seals. In: Le Boeuf BJ, Laws RM (eds) Elephant seals: population ecology, behavior, and physiology. University of California Press, Berkeley, pp 121–136
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118
- Lunn NJ, Boyd IL, Croxall JP (1994) Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *J Anim Ecol* 63:827–840
- Manly BFJ (1997) Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall, London
- McCann TS (1981) Aggression and sexual activity of male southern elephant seals, *Mirounga leonina*. *J Zool Lond* 195:295–310

- McCann TS (1982) Aggressive and maternal activities of female southern elephant seals (*Mirounga leonina*). *Anim Behav* 30:268–276
- McLaren IA (1993) Growth in pinnipeds. *Biol Rev* 68:1–79
- McMahon CR, Hoff J van den, Burton HR, Davis PD (1997) Evidence for precocious development in female pups of the southern elephant seal, *Mirounga leonina*, at Macquarie Island. In: Hindell MA, Kemper C (eds) *Marine mammal research in the Southern Hemisphere*, vol 1. Status, ecology and medicine. Surrey Beatty, Chipping Norton, pp 92–96
- McMahon CR, Burton HR, Bester MN (1999) First-year survival of southern elephant seals, *Mirounga leonina*, at sub-Antarctic Macquarie Island. *Polar Biol* 21:279–284
- McMahon CR, Burton H, McLean S, Slip D, Bester M (2000a) Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Vet Rec* 146:251–254
- McMahon CR, Burton HR, Bester MN (2000b) Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarct Sci* 12:149–153
- McMahon CR, Burton HR, Bester MN (2003) A demographic comparison of two southern elephant seal populations. *J Anim Ecol* 72:61–74
- Mellish JAE, Iverson SJ, Bowen WD (1999a) Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiol Biochem Zool* 72:677–690
- Mellish JAE, Iverson SJ, Bowen WD, Hammill MO (1999b) Fat transfer and energetics during lactation in the hooded seal: the roles of tissue lipoprotein lipase in milk fat secretion and pup blubber deposition. *J Comp Physiol B* 169:377–390
- Milner JM, Elston DA, Albon SD (1999) Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *J Anim Ecol* 68:1235–1247
- Pistorius PA, Bester MN, Kirkman SP, Taylor FE (2001) Pup mortality in southern elephant seals at Marion Island. *Polar Biol* 24:828–831
- Pomeroy PP, Fedak MA, Rothery P, Anderson S (1999) Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *J Anim Ecol* 68:235–253
- Pomeroy PP, Wilmar JW, Amos W, Twiss SD (2001) Reproductive performance links to fine-scale spatial patterns of female grey seal relatedness. *Proc R Soc Lond B* 268:711–717
- Reiter J, Le Boeuf BJ (1991) Life history consequences of variation in age at primiparity in northern elephant seals. *Behav Ecol Sociobiol* 28:153–160
- Reiter J, Panken KS, Le Boeuf BJ (1981) Female competition and reproductive success in northern elephant seals. *Anim Behav* 29:670–687
- Riedman ML, Le Boeuf BJ (1982) Mother-pup separation and adoption in northern elephant seals. *Behav Ecol Sociobiol* 11:203–215
- Rohwer S (1982) The evolution of reliable and unreliable badges of fighting ability. *Am Zool* 22:531–546
- Saether B-E (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol Evol* 12:143–149
- Schaffer WM (1974) Selection for optimal life histories: the effect of age structure. *Ecology* 55:291–303
- Seber GAF (1965) A note on the multiple recapture census. *Biometrika* 52:319–335
- Sokal RR, Rohlf FJ (1981) *Biometry. The principles and practice of statistics in biological research*, 2nd edn. Freeman, New York
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, Oxford
- Tobias J (1997) Asymmetric territorial contests in the European robin: the role of settlement costs. *Anim Behav* 54:9–21
- Trivers RL (1972) Parental investment and sexual selection. In: Campbell B (ed) *Sexual selection and the descent of man 1871–1971*. Aldine, Chicago, pp 136–179
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Program MARK: survival estimation from populations of marked animals* 46 [Suppl]:120–138