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Sex at sea: alternative mating system in an extremely polygynous mammal

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Polygyny is a widespread and evolutionarily significant mating system in vertebrates. The southern elephant seal, *Mirounga leonina*, has often been cited as being extremely polygynous, thus providing an important reference point for studies on mating systems. During the breeding season, these animals form terrestrial harems in which one dominant male controls tens to hundreds of females. Our current understanding of polygynous mating systems seems to imply that, unlike males, females are not under selection pressure to adopt alternative mating strategies, and in the case of the southern elephant seal, the possibility of mating at sea has not been considered. Furthermore, elephant seal females are thought to breed annually. Using a 25-year mark–recapture data set, we found that elephant seal females skipped breeding seasons, often returning to pup in the following breeding season. Females did not need to haul out on land in order to breed in the following season, thus providing evidence for mating at sea by virgin and multiparous females. Nonpolygynous, opportunistic mating at sea could be an important alternative mating strategy in a supposedly strictly polygynous species. This has implications for our understanding of elephant seal ecology, demography and behaviour and of the evolution of vertebrate polygyny in general. If polygyny does not preclude females from adopting alternative mating strategies, the term 'polygyny' may be misleading. Traditional concentration on male strategies has hampered our understanding of mating systems, in assuming that females capitulate to these strategies. We suggest similar misinterpretations could occur in other polygynous species.

The evolutionary, ecological and behavioural characteristics of species are underpinned by their mating systems (Orians 1969). In polygynous mammals, reproductive success is more variable in males than in females, and therefore competition between males for access to females is strong with only a few males gaining access to most of the females (Trivers 1972; Emlen & Oring 1977). Under these circumstances, alternative mating strategies (such as sneak copulations where access to females by fighting is likely to be unsuccessful) have been demonstrated in several species (e.g. Shuster & Wade 2003; Caudron et al. 2009). However, the significance of female alternative strategies has been largely overlooked until recently (Brennan et al. 2008; Morris et al. 2010), particularly in polygynous systems where it is assumed that it is adaptive for females to choose dominant males (Andersson 1994), or alternative male strategies function to coerce uncooperative females to mate with subordinate males.

Male alternative mating strategies have implications for the reproductive success of females. For example, in many polygynous species females are subject to harassment, either directly as males try to monopolize access to females, or indirectly because of aggressive interactions between males (e.g. Linklater et al. 1999; Cappozzo et al. 2008). Patterns of male harassment may be an important determinant of social structure (e.g. primates: Kappeler 1997; van Schaik & Kappeler 1997; equids: Linklater et al. 1999) in addition to more traditional determinants such as resource distribution (Emlen & Oring 1977). Consequently, females may not always choose to mate with dominant males and the high reproductive skew observed in polygynous mating systems may arise through dominant males monopolizing access to females, thereby restricting female choice (Reichard et al. 2005, 2007).

Females are thought to gain genetic benefits in polygynous mating systems by mating with the monopolizing male. Many pinniped species display behaviour where males compete to monopolize females and have traditionally been used as models of the polygynous breeding/mating system (Bartholomew 1970; Cassini 1999). In particular, southern elephant seals, *Mirounga leonina*, are extremely polygynous with females aggregating in harems on land, guarded and mated by adult males at ratios (females:males) from 9:1 to 277:1, depending on the locality (e.g.

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Carrick et al. 1962; Wilkinson & van Aarde 1999). Theory predicts that such extreme polygyny would promote alternative male mating strategies, since reproductive success is highly dependent on social status or 'ownership' (Maynard Smith 1979; Shuster & Wade 2003). Theory also predicts that the vast majority of females will mate only in a polygynous harem situation, or be coerced by sneaky males nearby. The role of female choice is thus minimized within alternative mating strategy studies (e.g. Waltz & Wolf 1984; Caudron et al. 2009).

In southern elephant seals, extreme polygyny is thought to have arisen because adult females annually come ashore for a prolonged period of time ('haul out') to give birth and subsequently to mate, usually with the dominant male or 'beachmaster' (Bartholomew 1970; Cassini 1999; Fabiani et al. 2004). The limited availability of terrestrial breeding sites (islands) within their oceanic ranges causes individuals to aggregate at suitable sites (Bartholomew 1970; Cassini 1999). Females show fidelity to these sites and are thus philopatric, although the extent varies depending on their breeding performance (Switzer 1997; McMahon & Bradshaw 2004). Polygyny is maintained by the return of highly philopatric females (e.g. Hofmeyr 2000; Fabiani et al. 2006) apparently aggregating to reduce male harassment (Galimberti et al. 2000). Owing to intense male–male competition the observed mate (alpha male) is often the largest, most aggressive harem holder (Andersson 1994) gaining 'fitness' benefits by leaving many descendants (e.g. Hoelzel et al. 1999; Galimberti et al. 2002). Females in these harems presumably also benefit as they will have mated with a male of sufficient quality to have defended a harem, traits that may be inherited by the female's offspring, thereby improving their quality. High natal site fidelity shown by females and the observed success of alpha males in obtaining most matings in a harem result in genetically differentiated populations within the species' range (Slade et al. 1998; Hoelzel et al. 1999). These observations imply that copulation opportunities for both sexes are dependent upon the polygynous mating system. However, alternative mating strategies by females away from the harem have not been considered. Furthermore, if some females mate off the harem, there is increased scope for alternative mating strategies by males.

Many facets of southern elephant seal biology support the assumption of extreme polygyny. Copulation and conception (followed by delayed implantation) occur approximately 1 year before parturition (Laws 1956). It is assumed that most adult females return to terrestrial sites to breed (pup and mate) every year after primiparity with no interruptions between years (e.g. Laws 1956; Hindell 1991; Wilkinson 1991; Le Boeuf & Laws 1994; Pistorius et al. 2001, 2004, 2008; McMahon et al. 2003, 2005, 2009; de Bruyn 2009). However, only a few identifiable virgin females have ever been observed to mate on land (Le Boeuf & Laws 1994), so it is assumed that most primiparous females mate at sea even though this has never been witnessed (Laws 1956; Le Boeuf & Laws 1994). This indicates that not all mating is necessarily terrestrial, raising the possibility that some postprimiparous mating may also occur away from terrestrial harems. This possibility implies an alternative mating strategy to the extreme polygyny model, and observable consequences can be predicted, which are (1) that a significant portion of multiparous females have interrupted breeding schedules (skip a birthing period on land) and do not haul out at their regular site to mate, such that mating may have occurred at sea, similar to primiparous females, (2) that females are not breeding at other terrestrial sites, (3) that females returning to their natal sites to breed are observed, and (4) that a significant portion of males need to be available at sea, representing an additional male strategy not associated with harems. We therefore tested whether female southern elephant seals may be adopting an alternative mating strategy (incorporating a significant proportion of any given population), and empirically tested this hypothesis using an intensive mark–recapture data set collected over 25 years.

METHODS

Study Area and Mark–Recapture Experiment

We assessed breeding histories of adult female southern elephant seals from 15 pooled cohorts (1983–1997) born at sub-Antarctic Marion Island (46°54′S, 37°45′E) and double tagged in their hindflippers immediately after weaning. Standard (50×10 mm and 1 mm thick, with a piercing pin 4 mm thick) plastic Jumbotags (Dalton Supplies Ltd, Henley-on-Thames, U.K.; http://www.dalton.co.uk/co.uk/products/pages_pr/research/r_jumbo.htm) were uniquely embossed with a three-digit number, and colour-coded to denote the year of application (see de Bruyn et al. 2008 for details). Fitting plastic identification tags to pinnipeds is an accepted long-term marking method, with no deleterious long-term effects (Erickson et al. 1993). Tag loss rates (Oosthuizen et al. 2010) are irrelevant for our purposes, because only skipped seasons prior to the last resighting of tagged animals are considered. All elephant seals on all 54 beaches where they haul out at Marion Island were checked for tags at least every 7 days during the breeding season (mid-August–mid-November) and at least every 10 days during the remainder of the year from 1983 to 2007. Moreover, recent efforts to identify mother–pup relationships required additional tag resighting occasions at intervals of less than 7 days (ca. 2 days) during the 2006–2009 breeding seasons (de Bruyn et al. 2008). During the breeding season, adult females are coded on each observation occasion, as (1) 'preparturient', (2) 'accompanied by a pup' or (3) 'hauled out to mate only'. Categories 1 and 3 are double-checked at the end of the breeding season against all other records of the female during that breeding season (e.g. a record of category 3 observed in the data set as preceding a record of category 2, clearly requires a change of the former entry to category 1).

Detectability analyses were performed in the R programming environment (R Development Core Team 2007), using the 'mra' mark–recapture analysis package (McDonald 2010). Capture histories for all females observed at weekly intervals during breeding seasons (1990–2007) were constructed. Breeding seasons never exceeded 6 weeks in length from observation of the first breeding female to that of the last departing female (Kirkman et al. 2004). Each particular breeding season (6 weeks) was reasonably assumed to be a closed population, with no additions or subtractions of individuals from the 'population' during the season. Because the objective of the analysis was finding the probability of detecting any given female in a specific breeding season if she was present, each female's capture history regardless of specific breeding season could be pooled into one 'pseudo breeding season', with each individual assigned a unique ID. In this way 3689 individual histories could be used for this 'breeding season'. Two biologically sensible Huggins closed population models (Huggins 1989) were fitted to the data: (1) a constant capture model (M(0)) and (2) a time-varying capture model (M(t)). Probabilities of detecting a female if she was present at Marion Island during any given breeding season (P_{obs}) was derived from the most parsimonious model, the latter selected by using the Akaike information criterion corrected for small samples (AIC_c; Burnham & Anderson 1998). The variance in P_{obs} was assessed by 1000 bootstrap iterations, with replacement, fitted to the most parsimonious model and an estimate of standard deviation and 95% confidence intervals for P_{obs} was obtained.

To assess the number of skipped breeding seasons for individual females over their lifetimes we used only females that had bred at