

**Article title** - 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 an example of an animal with an extremely polygynous mating system, 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 selective pressure to adopt alternative mating strategies, and in the case of the southern elephant seal, the possibility of mating at sea, off these harems, has not been considered. Furthermore, elephant seal females are thought to breed annually from primiparity to death. We use a 25-year mark-recapture dataset to show that elephant seal females skip breeding seasons, often returning to pup in the following breeding season. We show that elephant seal females do 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. Non-polygynous, 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, 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.

**Keywords:** polygyny, pinniped, southern elephant seal, mating system, Marion Island, animal behaviour, detectability analysis

The evolutionary, ecological and behavioural characteristics of species are underpinned by their mating systems (Orrians 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. Caudron et al. 2009; Shuster & Wade 2003). 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 monopolise access to females, or indirectly due to 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 like 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 monopolise 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. Wilkinson & van Aarde 1999; Carrick et al. 1962). 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 (‘haulout’) in order to give birth and to subsequently 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). Due 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 descendents (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 results 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) occurs approximately one 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 post-primiparous 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 (skips a birthing period on land) and do not haulout 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 test whether female southern elephant seals may be adopting an alternative mating strategy (incorporating a significant proportion of any given population), and empirically test this hypothesis using an intensive mark-recapture dataset 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 to 1997) born at sub-Antarctic Marion Island (46°54'S, 37°45'E) and double tagged immediately post-weaning in their hindflippers. Standard (50mm x 10mm x 1mm, with a 4mm thick piercing pin) plastic Jumbotags® ([http://www.dalton.co.uk/co.uk/products/pages\\_pr/research/r\\_jumbo.htm](http://www.dalton.co.uk/co.uk/products/pages_pr/research/r_jumbo.htm)) (Dalton Supplies Ltd., Henley-on-Thames, UK) 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 seven days during the breeding season (mid-Aug to mid-Nov) 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 seven days (~ 2 days) during the 2006 to 2009 breeding seasons (de Bruyn et al. 2008). During the breeding season, adult females are coded on each observation occasion, as a) 'pre-parturient', b) 'accompanied by a pup' or c) 'hauled out to mate only'. Categories a) and c) 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 (c) observed in the dataset as preceding a record of (b), clearly requires a change of the (c) entry, to (a)).

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 to 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 probability of detecting any given female in a specific breeding season if she was present, was the objective of the analysis, 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 small sample corrected Akaike Information Criterion ( $AIC_c$ ) (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 least once ( $n = 1032$ ) and belonged to cohorts that had attained at least 10 years of age. A simple bookkeeping approach using ‘Pivot tables’ in Microsoft Excel® was implemented to derive breeding season attendances (annually) between the first and last observed breeding occasion for each individual, and were plotted relative to the breeding histories of all other individuals. The relative percentages of females breeding annually from primiparity to ‘death’ (uninterrupted), annually (for at least two seasons) before a missed breeding season (but with subsequent return) and continuously interrupted breeding schedules respectively, were calculated.

#### *Tracking and dive analysis*

Fifty-three satellite-linked tracking devices were deployed on female southern elephant seals at Marion Island during the last decade (1999 – 2009), two of which (individuals GG335 and BB193) were fortuitously tracked using SMRU devices (see below) during skipped breeding seasons. Different manufacturers provided tracking devices, namely; Telonics (Telonics Inc., Arizona, USA), SMRU (Sea Mammal Research Unit, St. Andrews, UK), Wildlife Computers (Wildlife Computers, Redmond, WA, USA) or Sirtrack (Havelock North, New Zealand). The heaviest device weighed 550g and so represented 0.13% of the mean departure mass of the adult female seals in this study (<0.25% of the smallest individual = 220kg). Seals were immobilised using a mass-specific dosage of ketamine-hydrochloride, administered



intramuscularly using a custom-designed remote injection device (Bester 1988). Transmitters were attached to the dorsal, cranial pelage of each elephant seal using quick setting epoxy resin (Araldite AW2101, CIBA-GEIGY Ltd.). Transmitters were either removed from sedated animals by shaving the device off the fur or during the annual moult when devices are shed naturally with the moulting pelage. No short-term deleterious effects were evident with immobilisation, device deployment or retrieval, while tracking devices attached to elephant seals are known not to affect individual mass gain or survival in the long-term (McMahon et al. 2008). Southern elephant seal tracks were filtered to remove locations requiring unrealistic swim speeds (speeds > 10 km.h<sup>-1</sup>) and then averaged to find a daily location (Tosh et al. 2009 and references therein). Dive data analyses followed McIntyre et al. (2010). Accordingly, day-and night-time summaries of various dive parameters (mean ± SD values of dive depths, dive durations, surface durations, bottom time and time-at-depth) were calculated on a monthly scale. Bottom time was defined as the amount of time spent within the deepest 20% of each dive (Bailleul et al. 2008). Time-at-depth index calculations followed Fedak et al. (2001) and provided a depth and duration independent index of the activity centre of dives (e.g. values approaching 1 indicate a maximising of time close to the deepest point, and values approaching 0.5 indicate similar amounts of time spent at all depths).

All flipper tagging and satellite-device deployment/retrieval procedures were reviewed and approved by the Animal Use and Care Committee of the University of Pretoria (AUCC 040827-024 and AUCC 040827-023) and fieldwork was performed under Prince Edward Island's Research Permits R8-04 and R04-08. All procedures described conform to Antarctic Treaty legislation and to the Scientific Committee on Antarctic Research code of conduct.

## Results

### *Detectability analysis and Breeding season attendance*

Table 1 shows the likelihood of the two most biologically sensible models in fitting the data. The time varying model  $M(t)$  was most parsimonious according to  $AIC_c$  and was used to calculate detectability probabilities. The probability of detecting any given female somewhere on Marion Island, if she was present during the breeding season during at least one weekly resighting occasion in that season was 96.29%, SE = 0.15% (95% CI: 95.99 – 96.57%).

**Table 1.** Model outputs for the constant capture ( $M(0)$ ) and time varying ( $M(t)$ ) Huggins closed population capture models. Akaike Information Criterion ( $AIC_c$ ), number of estimable coefficients ( $EC$ ), Log likelihood ( $LL$ ) and Deviance ( $Dev$ ) are given. A total of 3689 individual capture histories were used for each model.

<i>Model</i>	<i>EC</i>	<i>LL</i>	<i>Dev</i>	<i>AIC<sub>c</sub></i>
M(0)	1	-14885.3	29770.6	29772.6
M(t)	6	-13220.2	26440.3	26452.34

A total of 1032 (28% of total tagged at weaning between 1983 and 1997) adult female southern elephant seals were observed to return to the island to pup and mate within the harem system between 1983 and 2007. A cumulative total of ~16 000 possible breeding occasions (all females for all breeding seasons) was observed between 1983 and 2007, and only during 140 (0.9%) of these did females haul out only to mate (i.e. did not pup). Thus, females virtually always haul out to give birth (99.1% of observed breeding occasions) and after weaning their pup they would mate in the harem system before departing to sea. Only one female participated in 15 consecutive breeding seasons, while another female bred until age 20, skipping 5 breeding seasons before that age. A total of 794 females participated in more than one breeding season. The relative percentages of females breeding annually from

primiparity to 'death' (uninterrupted), annually for at least 2 seasons before a missed breeding season (with subsequent return for a following breeding season/s), and continuously interrupted are shown as relative percentages (Fig. 1). A total of 632 females did not return for every consecutive breeding season over the duration of their breeding opportunities (>8000 possible breeding occasions), translating into a conservative estimate of up to 200 marked females of breeding age not being present at the island during any given breeding season. Approximately 235 (range: 191 – 266) marked cows annually were observed to participate in the 2000 to 2007 breeding seasons (de Bruyn 2009). On the occasions that the females that otherwise skipped breeding seasons (632 individuals) were observed at the island, 83 individuals were observed ashore only to mate at Marion Island. This number is unlikely to be inflated by tagged females potentially not being detected, e.g. during possible, but unlikely, haulout periods shorter than the 2- to 7-day intervals between dedicated tag-resightings (see above). Thus, <1% of females participating in the haulout did not give birth. Furthermore, 549 females (69% of all females observed to breed more than once between 1983 and 2007) that missed a breeding haulout (and were not ashore to mate) returned in subsequent years to give birth.

#### *At-sea mating*

The at-sea tracks of two individuals; GG335, a multiparous cow (8 years old in 2008) that skipped a breeding season and BB193, a virgin two-year-old, both of whom returned to pup in the following season, prove their absence from any island(s) and consequently their probable mating at sea (Fig 2). GG335 showed little variation in dive behaviour over the course of four months around the time (in 2008) when she must have copulated, although diurnal time spent at the sea surface during October

(peak adult female haulout ashore with highest sexual activity (Wilkinson 1991)) was slightly higher (Table 2). Additionally, she hauled out onto ice floes (n=9 occasions), between mid-August and mid-November. These haulouts were of short duration (mean = 3.82h, range = 0.75 – 11.62h). BB193's device malfunctioned prematurely, but she was too far away (given a likely mean speed of 35.23 [SD - 32.74] km.day<sup>-1</sup>; taken from earlier in her track) from any terrestrial site (Bouvetøya being the closest at ~1500km, opposite to the direction of travel at the time), and nowhere near ice, to have mated on a solid substrate, during the likely period of conception (October 2004).

**Table 2.** Summary dive statistics for GG335 during Aug-Nov 2008. Values are reported as means ( $\pm$  SD). TAD = Time at Depth Index. Bottom time was calculated as the estimated time (% of total dives or actual time in min) spent within the deepest 20% of each dive.

PARAMETER	DAY				NIGHT			
	AUG	SEPT	OCT	NOV	AUG	SEPT	OCT	NOV
<b>Max. depth (m)</b>	763.2 $\pm$	678 $\pm$	625.8 $\pm$	612.3 $\pm$	503.7 $\pm$	462.6 $\pm$	369.2 $\pm$	435.8 $\pm$
	117.3	166.7	141.8	160.4	187.9	149.3	189.4	133.5
<b>Dive duration (min)</b>	45.9 $\pm$	47.4 $\pm$	44.9 $\pm$	41.7 $\pm$	36.5 $\pm$	30.3 $\pm$	25.4 $\pm$	29.9 $\pm$
	7.8	11.8	10.4	10.7	13	12.6	13.4	6.5
<b>Surface duration (min)</b>	2.3 $\pm$	2.4 $\pm$	2.7 $\pm$	2.5 $\pm$	2.2 $\pm$	2.4 $\pm$	2.3 $\pm$	2.4 $\pm$
	0.3	0.6	0.9	0.8	0.9	1.1	1.2	0.9
<b>Bottom time (%)</b>	35.1 $\pm$	33.1 $\pm$	40.7 $\pm$	42.6 $\pm$	39.2 $\pm$	39.4 $\pm$	37 $\pm$	38 $\pm$
	22.3	26.1	26.5	26.3	26.2	23.6	26.9	27.6
<b>Bottom time (min)</b>	16.3 $\pm$	15.5 $\pm$	18.5 $\pm$	18.3 $\pm$	14.4 $\pm$	12.4 $\pm$	10.6 $\pm$	11.4 $\pm$
	10.9	13.3	13.4	12.9	11.2	9.4	9.8	9.1
<b>TAD</b>	0.79 $\pm$	0.78 $\pm$	0.8 $\pm$	0.82 $\pm$	0.75 $\pm$	0.75 $\pm$	0.72 $\pm$	0.77 $\pm$
	0.09	0.1	0.11	0.1	0.15	0.14	0.18	0.12

## **Discussion**

Female alternative mating strategies may be important determinants of reproductive performance, but have been largely overlooked until recently (Knott et al. 2010; Morris et al. 2010). Female choice has been assumed to match male strategies, since females mating with the winners of male-male contests are assumed to provide a genetic benefit to their offspring (Andersson 1994; Reichard et al. 2005). Therefore, in extremely polygynous species like the southern elephant seal, it is assumed that females choose these victorious males, and avoid alternative male strategies adopted by less successful males (e.g. Kiyota et al. 2008). Studies have suggested that females may also select larger harems to reduce harassment (Galimberti et al. 2000), suggesting that female choice results from factors other than direct genetic benefits (Wiley & Poston 1996). The ability of females to adopt alternative mating strategies may not necessarily be linked to mate choice but to the ability to adapt to an environment with patchily distributed resources (Weir & Rowlands 1973).

We show that interrupted breeding is more common than previously thought in southern elephant seal females at Marion Island. Mature females could skip breeding seasons if they (a) remain at sea (if no pup is born) where she then mates, (b) haul out to breed elsewhere, or (c) are present at the natal site, but not detected. Neither of the latter options are likely. Females are highly philopatric to initial breeding sites (Hofmeyr 2000; Fabiani et al. 2006) and are physiologically capable of breeding annually (Laws 1956). It is unlikely that they are hauling out to breed elsewhere because they would be utilising unfamiliar habitats both terrestrially and pelagically. Alternating breeding sites may require knowledge of multiple foraging grounds,

unlikely in a species in which the exploitation of patchily distributed food resources shows foraging site fidelity (Bradshaw et al. 2004), and variability in foraging behaviour is observed between populations (e.g. Campagna et al. 1999; Biuw et al. 2007; Tosh et al. 2009). Although some individuals could have been present but not recorded (see Gimenez et al. 2008), our intensive and repetitive resighting schedule results in a high detection probability (high detection probability:  $p_{obs} = 0.9629$ ,  $SD = 0.0015$ ), suggesting that almost all individuals will be sighted if they are present.

Uninterrupted breeding is assumed because almost all females on land give birth and also mate. However, our observations suggest that most females (>99%) only haul out terrestrially if giving birth and raising a pup. Otherwise, she remains at sea, avoiding the terrestrial mating harems. Our two satellite-tracked individuals probably mated pelagically and not near the shore or other terrestrial colonies. The older female may have mated at or near the sea surface, since aquatic mating is a common strategy for the majority of phocid seals (Boness et al. 2002). Alternatively, she may have mated on an ice floe, a substrate sometimes utilized for breeding by southern elephant seals inshore at Signy Island (Laws 1956). The primiparous female was too far from land or ice, and therefore must have mated pelagically. Without mating opportunities at sea, a female would forfeit an additional breeding opportunity the following year if she was solely dependent on a polygynous scenario for mating.

We therefore suggest that an alternative mating system is operating based on non-polygynous opportunistic sexual encounters at sea. Adult females showing multi-year fidelity to foraging regions (Bradshaw et al. 2004), may include those that skip a pupping season. Since up to 75% of the adult male population is at sea during the

breeding season (Le Boeuf & Laws 1994), exploiting profitable foraging areas (Biuw et al. 2007), frequent fortuitous encounters with adult females seem likely (see Harcourt et al. 2007 for a Weddell seal, *Leptonychotes weddellii*, example). The benefits of continued foraging and the availability of males, that probably use scramble competition (Boness et al. 1993, 2002) to access females, appears to be more important to a non-pregnant female than the indirect benefits of finding a “good mate” ashore within the aggressively competitive polygynous system in southern elephant seals (Boness et al. 1993, 2002; Galimberti et al. 2000). Furthermore, females may actively avoid the land-based polygynous mating system when not required to haul out to give birth. Previous studies have shown that harassment by males on these harems is an important determinant of harem choice by female seals (Galimberti et al. 2000; Cappozzo et al. 2008). We propose that non-pupping females avoid the mating harems in order to gain foraging benefits and reduce harassment. Females may only haul out when required to do so to give birth, enabling males to defend harems and dominate particular areas.

Elephant seals have always been considered as the model species of extreme polygyny, yet with basic long-term monitoring data, we show that it is possibly not the only important mating system available to them. Both males and females are potentially using alternative strategies not associated with land-based polygynous contest-based harems. Over the course of 25 years, more than half the breeding females in our sample demonstrated repetitively interrupted breeding histories, and probably mated at sea during their non-pupping season. Re-evaluation of demographic analyses of southern elephant seal populations which have been based on the assumption of uninterrupted breeding histories and focussed on terrestrial breeding

behaviour is now necessary. It is possible that focussing on the most obvious male strategy without considering the possibility of female alternative strategies has led to a misinterpretation of the elephant seal mating system.

Most studies on polygynous mating systems have focussed on male mating strategies, assuming that females benefit from mating with the most dominant males. Our study shows that females may also employ alternative mating strategies, and other recent studies have shown that female strategies are more varied than previously assumed (e.g. Brennan et al. 2008; Morris et al. 2010). Furthermore, male harassment of females is increasingly recognized as a major determinant of observed grouping and mating patterns (e.g. Linklater et al. 1999; van Schaik & Kappeler 1997). Consequently, we need to reassess the assumptions that females in extremely polygynous species benefit by assessing competitive males and employ only limited alternative strategies. We suggest similar re-evaluations of extreme polygyny should be undertaken by focussing on variation in female as well as male strategies.

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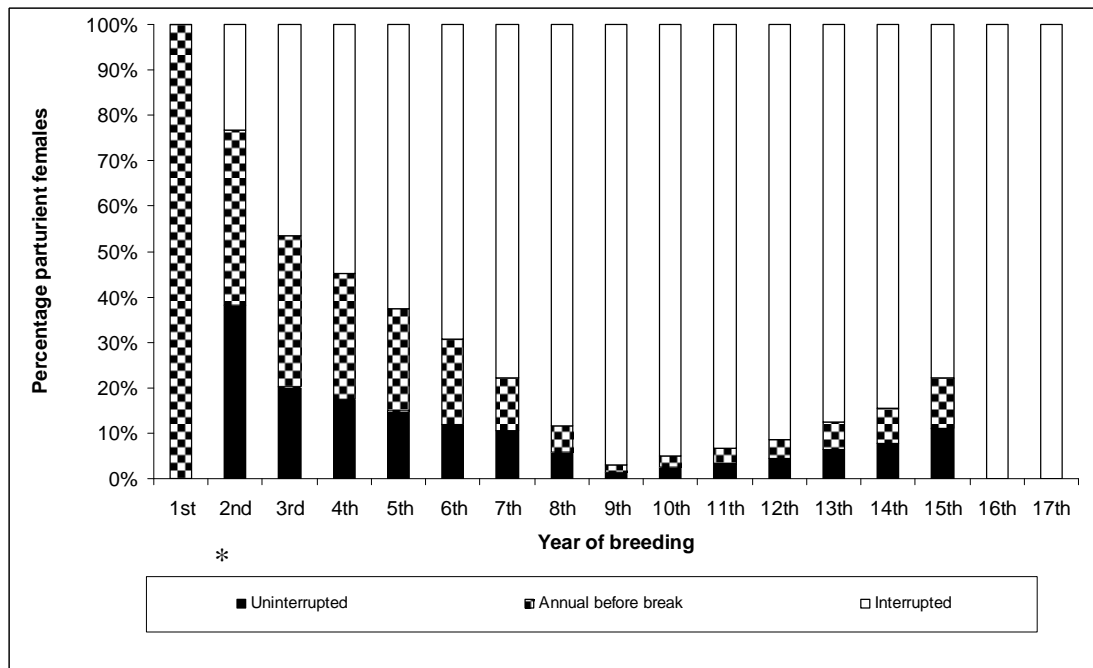


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**Figure 1.** Relative percentages of breeding female southern elephant seals ( $n = 1032$ ; from cohorts 1983 to 1997 inclusive) categorised as: (1) Uninterrupted breeding – females that bred annually from primiparity to disappearance from the study ('death'); (2) Annual before break - breeding annually for at least two seasons, then skipped a season ahead of subsequent resumption of breeding; or (3) Interrupted breeding – random intervals among breeding seasons. "Year of breeding" represents breeding occasions from first to last (not considering actual calendar year), regardless of the female's age at primiparity (only female primipari  $<6$  yrs were considered). The increasing proportion of uninterrupted breeding in later years ( $>9$  years) is a result of diminishing numbers of breeding females beyond this age, but comparatively more with uninterrupted schedules persisting.

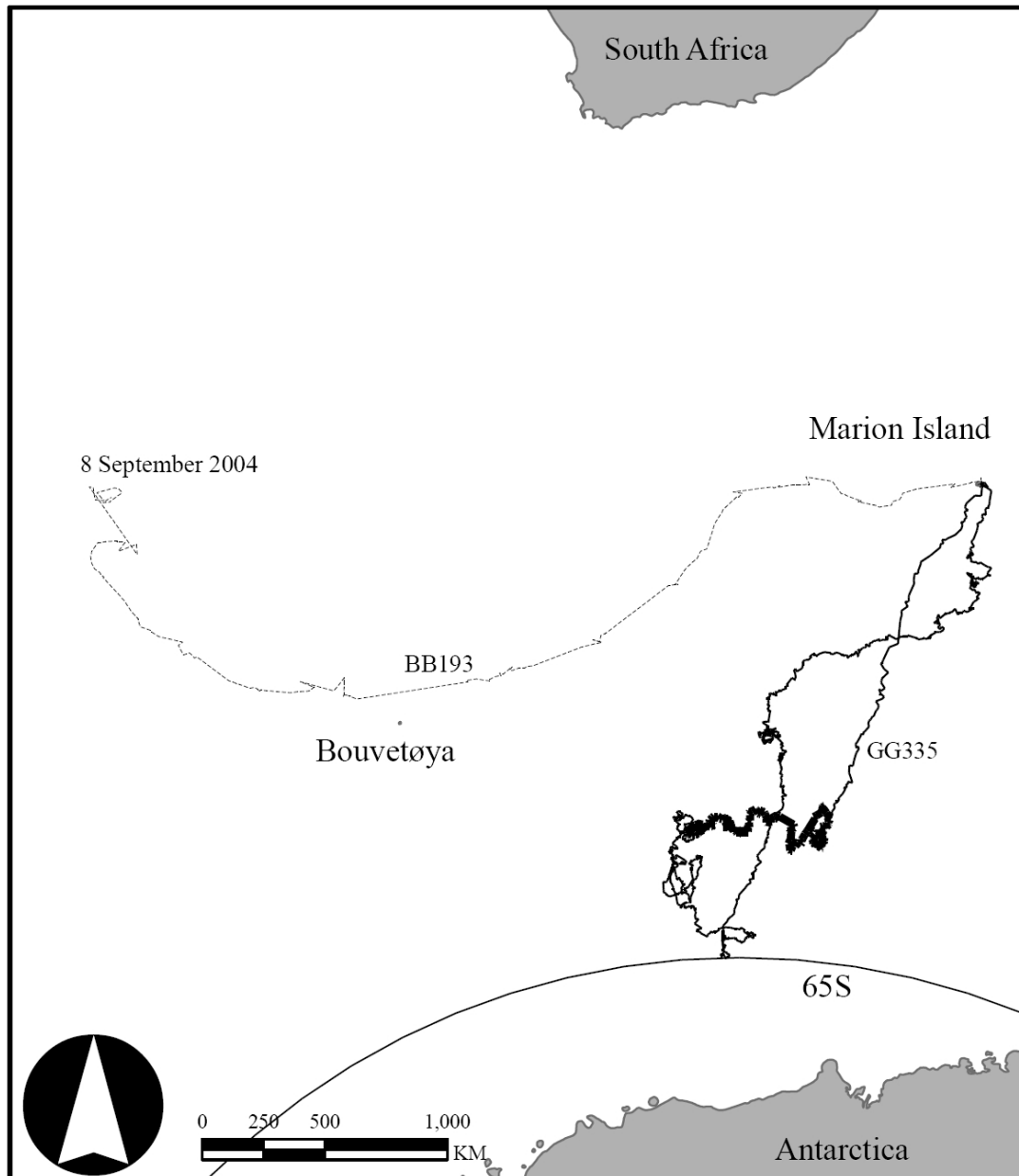
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**Figure 2.** The movements of BB193 (2004) and GG335 (2008) at sea. BB193 returned to Marion Island at the end of 2004 to moult and pupped in 2005; GG335 returned at the end of 2008 to moult and pupped during the 2009 breeding season. Both animals were absent from Marion Island during the preceding breeding season. The portion of the track corresponding to the duration of the breeding season is indicated in bold for GG335's track. BB193's track ended at the start of the corresponding time period of the breeding season at Marion Island.



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