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Genetic tagging reveals extreme site fidelity in territorial male Antarctic fur seals *Arctocephalus gazella*

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Abstract

Genetic tagging, the identification of individuals using their genotypes, provides a powerful tool for studying animals that are difficult to observe or identify using conventional techniques. However, despite being widely adopted by conservation biologists, the full potential of this approach has yet to be realized. Here we used genetic recapture data to quantify male site fidelity at a colony of Antarctic fur seals where an aerial walkway provides unprecedented access and individual positions are determined daily to 1 m accuracy. Because males are too large and aggressive to be captured and fitted with conventional tags, we remotely collected 770 tissue samples over eight consecutive seasons and used nine-locus microsatellite genotypes to reveal 306 genetic recaptures among 464 unique individuals. Within seasons, males are highly site-faithful, with any movements that occur tending to take place before the period when females come into oestrus. Of those males that return to breed over successive seasons, almost half return to within a body length of where they were before. The discovery of such extreme site faithfulness has implications for the population structure and mating system of fur seals and potentially other colonially breeding species.

Keywords: genetic tracking, microsatellite, territory, site faithfulness, mating system, resource-defence polygyny, prior residence, male-male competition, dear enemy, genetic structure, pinniped

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Introduction

Individual identification forms the keystone of much behavioural and ecological research. However, individuals of many species are difficult to capture and tag effectively, elusive or live in inaccessible sites. Consequently, biologists are increasingly turning to genetic tagging, in which individuals are identified using their genotypes (Palsböll 1999). Genetic tags are permanent, enabling individuals to be followed throughout their lives, and provide a theoretically unambiguous means of identification. Furthermore, the development of hypervariable microsatellite markers that are both ubiquitous in eukaryote genomes and amplifiable from small amounts of DNA has made genetic tagging increasingly accessible.

Used in conjunction with noninvasive sample collection, genetic tagging has proven a particularly powerful tool for studying natural populations of threatened species. So far, conservation geneticists have used this approach for estimating population size (e.g. Taberlet *et al*. 1997; Kohn *et al*. 1999; Ernest *et al*. 2000; Dallas *et al*. 2003), monitoring population dynamics (Prugh *et al*. 2005), and characterizing dispersal (Palsböll *et al*. 1997) and hybridization (Adams *et al*. 2003). However, the full potential of genetic tagging remains to be fulfilled. For example, in behavioural studies genetic tagging could in principle be combined with spatial data to study spatial aspects of behaviour, such as site fidelity.

Site fidelity is an important component of mammalian territorial behaviour that may profoundly influence mate choice, metapopulation dynamics and population genetic structure (e.g. Matthiopoulos *et al*. 2005). In mating systems characterized by intense male–male competition, strong site fidelity may be adaptive for a number of reasons. First, studies of numerous species ranging from butterflies to elephant seals show that resident males consistently win over intruders (Davies 1978; Baugh & Forester 1994; Haley 1994; Cutts *et al*. 1999). Hence, fidelity to a site may confer a 'prior residence' advantage. Second, maintaining strong

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fidelity across seasons may facilitate the reoccupation of previously held territories (Baird *et al*. 2001; Forstmeier 2002). Finally, site fidelity may be sufficient to create highly stable neighbourhood networks. Having familiar neighbours may reduce overall levels of conflict (the 'dear enemy' phenomenon, Beletsky & Orians 1989) because males have already evaluated each other, plus neighbours can cooperatively exclude incomers.

Pinnipeds make excellent subjects in which to test hypotheses relating to territory site fidelity because (i) territory quality is not a confounding factor as in many birds; and (ii) they are among the most polygynous of all species. However, relatively few empirical data are available because pinnipeds frequently live in inaccessible colonies and adults are often large and aggressive, limiting or often precluding the use of conventional identification methods. Consequently, published studies are few and tend to be limited to relatively small numbers of individuals, few seasons, and often just one sex. These studies have demonstrated varying degrees of site fidelity. Male Hooker's sea lions return to the same breeding colony year upon year, but do not show fidelity to 40 m × 80 m subsectors (Beentjes 1989). Grey and harbour seals show greater levels of site specificity, although this can be difficult to quantify because of the large size of territories (covering many tens or hundreds of square metres) and variation both within and among years in their shape and size (Twiss *et al*. 1994; Van Parijs *et al*. 2000; Hayes *et al*. 2004). Qualitative observations of Alaska fur seals by Kenyon (1960) indicate that fidelity may be strong ('a well worn spot develops where the bull habitually tries to sleep or rest'). However, perhaps the most comprehensive study of site fidelity comes from Gentry (1998). His analysis of over 1000 northern fur seals found that males typically occupy between three and seven 25 m^2 subsectors within a season, and usually return to within 10 m of territories held in previous seasons.

A long-term study of an Antarctic fur seal colony at Bird Island, South Georgia is ideally placed to examine territorial site fidelity in a sexually dimorphic, strongly polygynous pinniped. Antarctic fur seals breed at high-density rookeries on sub-Antarctic islands and exhibit resource-defence polygyny (Bonner 1968; McCann & Doidge 1987). Adult males begin to establish territories on breeding beaches during early November, about 1 month before the arrival of females, each carrying a fetus conceived the previous season (McCann 1980). Females give birth 2 days after coming ashore and then come into oestrus 6–7 days later and are mated (Duck 1990). Mating is polygynous and territorial tenure is a key predictor of paternity (Hoffman *et al*. 2003). However, holding a territory is costly because males fast throughout their tenure, losing weight at a rate of 1.5 kg/day (Boyd & Duck 1991) and injuries incurred during territorial disputes constitute a major cause of death (Baker & McCann 1989).

To quantify male site fidelity in Antarctic fur seals, we focused on a well-studied breeding colony where unprecedented access is provided by an aerial walkway and individual positions are determined daily to 1 m accuracy. Because adult males are too large and aggressive to be captured and fitted with plastic tags, we employed genetic tagging, collecting over 700 tissue samples and then using nine-locus microsatellite genotypes to reveal recaptures. We also used data from a tagged population of over 500 adult females to compare the strength of both inter- and intra-annual site fidelity for males and females. Specifically, we test the hypothesis that in a strongly polygynous terrestrially breeding pinniped, territorial males will exhibit strong fidelity, perhaps stronger than females.

Materials and methods

Study site, individual identification and observational data

This study was conducted at Bird Island, South Georgia (54°00'S, 38°02'W) during the austral summers of 1994/1995–2001/2002 (hereafter, breeding seasons are referred to by the year in which they began). The study population was located at a small cobblestone breeding beach, separated from adjacent breeding sites by a cliff on the east side, open sea on the west and rocky ridges to the north and south. The beach covered an area of 440 m^2 at high tide (Lunn & Boyd 1993). An elevated scaffold walkway (Doidge *et al*. 1984) provided access to all parts of the beach and enabled animals to be observed and tissue-sampled with minimal disturbance.

Adult territorial males were too large and aggressive to be fitted with plastic identification tags. Consequently, each season males occupying territories were individually marked using small patches of gloss paint (Arnould & Duck 1997). These marks generally persisted for the full duration of the season, but were re-applied if they became faint. To monitor the presence and locations of territorial males on the beach, daily surveys were made from 01 November until the end of the pupping period (early January). The locations of animals were recorded to the nearest square metre relative to grid markings painted on the scaffold walkway.

Tissue sampling, DNA extraction and microsatellite genotyping

The majority of males holding territories on the study beach and surrounding rocks were remotely sampled using a biopsy dart system (see Hoffman *et al*. 2003). However, because males present on the rocks were too far away from the grid markings painted on the scaffold walkway to accurately pinpoint their locations, spatial analyses were restricted to animals present in the central study area, where

Table 1 Numbers of tissue samples collected from territorial males present in the central study area during 1994–2001

Year	Number of tissue samples collected
1994	109
1995	131
1996	66
1997	27
1998	0
1999	125
2000	149
2001	163
Total	770

a total of 770 tissue samples were collected (Table 1). Sampling equipment was cleaned using ethanol between uses. Skin samples were stored individually in the preservative buffer 20% dimethyl sulphoxide (DMSO) saturated with salt (Amos & Hoelzel 1991) and stored at –20 °C. Total genomic DNA was extracted using an adapted Chelex 100 protocol (Walsh *et al*. 1991) and genotyped using a panel of nine dinucleotide-repeat microsatellite loci as described in detail elsewhere (Hoffman & Amos 2005). These loci exhibited clear banding patterns and were highly polymorphic, yielding up to 19 alleles per locus. None of the loci showed significant deviations from Hardy–Weinberg or linkage equilibrium following sequential Bonferroni correction for multiple statistical tests (e.g. see tables 2 and 3 respectively in Hoffman *et al*. 2006). The genotyping error rate, assessed by independently re-genotyping 190 individuals at all nine loci was low, at 0.0038 per reaction or 0.0022 per allele (Hoffman & Amos 2005).

Identity checking

To identify adult males that may have been sampled more than once among and/or within years, microsatellite data were checked for duplicate entries using the program IDENTITY (Allen *et al*. 1995). Since it is possible for different individuals to have identical multilocus genotypes where too few loci are used, we first calculated the probability of identity (P_{ID}, Paetkau & Strobeck 1994) across all individuals and all loci. This was very low (1.354×10^{-12}), indicating that identical genotypes almost certainly represented resampled individuals. Due to the possibility of relatives being present in the population, we also took the conservative measure of calculating the P_{ID} among siblings ($P_{ID\,Sib}$, Waits *et al*. 2001). This was sufficiently low (1.20×10^{-4}) to distinguish even full siblings with high confidence. Finally, since genotyping errors can lead to overestimation of the number of individuals present in a population (Creel *et al*. 2003; Waits & Leberg 2003), we checked autoradiographs for scoring errors whenever any two genotypes mismatched at a single locus, thereby identifying a small number of errors (n = 23) that were subsequently corrected. Resulting records of genetic identity were compared with field data and, whenever genetic analysis revealed mistaken identity, field records were modified accordingly.

Spatial analyses

All spatial analyses were restricted to years in which males were sampled enabling unequivocal identification. Individual seals were present for very different lengths of time, some coming ashore for much of the season while others were present for only one or a few days. Similarly, while some individuals were sighted in several years, many were only recorded in one or two seasons. Consequently tabulation of all possible differences in location, whether within or between years, will give undue weight to those animals who stay longer and have greater longevity. To avoid this bias we restricted our analyses to consecutive recorded locations both within and among seasons, and those chose a random single value from each distribution to represent each animal. In practice, the resulting distribution appeared virtually identical to the full data set where all observations were used. Comparisons between seasons required a single location for each season, and these were taken as the coordinate given by the average X-value and the average Y-value on the grid.

Adult female site fidelity

For comparison against territorial males, we also collected spatial data for adult females observed on the beach during the study period. To enable identification, 581 randomly selected adult females were tagged using cattle ear tags (Dalton Supplies) placed in the trailing edge of the foreflipper (Lunn *et al*. 1994). Due to time constraints, it was not possible to record the daily locations of females throughout the study. Therefore, interannual site fidelity was calculated using the pupping locations of tagged females. To estimate within-season spatial fidelity, daily observations were collected for all tagged females present on the study beach during 2001.

Results

We used genetic tagging to quantify territorial male site fidelity in a natural population of Antarctic fur seals. A total of 770 tissue samples were collected in the central study area over eight consecutive breeding seasons (Table 1). These samples were genotyped at nine highly polymorphic microsatellite loci, yielding 306 genetic recaptures among 464 unique individuals (Table 2). Given that paint marks were used to identify individuals only in the short term, the majority of recaptures (n = 274, 89.5%) were among

Table 2 Summary of genetic recapture data for 464 Antarctic fur seal males observed in the central study area during 1994–2001

Number of times male sampled	Number of males (among seasons)	Number of males (within seasons)	Number of males (total)
1	286	432	275
2	109	32	106
3	51	0	59
4	10	0	16
5	7	0	6
6	1	0	2
> 1	178	32	189

seasons, with each individual being sampled up to a maximum of six times. The remaining 32 recaptures were within seasons, indicating that paint-marks occasionally fade or are lost within a season.

Intra-annual site fidelity

To examine whether males show fidelity to particular locations on the study beach within years, we calculated for each male a distribution of distances between consecutive locations and then randomly selected one distance per male. The analysis was restricted to individuals that were observed on 2 or more days (n = 437). Figure 1a shows that over 80% of males moved less than 2 m between consecutive

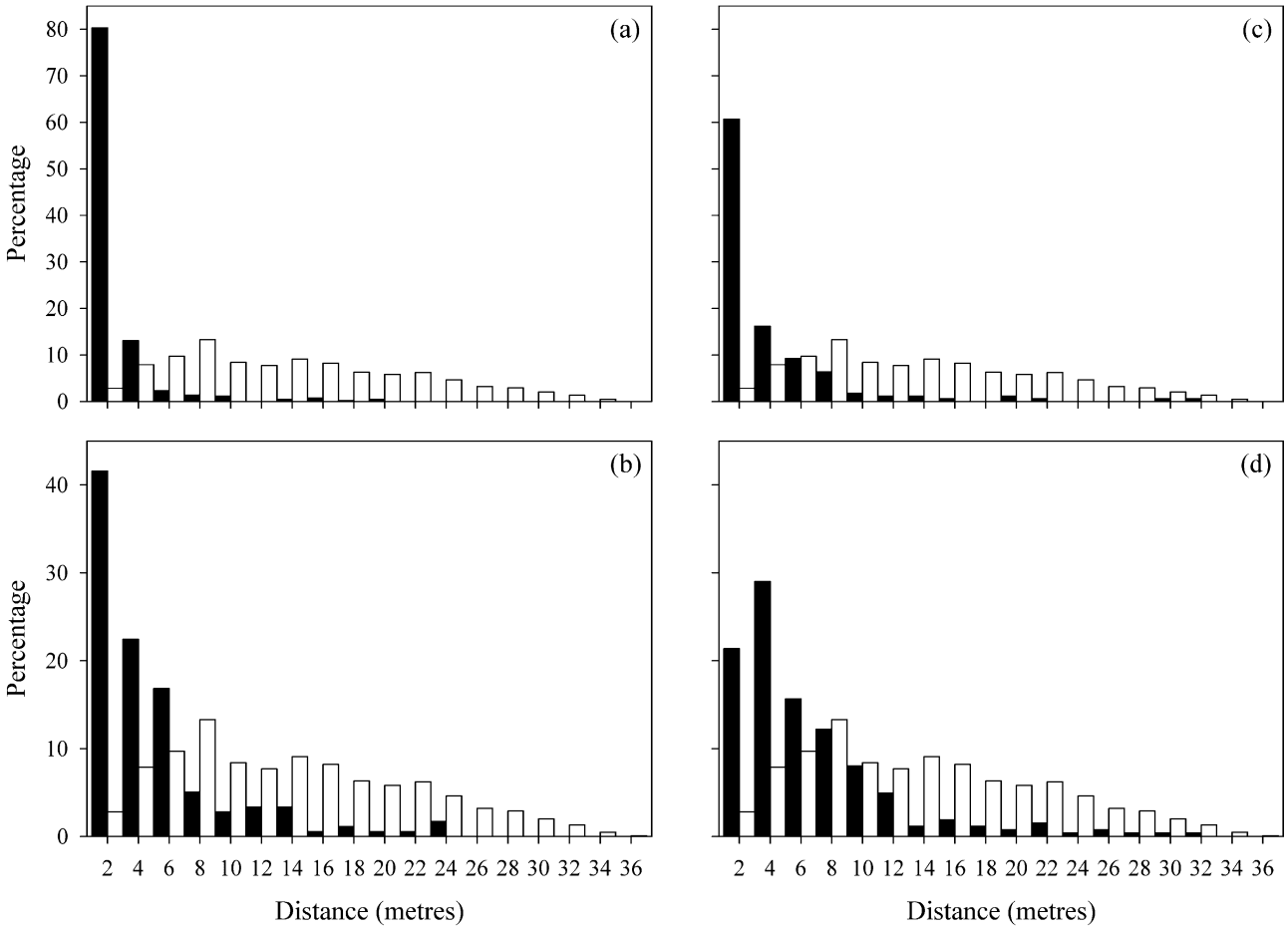

Fig. 1 Summary of distances between consecutive recorded locations for 464 tissue-sampled territorial males and 581 tagged adult females observed in the central study area during 1994–2001. (a) males within seasons (n = 437); (b) males among seasons (n = 178); (c) females within seasons (n = 173); (d) females among seasons (n = 262). Numbers of comparisons are smaller than the total number of animals because many individuals were only sighted in one season and/or for a single day within a season. Because animals came ashore for varying numbers of seasons and days within seasons, we weighted each individual equally by choosing a random single value from each distribution to represent each animal. For interannual comparisons, male locations for any given season were calculated by averaging the X- and Y-coordinates of all daily locations, and female locations were taken as their pupping coordinates. The female intra-annual distribution is based on a single season (2001). A randomised distribution (white bars) representing distances between 1000 randomly selected individuals in random years is included for comparison.

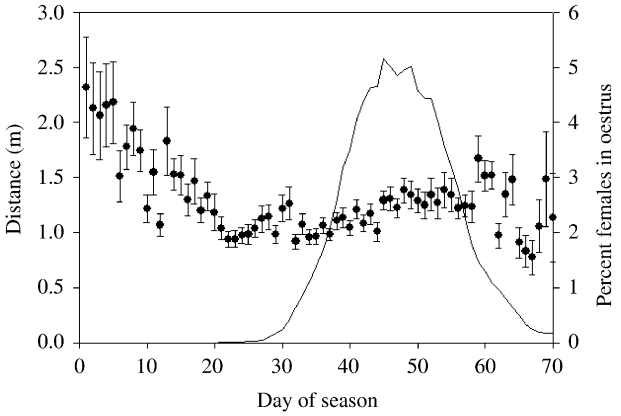

Fig. 2 Within-season profile showing daily changes in location (mean distance ± 1 SEM) by day, averaged over all years and all males, relative to the proportion of females estimated to be in oestrus.

sightings. A random distribution representing geographic distances among 1000 randomly selected individuals in random years is clearly different, with body length displacements constituting a small minority of all values.

To determine whether there is any pattern to any movements made within seasons, we plotted daily changes in location by day, averaged across males and across seasons (Fig. 2). The resulting pattern suggests that most movement occurs at the start of seasons, with any movement of males in the middle of the season being indistinguishable from measurement error. The implication is that most key disputes are resolved early, and that the arrival of receptive females reduces rather than stimulates attempts to improve territory size or position. Since males vary greatly in when they arrive and how long they spend ashore, it is unclear whether all males show the same pattern, regardless of when they arrive. To test this possibility, we re-plotted the data with every male's tenure normalized to a scale of 1% = arrival day through to 100% = departure day. When this was carried out, the pattern was largely destroyed (data not shown), suggesting that patterns of male movement are dictated by time relative to the start of the season and do not simply reflect increased restlessness near arrival and departure.

Interannual site fidelity

To examine variation in territory locations among years, we calculated distances between mean locations between one season and the next over all seasons for each male, and then to ensure that all males contribute equally to the distribution, randomly selected one observation to represent him. Analyses were restricted to males sampled during 2 or more years ($n = 178$). Remarkably, over 40% of males returned to within 2 m (one body length) and over 80% to within 6 m of sites that they occupied the season before (Fig. 1b).

Adult female site fidelity

For comparison against territorial males, we examined location data for 581 tagged adult females that came ashore during the study. Intra-annual comparisons were restricted to 217 females observed during 2001, of which 173 were sighted on two or more days. Female movements within seasons were again far smaller than expected by chance (Fig. 1c), but the degree of site faithfulness was significantly lower than that of males (mean distance moved = 3.04 m for females vs. 1.56 m for males; Mann–Whitney U test, $U = 47438$, $n_1 = 173$, $n_2 = 437$, $P < 0.0001$). A similar pattern was obtained for interannual comparisons (Fig. 1d, $n = 262$ females pupping in two or more seasons), with females exhibiting lower levels of site fidelity than males (mean distance moved = 5.72 m for females vs. 4.22 m for males; Mann–Whitney U test, $U = 29392$, $n_1 = 178$, $n_2 = 262$, $P < 0.0001$).

Discussion

Using genetic tagging, we reveal an extraordinary tendency not only for territorial males to remain more or less in one place during a season but also to return to within little more than one body length of where they were in previous seasons. Any movement that does occur within seasons also tends to take place before the period when most females come into oestrus. Such extreme site fidelity has the potential to exert a powerful influence on the population structure and mating system of the species.

Previous non-genetic studies of site fidelity in male pinnipeds have for the most part relied on small sample sizes due to logistic difficulties of tagging permanently such large and often aggressive animals. The picture that emerged was variable, with site fidelity varying from Hooker's sea lions who return simply to the same beach, down to northern fur seals that occupy between three and seven 25 m^2 sectors within a season, and tend to return to within approximately 10 m of these areas across seasons (Gentry 1998). Such fidelity is strong, but our study reveals what we believe is the most extreme case yet documented, with almost half of all males returning to within a body length of their position the previous season. Indeed, we are not aware of this level of site fidelity being exceeded by either sex. One possible reason why movements are so slight could be that the study beach is relatively small (440 m^2 at high tide, Lunn & Boyd 1993), thereby limiting where animals can sit. However, this seems an unlikely explanation because the observed distribution of movements is far smaller than the range of given by the randomized distribution and also females breeding on the same beach show lower levels of fidelity.

A further surprise is that males show greater site fidelity than females. Although there are a few exceptions, the

commonest pattern in mammals is for females to show the strongest site fidelity/philopatry. By implication, the extreme site fidelity shown by male fur seals may be adaptive for males. Most obviously, fidelity to a site may confer a 'prior residence' advantage, as in northern elephant seals (Haley 1994), or facilitate the reoccupation of territories held in previous seasons (Baird *et al*. 2001). Additionally however, when movement is minimized any given male has a relatively small repertoire of neighbours and may well be able to know his place in the dominance hierarchy without having to engage in potentially damaging combat. Testing this hypothesis would require extensive field observations of the number of aggressive interactions experienced by a male relative to his propensity to shift position both within and between years.

Extreme site faithfulness may have important consequences for both colony genetic structure and the mating system of the species. Kenyon notes that photographs taken of an Alaskan fur seal colony during the 1890s 'show virtually the same pattern of distribution of harems as today' (1960), and that this 'bears no relation to geographic features'. This supports our observations and raises the possibility that strong fidelity, especially if coupled with natal philopatry, could generate genetic structures that remain stable over time. In a polygynous breeding system where relatively homozygous individuals appear less fit (Hoffman *et al*. 2004), selection should favour behaviours that minimize inbreeding and one way to achieve this could involve a stable structure within which related individuals of opposite sex tend not to be neighbours. Future research will address these and related topics.

Conclusion

We have used genetic tagging to show that male Antarctic fur seals are remarkably site-faithful, both within and among seasons. It is not known how they achieve this, but in such an aggressive species the benefits of strong male site fidelity could be numerous and the potential impacts upon both the mating system and colony genetic structure profound.

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