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Alternative mating tactics in the New Zealand fur seal (*Arctocephalus forsteri*): when non-territorial males are successful too

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Abstract. In polygynous mammals, the status of many males does not allow them to have a high social rank and theory predicts selection for alternative mating tactics. Alternative tactics were suggested to explain discrepancies between mating and paternity successes in several pinniped species. However, information on alternative tactics in fur seals is limited. Here, we focus on the polygynous New Zealand fur seal, *Arctocephalus forsteri*, predicting that competition for females is likely to cause a diversification of male mating tactics and that non-territorial tactics can yield reproductive success. We describe the behaviour of 38 males in a medium to large colony. Paternity success was assessed using CERVUS and PASOS, from a pool of 82 pups sampled at the study site and at neighbouring breeding areas. To see whether size is correlated with mating tactic, the length of 17 males was estimated using photogrammetry. Cluster analysis identified three male behavioural profiles: one corresponding to large territorial males and two illustrating alternative tactics employed by smaller non-territorial males. Of the 13 pups born at the study site that were assigned a father, eight were sired by three territorial males and five were sired by non-territorial males. Our study highlights that holding a territory is not a necessary condition for reproductive success in all otariids.

Additional keywords: alternative tactics, fur seals, male mating strategy, pinnipeds, reproductive success.

Introduction

In polygynous mammals, reproductive success is typically more variable in males than in females and it is usually females that provide parental care. Competition between males is strong, with the more competitive males achieving more matings than their rivals (Darwin 1871; Trivers 1972; Emlen and Oring 1977). Only a subset of all males gain reproductive access to females, depending on their individual status. Status is determined by conditional factors such as genetics, ontogeny, age, size, disease and pathogen load. When differences in status create differences in male relative fitness, selection is predicted to favour the development of alternative mating tactics (Maynard Smith 1982; Gross 1996; Shuster and Wade 2003; Tomkins and Hazel 2007; Oliveira *et al*. 2008).

Several theories, based on game theory (Maynard Smith 1982), have been developed around alternative reproductive phenotypes in relation to their costs and benefits to evolutionary fitness (reviewed in Gross 1996; Shuster and Wade 2003; Oliveira *et al*. 2008). The simplest explanation is genetic polymorphism for several strategies, but this is rare (Gross 1996). Other explanations propose the existence of alternative tactics within a genetically monomorphic strategy (Maynard Smith 1982; Gross 1996). To date, almost all alternative reproductive phenotypes within the sexes have been explained as alternative tactics within a so-called conditional strategy (Gross 1996). This theory proposes that individuals adopt tactics according to their relative status (competitive ability) in the population. A classic example of conditional strategy is the use of fighting or sneaking as alternative mating tactics depending on body size (Gross 1996). This 'status-dependent selection' model assumes that individuals are genetically monomorphic with respect to their ability to express an alternative life history (Shuster and Wade 2003).

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Adoption of a particular maturation phenotype depends upon individuals achieving a specific 'threshold' condition or status (Gross 1996). Shuster and Wade (2003) likewise argue that in strongly polygynous systems, sexual selection will favour alternative mating tactics in males whose status does not favour competitive abilities. Numerous examples of alternative mating tactics have been documented in an increasing list of vertebrate taxa (for a review see Oliveira *et al.* 2008), including mammals (Rasa 1989; Clark *et al.* 1997; Hogg and Forbes 1997; Soltis *et al.* 1997; Linklater *et al.* 1999; Coltman *et al.* 1999*a*; Heckel and von Helversen 2002).

The mammalian systems studied thus far show several common tactics employed by males, including sneaking, satellite, and helper behaviours. Sneaky mating is a common tactic observed in many animal systems (Gross 1996). In elephant seals, *Mirounga* spp., for example, males similar in size to females may attempt to mimic female behaviours to obtain copulations (Hoelzel *et al.* 1999). Satellite tactics, well documented in feral horses and deer, utilise less subterfuge. Satellite males are generally subdominant individuals who would not be capable of monopolising females or holding a territory that contains resources females need. They can, however, gain some opportunity for matings by occupying the periphery of a breeding territory or harem and waiting for females to leave the security of these areas, or waiting for the dominant males to be distracted or otherwise engaged (Coltman *et al.* 1999*a*, 1999*b*; Linklater *et al.* 1999; Gemmell *et al.* 2001). In a few extreme cases, such satellite males gain significant reproductive opportunity via the formation of coalitions or alliances. Such behaviours have been documented in lions (Packer *et al.* 1991), cheetahs (Caro 1994), horses (Feh 1999; Linklater and Cameron 2000) and dolphins (Connor *et al.* 2001).

Because pinnipeds are predisposed to polygyny, they have been traditionally used as models to study polygyny in mammals, showing some of the most dramatically skewed sex ratios (Clutton-Brock 1989). The pinnipeds' environmental potential for polygyny is high because most species display female spatial clustering during a synchronous birthing season, giving some males the opportunity to gather numerous mating opportunities in a short time (Emlen and Oring 1977). Pinnipeds are marine feeders but come onshore for parturition and postnatal pup care, with females in most systems exhibiting strong natal philopatry and breeding-site fidelity, the latter of which also extends to males (Riedman 1990). Molecular techniques to measure paternity have been introduced with success to investigate the primary mating tactic in several species. However, very few studies have specifically addressed the presence of alternative mating tactics in pinnipeds, although such tactics have been inferred on several occasions (e.g. Coltman *et al.* 1999*b*; Gemmell *et al.* 2001; Van Parijs *et al.* 2001; Harcourt *et al.* 2007). In one such study, Lidgard *et al.* (2004) compared the success of two out of four male mating tactics they described in the grey seal, *Halichoerus grypus* (Sable Island, Canada). The fertilisation rate for males using one alternative tactic (i.e. mating with departing females), while lower than for males using the primary tactic, was significantly higher than zero. This indicates the potential fitness value of alternative tactics in a population of polygynous mammals.

Thus far, the studies providing circumstantial evidence for alternative mating tactics in pinnipeds all highlight a lack of strong correlation between access to females and reproductive success (grey seal, *Halichoerus grypus*: Amos *et al.* 1993; harbour seal, *Phoca vitulina*: Coltman *et al.* 1998; Ambs *et al.* 1999; northern elephant seal, *Mirounga angustirostris*: Hoelzel *et al.* 1999; Worthington Wilmer *et al.* 1999; Antarctic fur seal, *Arctocephalus gazella*: Gemmell *et al.* 2001). In all cases, many pups could not be assigned to the males using the primary tactic, meaning that those pups had been sired either by males that did not have apparent access to females (i.e. males using an alternative tactic) or by males that used the primary tactic away from the study site (in the water or at another breeding site). In two more recent studies, improved methodologies (increasing sample size and extending the temporal scale of the study to incorporate further breeding seasons: Hoffman *et al.* 2003; or better matching the pool of males sampled for genetics and for behaviour: Twiss *et al.* 2006) still left ~40% of the paternities unassigned to males using the primary tactic. In a study of hybridisation between three species of *Arctocephalus* fur seals on Macquarie Island, Lancaster *et al.* (2007) assigned two hybrid pups to non-territorial males.

The New Zealand fur seal, *Arctocephalus forsteri*, is a polygynous, annual colonial breeder, with an apparent high degree of breeding-site fidelity observed in both sexes (Stirling 1971; Bradshaw *et al.* 2000; Boren *et al.* 2006). Females' gregariousness and specific habitat choice favours their repeated return to a preferred site (Ryan *et al.* 1997; Bradshaw *et al.* 1999). Males come ashore to establish territories at the beginning of the breeding season (austral spring), while females haul out several weeks later to give birth (Mattlin 1978). Females are in oestrus about one week after parturition, mate with males and start alternating between foraging at sea and nursing their pup onshore. The degree of polygyny ranges from 4 to 10 females per male (Mattlin 1978). Like all otariids, New Zealand fur seal females breed in denser clusters than do phocids, because female otariids need to feed at sea in between sessions on land when they suckle their pup. Female clustering occurs due to the need to give birth on land near highly productive marine food resources. Additionally, the New Zealand fur seal is a temperate-zone species with a synchronised birthing season (Gentry and Kooyman 1986). Because of female clustering and synchronised breeding, the environmental potential for polygyny of the New Zealand fur seal is high, which makes it an ideal pinniped species to investigate male mating tactics under strong polygyny.

The objective of this study was to investigate whether New Zealand fur seals display alternative tactic(s) aside from the primary territorial tactic. Following the initial arguments of Gross (1996) and Shuster and Wade (2003), we expected that high competition for females in this species should favour a conditional mating strategy within which males adopt one of several mating tactics according to their status. Because males adopt a tactic in order to increase their individual fitness, all observed tactics should yield at least some reproductive success (i.e. produce offspring). To test this hypothesis, we sorted males into objectively defined behavioural tactics and assessed their success using microsatellite genotyping. We correlated these data with male body length (as an estimator of male size), which is a major determinant of male success in many polygynous species (Andersson 1994).

Materials and methods

Study site

The Ohau Point breeding colony (42°25′0″S, 173°40′60″E), New Zealand, is a 50–100-m-wide and ~1-km-long colony backed by a steep hill. Its annual pup production in 2002–03 was ~300 pups and ~450 pups in 2003–04 (Boren *et al*. 2006), making it a medium-to-large colony for this species (L. Boren, pers. comm.). The substrate of irregular-sized and -shaped rocks creates small caves and crevices, together with rocky platforms and tide pools. This expanding colony offers fur seals suitable breeding habitat, plenty of space and close access to foraging grounds (Boren *et al*. 2006). We divided the colony into three areas: the study site (which covers ~1500 m^2, i.e. ~20% of the area of the whole colony and hosts ~16% of the colony annual pup production), North and South (the neighbouring breeding areas on each side), each of which are separated by natural landmarks (rocky/boulder ledges) and by adult haul-outs with no territories and no pupping. As an important element of colony structure, seal density was measured by dividing the total number of seals that were present during the highest of three daily counts, by the estimated study site area (1500 m^2).

Behavioural sampling

A total of 330 h of observation spread over 65 days was conducted at the study site from 30 October 2002 to 2 January 2003 inclusive (covering approximately the whole breeding season, i.e. the number of days between the establishment of the first territories and the end of the last territorial activities). Seals were observed by using binoculars and a spotting scope from a cliff-top hide ~25 m away from the colony, from 0900 to 1700 hours. For most days, eight consecutive hours of observations were carried out by two observers alternating every 2 h, except when the weather (wind and/or rain) made observations impossible. Data from days with less than two successive hours of observations were not analysed. Observer bias was not investigated since both observers were experienced with the study species and site, and cross-checked protocols for data collection during regular overlapping sessions. The total number of males that spent time at the study site during the whole study period was ~50, but could not be determined exactly since not all males were identified. Of the males that stayed in the study area long enough to be described with reliable features (~30 min), 43 focal males were identified by natural markings (e.g. flipper scalloping, nose or body scars: McConkey 1999) or artificial markings (white and yellow road oil-based paint (Resene) applied with a sponge mounted on a 2.5-m metal pole, diameter 1.8 cm). Intrusions in the colony for paint marking of males were less than 1 h each, by a maximum of two researchers and successive marking sessions were separated by at least two days without human disturbance, in order to limit the potential impact of marking on male behaviour. The paint marking was done at the beginning of the season and stopped after the first pup was born in the study area, to reduce disturbance to mothers. Unlike other taxa (e.g. many bird species), pinnipeds do not use complex body colour patterns that could be disturbed by paint marks. Considering the small proportion of the body area that was paint-marked, the wind-swept coastline and the strong natural body odour of males, we considered the impact of the temporary smell of drying paint to be negligible.

All interactions involving focal males at the study site were recorded as behavioural events (Continuous All Occurrence Sampling: Altmann 1974). Interactions and how they were pooled for analysis are detailed in Table 1 (see Stirling (1970) and Miller (1971) for descriptions of behaviours and vocalisations). The location and the time of all interactions were recorded together with the type (or identity, when it was known) of individual(s) with which focal male(s) interacted. The behavioural profile of study males was quantified using seven variables: (1) date of arrival (first day seen on the study site) counted from 30 October; (2) total number of days spent on the site (number of days that a male was recorded at the site; i.e. tenure duration for territorial males); (3) estimated area defended (m^2; a value of 1.0 was given to males that defended their resting spot only, but no area around it, nor any female); (4) overall frequency of aggressive intrasexual interactions (per hour); (5) overall frequency of submissive intrasexual interactions (per hour); (6) overall frequency of intersexual interactions (per hour); and (7) overall frequency of male dominance displays (per hour) (see Table 1).

Territory sizes were estimated using digital photographs of the study site processed with the software TurboCAD v4 (Fowler 2003). Limits of individual males' territories were based on their patrolling behaviour and location of all their daily intrasexual interactions, using scaling marks painted on rocks at known distances.

Male size

The size of a subsample ($n = 17$) of the focal males was estimated using basic photogrammetry (Baker 1960; Haley *et al*. 1991).

Table 1. The fur seal behaviours recorded in the present study

See Stirling (1970) and Miller (1971) for full descriptions of the behaviours. The behaviours were pooled into four categories (shown in bold) for analysis

Behaviours	Description
Intrasexual interactions	Walking towards, following, chasing, attacking, lunging at, fighting, investigating, having a low-intensity aggressive interaction with another male (e.g. investigating/sniffing followed by open-mouth threat). For each interaction, the focal male(s) was (were) classified as **aggressive** (the male initiating the interaction, the challenger) or **submissive** (the target, the defending male).
Intersexual interactions	Walking towards, investigating, withholding (herding), attempting to copulate and copulating with a female, accepting female advances (female biting male's neck, mounting on his back, soliciting) and vocalising to a female (whimpering).
Male displays	Vocalisations, either to another male or with no apparent target, and full-necking (upright display).

Body length from the tip of the nose to the tip of the tail was measured from digital photographs of individuals lying straight, perpendicular to the objective, using measures of natural rock marks as a scale. Body length (cm) estimated from several photographs of the same individual taken on different days over the season showed a maximum CV of 6.2% (*n* = 4 males, with 10 photographs taken on different days for each of the four males).

Genetic sampling

During the 2002–03 breeding season, male skin samples (*n* = 20) were collected from a distance using a crossbow-launched skin-sampling device (Gemmell and Majluf 1997). We were unable to sample all focal males, due to male turnover early in the season (November), and then later, to avoid disturbing pregnant females seeking a place to pup (December). Five of the 20 males sampled were defending a territory at South, where no behavioural data were collected. To investigate the result of male reproductive efforts, genetic samples were taken from mother–pup pairs during the 2003–04 breeding season, aiming at sampling all mother–pup pairs at the study site, and 10–20 pairs (~20% of the pairs present) randomly selected at North and at South, the two neighbouring breeding areas. For pups, a small piece of skin was taken from the trailing edge of the fore flipper using piglet ear-notch pliers (Majluf and Goebel 1992). For mothers, who were more mobile and skittish than males and pups, a crossbow-launched hair-sampling device was custom-designed with a sticking dart to pull hair (Caudron *et al.* 2007). Limitations in the number of mothers sampled was due to the fact that most were not individually marked and could be located only when interacting with their identified pup. A female was assumed to be the mother of a pup only if their interaction was long enough to ensure the female did not reject the pup, show any sign of hesitating between several pups or interact in a maternal fashion with another pup (a fostering rate of 0.22% was calculated in this colony: Dowell *et al.* (2008) and Haase (2007) found a similar rate of 0.17% in another colony of the same species). All genetic samples collected were stored in 70% ethanol and then in 90% ethanol one month later for long-term conservation.

Genotyping

In order to match mother–pup pairs and putative fathers, we genotyped all samples using 10 microsatellite markers. Whole genomic DNA was extracted from skin biopsies using an adapted Chelex 100™ protocol (Walsh *et al.* 1991) and from hair follicles as described in Caudron *et al.* (2007). Ten informative loci were amplified (Table 2), run and scored for skin samples (*n* = 111) as described by Robertson and Gemmell (2005). For hair samples (*n* = 45), microsatellite amplification was achieved using PCR conditions described in Caudron *et al.* (2007) and PCR products were size-fractionated on 6% denaturing polyacrylamide gels using a low-concentration alkali salt-conductive medium (Negro *et al.* 2006). Samples for which three or more loci did not amplify (*n* = 2 females out of 45 hair samples) were excluded from the dataset.

Identity checking

All files were checked for duplicate genotypes using the Identity function of CERVUS ver. 3.0 (Marshall *et al.* 1998; Kalinowski *et al.* 2007). The probability of an identical multilocus genotype occurring by chance in two unrelated individuals at all 10 polymorphic loci was calculated for each locus and across all loci using GenAlEx ver. 6 (Peakall and Smouse 2006) (Table 3), using the method of Paetkau and Strobeck (1994). As New Zealand fur seals tend to be philopatric, as a conservative measure the probability of identity assuming that all individuals are siblings was also calculated according to Evett and Weir (1998) as

Table 2. The 10 pinniped microsatellite loci used in the present study

The primer sequences, polymorphism characteristics and literature sources for each locus are shown. *N*, number of alleles

Locus	Primers sequence (5′→3′)	Allele size	*N*	Species	Reference
Hg1.4	F: CTCCAAGACGACTGAAACCC R: TACCATATCTTTGTGGCTCTG	187–209	7	Grey seal *Halichoerus grypus*	Gemmell *et al.* (1997)
Hg4.2	F: AATCGAAATGCTGAGCCTCC R: TGATTTGACTTCCCTTCCCTG	126–188	19	Grey seal *Halichoerus grypus*	Allen *et al.* (1995)
Hg6.1	F: TGCACCAGAGCCTAAGCAGACTG R: CCACCAGCCAGTTCACCCAG	143–166	10	Grey seal *Halichoerus grypus*	Allen *et al.* (1995)
Hg6.3	F: CAGGGGACCTGAGTGCTTATG R: GACCCAGCATCAGAACTCAAG	228–249	9	Grey seal *Halichoerus grypus*	Allen *et al.* (1995)
Pv9	F: TAGTGTTTGGAAATGAGTTGGCA R: ACTGATCCTTGTGAATCCCAGC	166–186	11	Harbour seal *Phoca vitulina*	Allen *et al.* (1995)
Pv11	F: GTGCTGGTGAATTAGCCCATTATAAG R: CAGAGTAAGCACCCAAGGAGCAG	151–173	11	Harbour seal *Phoca vitulina*	Goodman (1997)
3 E 3	F: GCATACTCTTCACCTACCAATGG R: CTCCAGCTAGCTTCCTCTCTTG	213–223	5	Harbour seal *Phoca vitulina*	Kappe (1998)
HI16	F: CACTTATCTCGCCCTATATCCA R: CAGCCACAGCCAACACAA	135–169	13	Leopard seal *Hydrurga leptonyx*	Davis *et al.* (2002)
Lc5	F: ATCTTCAGGCTTTCTTCT R: TTCACGGACTCAAATAAT	156–169	6	Crabeater seal *Lobodon carcinophagus*	Davis *et al.* (2002)
M11a	F: TGTTTCCCAGTTTTACCA R: TACATTCACAAGGCTCAA	135–182	18	Southern elephant seal *Mirounga leonina*	Hoelzel *et al.* (2001)
Overall		126–249	10.5		

Table 3. Genetic diversity measures for 10 microsatellite loci used to analyse individuals from the New Zealand fur seal, *A. forsteri*, colony at Ohau Point

A_N, allele number; He_O and He_E, observed and expected heterozygosity; F_{IS}, inbreeding coefficient; PIC, polymorphic information content; HW, Hardy–Weinberg disequilibrium (S: significant, i.e. $P < 0.05$ after sequential Bonferroni correction for multiple tests; NS: non-significant); PI, probability of identity between two unrelated individuals; P Excl (1), probability of parentage exclusion when only one parent is known; P Excl (2), probability of excluding two putative parents

Locus	A_N	He_O	He_E	F_{IS}	PIC	HW	Null allele frequency	PI	P Excl (1)	P Excl (2)	Error rate
Hg6.1	10	0.778	0.800	0.0589	0.827	NS	+0.0285	0.055	0.473	0.822	0
Hl16	13	0.793	0.829	0.0400	0.802	NS	+0.0197	0.054	0.480	0.829	0
Hg1.4	7	0.521	0.808	0.3636	0.780	S	+0.2084	0.064	0.444	0.805	–
Lc5	6	0.724	0.774	0.0511	0.734	NS	+0.0321	0.090	0.373	0.731	0
Hg4.2	18	0.860	0.858	0.0012	0.845	NS	–0.0076	0.030	0.579	0.906	0
Pv11	11	0.683	0.657	–0.0487	0.629	NS	–0.0228	0.143	0.272	0.673	0
M11a	18	0.793	0.817	0.0216	0.794	NS	+0.0115	0.056	0.475	0.834	0.0501
Hg6.3	9	0.731	0.791	0.0868	0.758	NS	+0.0418	0.075	0.413	0.776	0
Pv9	11	0.827	0.844	0.0192	0.822	NS	+0.0076	0.044	0.521	0.861	0
3 E 3	5	0.503	0.539	0.0641	0.500	NS	+0.0377	0.252	0.156	0.497	0
Overall	10.8	0.721	0.774		0.747			3.418×10^{-12}	0.996	0.999	0.0056

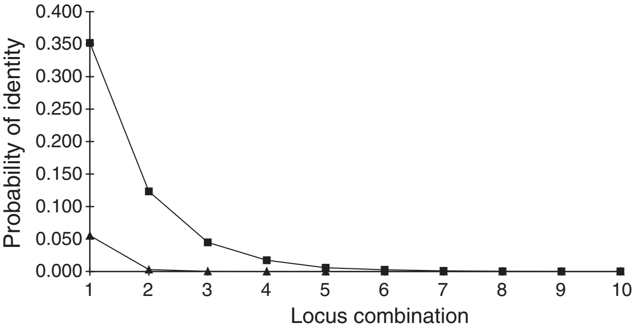

Fig. 1. Probabilities of identical genotypes between two unrelated (triangles) and sibling (squares) individuals. Locus combination means cumulative effect of loci.

implemented in GenAlEx (Fig. 1). Duplicate samples ($n = 3$ pups, $n = 1$ female) were excluded from the genotype files before analysis.

User-defined parameters and paternity allocation

Prior to paternity analysis, all 10 microsatellites were tested for their appropriateness as population genetic markers. Specifically, we tested for deviations from Hardy–Weinberg equilibrium and linkage disequilibrium (LD) using Genepop ver. 3.4 (Raymond and Rousset 1995), while null allele frequencies were estimated using CERVUS ver. 3.0 (Table 3). Probabilities of parentage exclusion (i.e. the average capability of a marker system to exclude any given relationship) were calculated according to Jamieson and Taylor (1997) using GenAlEx (Table 3).

We followed guidelines from S. S. Negro, L. Naduvilezhath and N. J. Gemmell (unpubl. data) to determine reliable user-defined parameter values to perform paternity testing. Specifically, we determined (1) the error rate in the genetic data, (2) the relatedness level in the study population, (3) the total number of candidate males. Then we (4) combined the paternity results from CERVUS and PASOS parentage programs and calculated the common assignment correctness (i.e. true common assigned and unassigned offspring divided by the total number of offspring) using simulated data with known parent–offspring relationship and based on the microsatellite data accumulated. The major cause of mismatches between offspring and their biological parents is through microsatellite genotyping errors (Hoffman and Amos 2005). To estimate the error rate of our dataset, we checked 43 mother–pup pairs for mismatches using CERVUS. The mean observed error across loci was 0.0142. One pair showed three mismatches at multiple loci, suggesting that the pair being sampled was not genuine. Excluding this pair, the mean observed error across loci was 0.0056. The relatedness estimator, R (Queller and Goodnight 1989) for our genetic data, was determined using GenAlEx ver. 6. Among the candidate fathers sampled, 10 were related with a mean R of 0.450. Finally, the total number of candidate fathers was determined using PASOS ver. 1.0 (Duchesne *et al.* 2005). The program estimated the missing portion of males (0.536) and hence calculates the total number of candidate males in the population ($n = 43$). The common assignment correctness (97%) and the proportion of common true assignments that can be resolved by both parental allocation programs (65%) were calculated in a side study (S. S. Negro, L. Naduvilezhath and N. J. Gemmell, unpubl. data) using simulated genotypes based on the same New Zealand fur seal population.

Statistical analysis

Agglomerative hierarchical clustering (Johnson 1967; Aldenderfer and Blashfield 1984) was used to sort N individual male behavioural profiles into meaningful, objective classes (Coltman *et al.* 1999*b*). Variables were standardised to minimise bias in weighting that may result from differing units and ranges. An $N \times N$ matrix was built using the Manhattan (City-block) distance, which examines the sum of the differences between the attributes of pairs of individuals. The matrix was visualised by a tree using Ward's linkage that clusters by assessing the group's variance (StatSoft 2005; Wishart 2006). (M)ANOVAs followed by *post hoc* Scheffé tests show the significantly different pair-wise comparisons between clusters. Variables were log-transformed as necessary to meet assumptions of parametric statistics (Sokal and Rohlf 1995). For data that could not be transformed (presented in the results as medians and ranges, instead of means ± s.e.), non-parametric Kruskal–Wallis tests were used. Chi-square test was used to compare the reproductive success of males of different sizes. Analyses were done using STATISTICA ver. 7.1 (StatSoft 2005).

Results

Male behaviour

The mean density at the study site was 0.02 seals m^{-2} ($n = 45$ days between 30 October and 24 December). Of ~50 males that spent time at the study site during the study period, 38 were identified and spent more than 3 h each at the study site (3 h was roughly the minimum for males to interact or to display at least once). The breeding behaviour of these 38 males was described using seven variables (Table 4). A large proportion of focal males (82%) did not defend any territory. Most were mobile, being observed in the study area at various locations during the breeding season.

To define behavioural profiles, males were sorted into objective classes, based on similarities in their breeding behaviour (StatSoft 2005). Clustering identified three classes of males (Fig. 2). Note that the variable 'territory area' was not used in the analysis, because it could not be normalised by transformation due to many males defending no area and hence scoring a value of zero. A MANOVA confirmed that the three classes significantly differed (Wilks' $F = 7.3$, d.f. = 12, $P < 0.01$) (Table 4). *Post hoc* (Scheffé) tests showed the following significant differences among all pair-wise comparisons: Class I males were characterised by a higher frequency of aggressive male–male interactions, of male–female interactions and of dominant displays than for the other classes, and a lower frequency of submissive male–male interactions. All (and only) the males of Class I defended a territory, corresponding to the primary territorial tactic. Class II males arrived later than Class III males, and stayed on-site for fewer days than the males of the two other classes. Class III males arrived earlier and stayed for more days than Class II males and did not defend any territory. Males of Classes II and III showed similar frequencies for the three other behavioural categories (submissive male–male interactions, male–female interactions and dominant displays). Classes II and III can be considered as alternative tactics which consist respectively in transience (i.e. making regular visits to the study site without any territory defence in this area) and residence at the study site without any territory defence.

The variable 'estimated size' was not included in the cluster analysis as we could only obtain it for a subsample of study males (body length range = 122–168 cm, median = 151 cm, $n = 17$). Size significantly varied between the male classes (Kruskal–Wallis H = 8.05, $P < 0.05$), with Class II males having significantly shorter body length than Class I males. Males of Class III had an intermediate average body length that did not significantly differ from the two other classes.

Only seven copulations were observed in the study area, over the total study period (330 h). A similarly low number of copulations was observed in all portions of the Ohau Point colony (Boren 2005).

Characterisation of microsatellite loci

Deviations from Hardy–Weinberg equilibrium were assessed using a Chi-square goodness-of-fit test, comparing observed genotype frequencies with expected genotype frequencies calculated from allele frequencies assuming Hardy–Weinberg equilibrium. One locus (Hg1.4) showed a significant deviation from Hardy–Weinberg equilibrium (homozygous excess), even after Bonferroni corrections for multiple comparisons (Sokal and Rohlf 1995), which could indicate the presence of a null allele at this locus; this locus was then omitted from the parentage testing. The probability of two unrelated individuals having identical genotypes for the nine polymorphic loci was negligible (3.418×10^{-12}) (Table 3). The probabilities of identity between

Table 4. The behavioural profiles of study males sorted by hierarchical clustering

A MANOVA on log-transformed data confirmed that the three classes differ significantly ($F = 7.3$, $P < 0.01$). The results of ANOVAs for each variable are detailed; Kruskal–Wallis was used for body length (only measured in a subsample of study males, could not be normalised). All pair-wise comparisons (Classes I and II, I and III, II and III) were performed by a *post hoc* Scheffé test. The symbols * and ° indicate which two classes significantly differ from each other. The variable 'Arrival date' is given as mean ± s.e. as its distribution does not significantly differ from normality

Variable	Class I: Territorial ($n = 7$ males) median (range)	Class II: Transient ($n = 16$ males) median (range)	Class III: Non-territorial resident ($n = 15$ males) median (range) unit	Notes
Time observed (h)	107.6 (30.7–285.2)	7.6 (3.0–35.5)	46 (14.9–185.2)	
Arrival date^{A} (Day 1 = 30 October)	14.4 ± 5.4	28 ± 3.4*	12.2 ± 2.9*	$P < 0.01$, univariate $F = 5.9$
No. of days onsite^{A}	16 (4–46)*	3 (2–8)*°	13 (4–34)°	$P < 0.01$, univariate $F = 12.8$
Mean territory area (m^{2})	79.2 (45.7–357)	n.a.	n.a.	
Aggressive intrasexual interactions^{A} (h^{-1})	1.6 (0.7–3.2)*°	0.6 (0.1–1.9)*	0.4 (0.2–1.4)°	$P < 0.01$, univariate $F = 9.4$
Submissive intrasexual interactions^{A} (h^{-1})	0.02 (0–0.2)*°	0.4 (0–1.6)*	0.4 (0.05–1.1)°	$P < 0.01$, univariate $F = 15.7$
Intersexual interactions^{A} (h^{-1})	1.9 (1.2–3.7)*°	0.6 (0–1.5)*	0.5 (0.3–0.9)°	$P < 0.01$, univariate $F = 5.1$
Dominance displays^{A} (h^{-1})	1.1 (0.4–2.1)*°	0.1 (0–0.7)*	0.2 (0–0.8)°	$P < 0.01$, univariate $F = 5.7$
Estimated body length (cm)	156.5 (128–168)* ($n = 6$)	125 (122–127)* ($n = 3$)	149.5 (128–166) ($n = 8$)	$P < 0.05$, K–W H = 8.05
Paternity (pups)	4 (4)*° ($n = 3$)	0.5 (0–1)* ($n = 4$)	1 (0–2)° ($n = 7$)	$P < 0.01$, univariate $F = 26.9$

[A] Clustering was based on these variables.

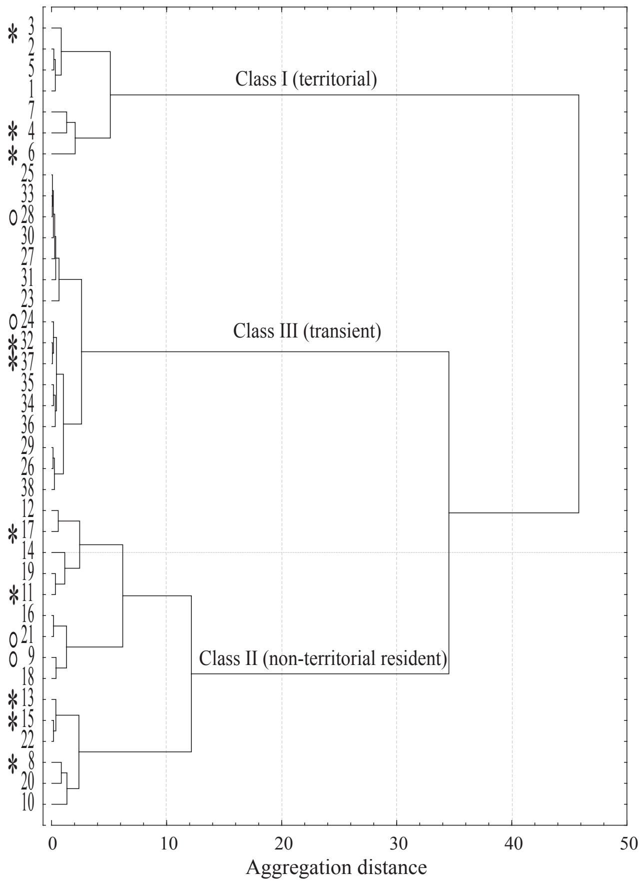

Fig. 2. Hierarchical clustering of male behavioural profiles (Manhattan distance, Ward's linkage: StatSoft 2005) suggesting three classes. Class I corresponds to territorial males. The other classes can be described as transient and non-territorial resident profiles. Genotyped males that were assigned pup(s) are indicated by *, genotyped males that were not assigned any pup are indicated by °.

unrelated and sibling individuals for increasing locus combinations suggest that identical genotypes were most likely the result of resampling. Duplicate samples were removed from the dataset.

Reproductive success of study males

Skin samples were obtained from 15 males at the study site (~30% of all males that spent time at the study site: Table 5). One of the males sampled was not included in the behavioural observations as he stayed for less than 3 h; he was not territorial. Of the 15 males sampled at the study site, only three defended a territory. The 12 others displayed a range of behaviours that included defending just a resting location or no defence at all. In all, 85 pup samples were genotyped, including 41 at the study site (88% of the total pup production at the study site), 25 at South and 19 pups at North (representing ~21% and 24% of the pup production in those areas respectively). For 42 of these samples, the attending mother was also sampled (mother–pup pairs). Of those 85 pups, analysis showed three were duplicates, so a total of 82 individual pups were genotyped. We could assign a father to 24 (29%) of the 82 genotyped pups based on the common father assignments by CERVUS and PASOS and on the assignment decisions. The number of assignments at 95% CL in CERVUS was small due to the high number of candidate males sampled being related among themselves and the mother sample not being available for many genotyped pups. Therefore, confidence level in CERVUS was set at 80% and the results combined with PASOS.

Of the 38 pups sampled at the study site (41 – 3 duplicates), 12 (32%) were assigned a known father that was observed at the study site in the year of conception and one pup was sired by a male sampled at South. Eleven additional pups that were not born at the study site but at neighbouring breeding areas (four at North and seven at South) were assigned a father sampled at the study site.

Out of 20 genotyped males, five males that were not territorial at the study site sired one pup born at the study site in the following season (Table 5). Each one of the three territorial males sampled at the study site ($n = 3$) sired pups at the study site (eight study-site pups in total, which means 21% of all pups sampled at the study site were sired by these three territorial males). In addition, two territorial males from the study site sired four pups born in other areas (two pups each).

For males that were both measured and genotyped, the average number of pups sired by large males ($\geq$156 cm, 3rd quartile for the 17 males measured) was three pups per male ($n = 4$). For medium males (<156 cm but >128 cm, 1st quartile for the 17 males measured) the average number of pups sired was one pup per male ($n = 5$). The number of pups sired by large males was significantly higher than the number of pups sired by medium-sized males ($\chi^2 = 20.0$, d.f. = 1, $P < 0.001$). Overlaying paternity results and behavioural profiles shows that males using any of the three tactics were assigned pups (Fig. 2): 100% of three genotyped Class I males, 71% of 7 genotyped Class III males and 50% of four genotyped Class II males sired pups. For the three territorial (Class I) males genotyped, the average reproductive success (2.7 pups per male) was higher than the overall average success at the study site (13 pups born at the study site to 15 potential sires genotyped from the study site, for an overall average success of 0.87 pup per male). For all non-territorial males, the average number of pups (0.33 pup per male) was much lower than the estimated average paternity for those males genotyped (0.87 pup per male). Nevertheless, of the 12 males that did not defend a territory at the study site and for which both behavioural and genetic data were collected, eight (67%) were found to have sired at least one pup.

Discussion

By combining ethology and molecular genetics to assess the paternity success of focal males, we found evidence of alternative mating tactics in a breeding colony of New Zealand fur seals. Three large territorial males sired 21% of the 38 pups genotyped at our study site. The success of these three territorial males was higher than the estimated average paternity for all males genotyped at the study site, in agreement with a skewed male success in polygynous systems. Males adopting a primary tactic for a long tenure typically achieve more successful matings than others (e.g. Boness and James 1979; Anderson and Fedak 1985; Arnould and Duck 1997; Wainstein 2000). However, our

Table 5. Main characteristics for the 44 study males (39 focal males at the study site and 5 males at South for which no behavioural data were collected)
Twenty of the males were sampled for genetics (and assigned 0–4 genotyped pups: 4th column). The behavioural classes found by clustering correspond to territorial males (I), transient males (II) and non-territorial resident males (III). SS, study site

Male	Site	Defends a territory?	No. of SS pups assigned	Behavioural class	Tenure duration (days)	Estimated body length (cm)[A]
1	SS	Y		I	4	128
2	SS	Y		I	16	168
3	SS	Y	2 + 2 at South	I	29	156
4	SS	Y	2 + 2 at North	I	46	160
5	SS	Y		I	7	
6	SS	Y	4	I	22	157
7	SS	Y		I	14	151
8	SS	N	1	II	34	155
9	SS	N	0	II	16	166
10	SS	N		II	4	
11	SS	N	1 at South + 1 at North	II	30	152
12	SS	N		II	10	
13	SS	N	1	II	31	142
14	SS	N		II	4	
15	SS	N	1	II	20	145
16	SS	N		II	15	128
17	SS	N	1 at South + 1 at North	II	10	
18	SS	N		II	6	
19	SS	N		II	20	155
20	SS	N		II	8	
21	SS	N	0	II	13	147
22	SS	N		II	8	
23	SS	N		III	8	127
24	SS	N	0	III	5	
25	SS	N		III	6	122
26	SS	N		III	4	
27	SS	N		III	5	
28	SS	N	0	III	8	
29	SS	N		III	2	
30	SS	N		III	3	
31	SS	N		III	3	
32	SS	N	1 at South	III	3	
33	SS	N		III	4	
34	SS	N		III	2	
35	SS	N		III	3	
36	SS	N		III	2	125
37	SS	N	1	III	3	
38	SS	N		III	3	
39	SS	N	2 at South	n.a.	?	
40	South	Y	0	n.a.	?	
41	South	Y	1	n.a.	?	
42	South	Y	0	n.a.	?	
43	South	Y	0	n.a.	?	
44	South	Y	0	n.a.	?	

[A] By basic photogrammetry, e.g. in Haley *et al.* (1991).

results also show that alternative mating tactics can coexist with the primary territorial tactic and provide non-territorial males some success. At the scale of this study, holding a territory was not a necessary condition for male New Zealand fur seals to sire pups. This confirms the findings of Lancaster *et al.* (2007) on Macquarie Island where 6 of 1007 fur seal pups sampled (0.6%) were assigned to non-territorial males.

In this study, we also found that four resident males (two males that held territories for 29 and 46 days respectively, and two non-territorial males) sired a total of eight pups born at neighbouring breeding areas (>100 m away, separated from the study site by non-breeding zones and boulder ledges). Although based on a small sample size and temporal scale, such observations are consistent with behaviours hypothesised to reduce inbreeding in systems that typically combine high reproductive skew and site fidelity. Under pressures to limit inbreeding, females may seek copulations with males other than their immediate neighbour (Hoffman *et al.* 2007).

By sampling pups outside our core study area, we found evidence of mixing between different areas of the colony (four resident males had pups in other parts of the 1-km-long colony that same year), possibly due to females moving within the colony for mating. This hypothesis is supported by our observations of three identified females regularly seen in one part of the colony without a pup during one breeding season, who pupped in another part of the colony the following season (Boren 2005). Lancaster *et al*. (2007) found that the propensity of fur seal females (antarctic, *A. gazella*, and subantarctic fur seals, *A. tropicalis*) to mate extraterritorially was related to their reproductive status: in that study, nearly half of all females that mated outside territories (9 of 20; 45%) did not give birth in the year of conception, and so were not induced to *post partum* oestrus in the breeding group. Because they were not tied to birthing sites in the breeding colony, they could enter oestrus outside the breeding group. Hoffman *et al*. (2003) also found that female antarctic fur seals observed without a pup had a significantly lower chance of conceiving with a territorial male than females who did have a pup. This may reflect greater freedom in mate choice by females that are not constrained to a male's territory by their pup.

However, at Macquarie Island, females mating with non-territorial males show a high probability of mating with a heterospecific male. Since females at Macquarie discriminate against heterospecific males (Goldsworthy *et al*. 1999; Lancaster *et al*. 2007), it seems unlikely that extraterritorial pups are produced as a result of female choice. Instead, Lancaster *et al*. (2007) suggest that nulliparous females mate with heterospecific subordinate males for two reasons: they come into oestrus after the peak of the breeding season when territorial males have left, or these females are young and inexperienced and haul out to breed in areas away from the main territorial areas.

In the present study, it was not possible to identify which females gave birth in the year of conception and to relate extraterritorial mating to late oestrus. As 90% of pupping takes place over six weeks at Ohau Point colony (Boren 2005), we approximate a similar duration for *post partum* oestrus. Only 4 of our 38 study males were on site long enough ($\geq$30 days) to mate with most receptive females. All the other study males managed to be present for only a part of the season, further justifying their use of alternatives to costly territoriality. The main costs of territoriality are two-fold. First, territorial male pinnipeds fast throughout their on-land tenure, losing weight at a regular rate (e.g. Boyd and Duck 1991). This fasting behaviour is favoured in pinnipeds because males may lose paternity and/or their territory if they go to sea to feed. However, otariids typically breed close to food resources because mothers must feed during lactation, as is the case at Ohau Point (Boren *et al*. 2006). Males can also access these resources providing they do not have a territory to defend. Second, injuries due to male fights constitute a major cause of death in male fur seals (e.g. Baker and McCann 1989). Non-territorial males at our study site typically engaged in fewer intrasexual interactions (including fights) than territorial males, again potentially avoiding a significant cost to their immediate and long-term fitness.

Most alternative mating tactics are conditional, and individuals are expected to exhibit the tactic that yields the greatest success relative to their status (genetics, size, experience, sex and stress hormones, health, etc.: Gross 1996). In most colonial pinnipeds, smaller males are common at the periphery of breeding groups (Bartholomew 1953; Le Boeuf 1974; Miller 1975; Boness and James 1979; McCann 1980) and are traditionally considered as socially 'inferior' (McLaren 1967) and/or immature. After reaching sexual maturity, male pinnipeds need a few more years before reaching their full body size and enough social experience to hold a territory ('delayed social maturation': Kiyota 2005). Their body mass is often correlated with their tenure duration and reproductive success (Boness and James 1979; Tinker *et al*. 1995; Arnould and Duck 1997). In the grey seal, for example, males using the primary reproductive tactic were the heaviest, had the highest proportion of body fat and energy reserves and could sustain the longest breeding tenures (Lidgard *et al*. 2005). Here, we tested whether the estimated male body length (as a rough estimator of body reserves) varied between mating tactics. The length of six territorial males (median = 156.5 cm, range = 128–168 cm) did not significantly differ from the length of nine territorial New Zealand fur seal males shot, aged and measured by Mattlin in 1978 (9–14 years old). Within the pool of males we measured, non-territorial males were smaller than territorial males (Table 4), in agreement with the fact that alternative tactics theoretically characterise individuals that do not have an optimal territorial phenotype. The potential for non-territorial males to successfully reproduce at the periphery of the group benefits these males that are less successful than territorial holders, but still 'do better' than having no mates at all (Dawkins 1980). Peripheral males that are socially immature but able to increase their lifetime reproductive success by siring a pup before becoming territorial could actually have a higher than average lifetime fitness (Gross 1996).

Aside from individual status, ecological factors (e.g. site topography, resources for thermoregulation) are highly influential determinants of fur seal mating systems (Carey 1991; Ryan *et al*. 1997; Bradshaw *et al*. 1999). They shape mating systems by influencing the aggregation of females and hence the potential for males to monopolise them (in mammals: Clutton-Brock and Harvey 1978; in pinnipeds: Boness 1991). Hoffman *et al*. (2003) concluded that there was no obvious alternative mating tactic in Bird Island antarctic fur seals, despite the inability to assign parentage to 39% of the study pups and the recognition that the mothers of those pups most probably did not mate at the study beach. The antarctic fur seal breeds in high densities on Bird Island, with an estimated density of 3.3 seals m^{-2} compared with 0.02–0.16 seal m^{-2} in the New Zealand fur seal (Mattlin 1978; Bradshaw *et al*. 2000; the present study). High density in core breeding areas might prevent antarctic fur seal males on Bird Island to use alternative tactics. In addition to specific (in) tolerance to crowding (Gentry 1975), local topography explains density differences in concert with colony developmental stage. In our study, territory sizes were larger than previously reported for the New Zealand fur seal (Miller 1974, 1975; Gentry 1975; Mattlin 1978), making it energetically impractical for territorial males to fully exclude subordinates. With the first pups born in 1990 and an exponential increase of 32% per annum (Boren *et al*. 2006), the Ohau Point colony is in the lower part of the density range of *A. forsteri* breeding colonies (Bradshaw *et al*. 2000) and is still currently growing exponentially (L. Boren, pers. comm.). This might partly explain the overall loose territorial setting allowing for non-territorial male tactics to be displayed (present study). The potential for alternative tactics in case of limited aggregation is illustrated in aquatically mating pinnipeds: in the water, females do not tend to aggregate and successful alternative male mating tactics coexist in the bearded seal, *Erignathus barbatus* (Van Parijs *et al.* 2003), the harbour seal, *Phoca vitulina* (Boness *et al.* 2006) and the Weddell seal, *Leptonychotes weddellii* (Harcourt *et al.* 2007). In land-breeding mammals, density is an important determinant for alternative mating tactics in many species, including bighorn sheep (Hogg 1984), Soay sheep (Clutton-Brock and Pemberton 2004) and feral horses (Linklater and Cameron 2000).

Finally, recent studies have shown important interannual variations in the functioning and genetic structure of pinniped breeding colonies. In the grey seal, the level of polygyny is influenced by interannual climatic variations (Twiss *et al.* 2007); in the antarctic fur seal, heterozygote/outbred males are more successful in low-pup-production years (Hoffman *et al.* 2004). Clearly, our study is limited by its temporal duration and it is possible that our study is not representative of the long-term trends occurring in the population, although the study years were not atypical in terms of other colony dynamics (Boren *et al.* 2006). In addition, because of the short temporal nature of our study, it may also have been affected by some annual turnover of females at the study site. While marked females are rare at our study site we observed little movement of established females between sites across years, confirming the strong breeding-site fidelity observed previously in this (Bradshaw *et al.* 2000; Boren *et al.* 2006) and other (Riedman 1990) pinniped species. Thus, any not previously observed females at our study site might be first-time breeders and clearly we have no idea where these females may have been mated, but it is unlikely to have been on our study beach. Consequently, we could never expect to determine paternity for all of the mother–pup pairs sampled. However, while such a discrepancy would be of concern when trying to document the full extent of reproductive success among males (Gemmell *et al.* 2001), this was not the intent of this study so such difficulties do not affect our key results. Our goal was simply to determine whether, as predicted by theory (Maynard Smith 1982; Gross 1996; Shuster and Wade 2003), alternative mating tactics exist in the intensely polygynous New Zealand fur seal.

The simple finding that no fewer than five non-territorial males obtained significant reproductive success through the course of our study shows quite clearly that alternatives to territoriality do exist and can provide fur seal males some reproductive success. We showed that a single sampling season study can be highly cost-effective for documenting poorly studied behaviours such as alternative mating tactics and whether they can provide some success in a medium to large colony of highly polygynous fur seals. Studies in a wide range of socio-ecological conditions, for example in both dense and mature populations and in more spread out, recolonising groups (Caudron *et al.* 2001), are essential, complementary approaches for bettering our understanding of the subtle mechanisms underlying pinniped polygyny.

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References

Aldenderfer, M. S., and Blashfield, R. K. (1984). 'Cluster Analysis.' (Sage Publications Inc.: Beverly Hills, CA.)

Allen, P. J., Amos, W., Pomeroy, P. P., and Twiss, S. D. (1995). Microsatellite variation in grey seals (*Halichoerus grypus*) shows evidence of genetic differentiation between two British breeding colonies. *Molecular Ecology* **4**, 653–662. doi:10.1111/j.1365-294X.1995.tb00266.x

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour* **49**, 227–266. doi:10.1163/156853974X00534

Ambs, S. M., Boness, D. J., Bowen, W. D., Perry, E. A., and Fleischer, R. C. (1999). Proximate factors associated with high levels of extraconsort fertilization in polygynous grey seals. *Animal Behaviour* **58**, 527–535. doi:10.1006/anbe.1999.1201

Amos, W., Twiss, S., Pomeroy, P. P., and Anderson, S. S. (1993). Male mating success and paternity in the grey seal, *Halichoerus grypus*: a study using DNA fingerprinting. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **252**, 199–207. doi:10.1098/rspb.1993.0066

Anderson, S. S., and Fedak, M. A. (1985). Grey seal males: energetic and behavioural links between size and sexual success. *Animal Behaviour* **33**, 829–838. doi:10.1016/S0003-3472(85)80017-8

Andersson, M. (1994). 'Sexual Selection.' (Princeton University Press: Princeton, NJ.)

Arnould, J. P. Y., and Duck, C. D. (1997). The cost and benefits of territorial tenure, and factors affecting mating success in male antarctic fur seals. *Journal of Zoology* **241**, 649–664. doi:10.1111/j.1469-7998.1997.tb05739.x

Baker, J. R., and McCann, T. S. (1989). Pathology and bacteriology of adult male antarctic fur seals, *Arctocephalus gazella*, dying at Bird Island, South Georgia. *The British Veterinary Journal* **145**, 263–275.

Baker, W. H. (1960). 'Element of Photogrammetry.' (The Ronald Press Company: New York.)

Bartholomew, G. A. (1953). Behavioral factors affecting social structure in the Alaska fur seal. In 'Transactions of the 18th North American Wildlife Conference'. pp. 481–502.

Boness, D. J. (1991). Determinants of mating systems in the Otariidae (Pinnipedia). In 'Behaviour of Pinnipeds'. (Ed. D. Renouf.) pp. 1–44. (Chapman and Hall: London.)

Boness, D. J., and James, H. (1979). Reproductive behaviour of the grey seal (*Halichoerus grypus*) on Sable Island, Nova Scotia. *Journal of Zoology* **188**, 477–500. doi:10.1111/j.1469-7998.1979.tb03430.x

Boness, D. J., Bowen, W. D., Buhleier, B. M., and Marshall, G. J. (2006). Mating tactics and mating system of an aquatic-mating pinniped: the harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology* **61**, 119–130. doi:10.1007/s00265-006-0242-9

Boren, L. J. (2005). New Zealand fur seals in the Kaikoura region: colony dynamics, maternal investment and health. Ph.D. Thesis, University of Canterbury, Christchurch, New Zealand.

Boren, L. J., Muller, C. G., and Gemmell, N. J. (2006). Colony growth and pup condition of the New Zealand fur seal (*Arctocephalus forsteri*) on the Kaikoura coastline compared with other east coast colonies. *Wildlife Research* **33**, 497–505. doi:10.1071/WR05092

Boyd, I. L., and Duck, C. D. (1991). Mass changes and metabolism in territorial male antarctic fur seals (*Arctocephalus gazella*). *Physiological Zoology* **64**, 375–392.

Bradshaw, C. J. A., Thompson, C. M., Davis, L. S., and Lalas, C. (1999). Pup density related to terrestrial habitat use by New Zealand fur seals. *Canadian Journal of Zoology* **77**, 1579–1586. doi:10.1139/cjz-77-10-1579

Bradshaw, C. J. A., Davis, L. S., Lalas, C., and Harcourt, R. G. (2000). Geographic and temporal variation in the condition of pups of the New Zealand fur seal (*Arctocephalus forsteri*): evidence for density dependence and differences in the marine environment. *Journal of Zoology* **252**, 41–51. doi:10.1111/j.1469-7998.2000.tb00818.x

Carey, P. W. (1991). Resource-defense polygyny and male territory quality in the New Zealand fur seal. *Ethology* **88**, 63–79.

Caro, T. M. (1994). 'Cheetahs of the Serengeti Plains: Group Living in an Asocial Species.' (University of Chicago Press: Chicago, IL.)

Caudron, A. K., Joiris, C. R., and Ruwet, J.-C. (2001). Comparative activity budget among grey seal (*Halichoerus grypus*) breeding colonies – the importance of marginal populations. *Mammalia* **65**, 373–382. doi:10.1515/mamm.2001.65.3.373

Caudron, A. K., Negro, S. S., Muller, C., Boren, L., and Gemmell, N. J. (2007). Hair sampling and genotyping from follicles: a minimally-invasive alternative for genetics studies in small, mobile pinnipeds and other mammals. *Marine Mammal Science* **23**, 184–192. doi:10.1111/j.1748-7692.2006.00084.x

Clark, M. M., Desousa, D., Vonk, J., and Galef, B. G. (1997). Parenting and potency: alternative routes to reproductive success in male Mongolian gerbils. *Animal Behaviour* **54**, 635–642. doi:10.1006/anbe.1997.0468

Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **236**, 339–372. doi:10.1098/rspb.1989.0027

Clutton-Brock, T. H., and Harvey, P. H. (1978). Mammals, resources and reproductive strategies. *Nature* **273**, 191–195. doi:10.1038/273191a0

Clutton-Brock, T. H., and Pemberton, J. R. (2004). 'Soay Sheep: Dynamics and Selection in an Island Population.' (Cambridge University Press: Cambridge.)

Coltman, D. W., Bowen, W. D., and Wright, J. M. (1998). Male mating success in an aquatically mating pinniped, the harbour seal (*Phoca vitulina*), assessed by microsatellite DNA markers. *Molecular Ecology* **7**, 627–638. doi:10.1046/j.1365-294x.1998.00373.x

Coltman, D. W., Bancroft, D. R., Robertson, A., Smith, J. A., Clutton-Brock, T. H., and Pemberton, J. M. (1999*a*). Male reproductive success in a promiscuous mammal: behavioural estimates compared with genetic paternity. *Molecular Ecology* **8**, 1199–1209. doi:10.1046/j.1365-294x.1999.00683.x

Coltman, D. W., Bowen, W. D., and Wright, J. M. (1999*b*). A multivariate analysis of phenotype and paternity in male harbor seals, *Phoca vitulina*, at Sable Island, Nova Scotia. *Behavioral Ecology* **10**, 169–177. doi:10.1093/beheco/10.2.169

Connor, R. C., Heithaus, M. R., and Barre, L. M. (2001). Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings of the Royal Society of London. Series B. Biological Sciences* **268**, 263–267. doi:10.1098/rspb.2000.1357

Darwin, C. R. (1871). 'The Descent of Man and Selection in Relation to Sex.' (Appleton: New York.)

Davis, C. S., Gelatt, T. S., Siniff, D., and Strobeck, A. (2002). Dinucleotide microsatellite markers from the antarctic seals and their use in other pinnipeds. *Molecular Ecology Notes* **2**, 203–208. doi:10.1046/j.1471-8286.2002.00187.x

Dawkins, R. (1980). Good strategy or evolutionary stable strategy? In 'Sociobiology: Beyond Nature/Nurture?' (Eds G. W. Barlow and J. Silverberg.) pp. 331–367. (Westview Press: Boulder, CO.)

Dowell, S. A., Boren, L. J., Negro, S. S., Muller, C. J., Caudron, A. K., and Gemmell, N. J. (2008). Rearing two New Zealand fur seal (*Arctocephalus forsteri*) pups to weaning. *Australian Journal of Zoology* **56**, 33–39. doi:10.1071/ZO07063

Duchesne, P., Castric, T., and Bernatchez, L. (2005). PASOS (parental allocation of singles in open systems): a computer program for individual parental allocation with missing parents. *Molecular Ecology Notes* **5**, 701. doi:10.1111/j.1471-8286.2005.01001.x

Emlen, S. T., and Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–223. doi:10.1126/science.327542

Evett, I. W., and Weir, B. S. (1998). 'Interpreting DNA Evidence.' (Sinauer Associates: Sunderland, MA.)

Feh, C. (1999). Alliances and reproductive success in Camargue stallions, *Equus caballus. Animal Behaviour* **57**, 705–713. doi:10.1006/anbe.1998.1009

Fowler, M. (2003). Spatial distribution of male New Zealand fur seals, *Arctocephalus forsteri*, during the breeding season. B.Sc.(Honours) Thesis, Southampton College, Long Island University, New York.

Gemmell, N. J., and Majluf, P. (1997). Projectile biopsy sampling of fur seals. *Marine Mammal Science* **13**, 512–516. doi:10.1111/j.1748-7692.1997.tb00661.x

Gemmell, N. J., Allen, P. J., Goodman, S. J., and Reed, J. Z. (1997). Interspecific microsatellite markers for the study of pinniped populations. *Molecular Ecology* **6**, 661–666. doi:10.1046/j.1365-294X.1997.00235.x

Gemmell, N. J., Burg, T. M., Boyd, I. L., and Amos, W. (2001). Low reproductive success in territorial male Antarctic fur seals (*Arctocephalus gazella*) suggests the existence of alternative mating strategies. *Molecular Ecology* **10**, 451–460. doi:10.1046/j.1365-294x.2001.01186.x

Gentry, R. L. (1975). Comparative social behaviour of the eared seals. *Rapports et Proces-Verbaux des Reunions – Conseil International pour L'Exploration de la Mer* **169**, 188–194.

Gentry, R. L., and Kooyman, G. L. (1986). 'Fur Seals. Maternal Strategies on Land and at Sea.' (Princeton University Press: Princeton, NJ.)

Goldsworthy, S. D., Boness, D. J., and Fleischer, R. C. (1999). Mate choice among sympatric fur seals: female preference for conphenotypic males. *Behavioral Ecology and Sociobiology* **45**, 253–267. doi:10.1007/s002650050560

Goodman, S. J. (1997). Dinucleotide repeat polymorphisms at seven anonymous microsatellite loci cloned from the European harbour seal (*Phoca vitulina vitulina*). *Animal Genetics* **28**, 310–311.

Gross, M. R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology & Evolution* **11**, 92–98. doi:10.1016/0169-5347(96)81050-0

Haase, T. J. (2007). Suckling an additional pup to weaning in the New Zealand fur seal. *Marine Mammal Science* **23**, 176–183. doi:10.1111/j.1748-7692.2006.00078.x

Haley, M. P., Deutsch, C. J., and Le Boeuf, B. J. (1991). A method for estimating mass of large pinnipeds. *Marine Mammal Science* **7**, 157–164. doi:10.1111/j.1748-7692.1991.tb00562.x

Harcourt, R. G., Kingston, J. J., Waas, J. R., and Hindell, M. A. (2007). Foraging while breeding: alternative mating strategies by male Weddell seals? *Aquatic Conservation: Marine & Freshwater Ecosystems* **17**, S68–S78. doi:10.1002/aqc.915

Heckel, G., and von Helversen, O. (2002). Male tactics and reproductive success in the harem polygynous bat *Saccopteryx bilineata. Behavioral Ecology* **13**, 750–756. doi:10.1093/beheco/13.6.750

Hoelzel, A. R., Le Boeuf, B. J., Reiter, J., and Campagna, C. (1999). Alpha-male paternity in elephant seals. *Behavioral Ecology and Sociobiology* **46**, 298–306. doi:10.1007/s002650050623

Hoelzel, A. R., Campagna, C., and Arnbom, T. (2001). Genetic and morphometric differentiation between island and mainland southern elephant seal populations. *Proceedings of the Royal Society of London, Biological Sciences* **268**, 325–332.

Hoffman, J. I., and Amos, W. (2005). Microsatellite genotyping errors: detection approaches, common sources and consequences for paternal exclusion. *Molecular Ecology* **14**, 599–612. doi:10.1111/j.1365-294X.2004.02419.x

Hoffman, J. I., Boyd, I. L., and Amos, W. (2003). Male reproductive strategy and the importance of maternal status in the antarctic fur seal *Arctocephalus gazella. Evolution* **57**, 1917–1930.

Hoffman, J. I., Boyd, I. L., and Amos, W. (2004). Exploring the relationship between parental relatedness and male reproductive success in the antarctic fur seal *Arctocephalus gazella. Evolution* **58**, 2087–2099.

Hoffman, J. I., Forcada, J., Trathan, P. N., and Amos, W. (2007). Female fur seals show active choice for males that are heterozygous and unrelated. *Nature* **445**, 912–914. doi:10.1038/nature05558

Hogg, J. T. (1984). Intrasexual competition in bighorn sheep: multiple creative male strategies. *Science* **225**, 526–529. doi:10.1126/science.6539948

Hogg, J. T., and Forbes, S. H. (1997). Mating in bighorn sheep: frequent male reproduction via a high-risk 'unconventional' tactic. *Behavioral Ecology and Sociobiology* **41**, 33–48. doi:10.1007/s002650050361

Jamieson, A., and Taylor, S. C. S. (1997). Comparisons of three probability formulae for parentage exclusion. *Animal Genetics* **28**, 397–400. doi:10.1111/j.1365-2052.1997.00186.x

Johnson, S. C. (1967). Hierarchical clustering schemes. *Psychometrika* **32**, 241–254. doi:10.1007/BF02289588

Kalinowski, S. T., Raper, M. L., and Marshall, T. C. (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Molecular Ecology* **16**, 1099–1106. doi:10.1111/j.1365-294X.2007.03089.x

Kappe, A. (1998). Detection of genetic variation: application of molecular techniques in conservation biology. Ph.D. Thesis, Groningen University, The Netherlands.

Kiyota, M. (2005). Site fidelity, territory acquisition and mating success in male northern fur seals (*Callorhinus ursinus*). *Mammal Study* **30**, 19–27. doi:10.3106/1348-6160(2005)30[19:SFTAAM]2.0.CO;2

Lancaster, M. L., Goldsworthy, S. D., and Sunnucks, P. (2007). Multiple mating strategies explain unexpected genetic mixing of New Zealand fur seals with two congenerics in a recently recolonized population. *Molecular Ecology* **16**, 5267–5276.

Le Boeuf, B. J. (1974). Male–male competition and reproductive success in elephant seals. *American Zoologist* **14**, 163–176.

Lidgard, D. C., Boness, D. J., Bowen, W. D., McMillan, J. I., and Fleischer, R. C. (2004). The rate of fertilization in male mating tactics of the polygynous grey seal. *Molecular Ecology* **13**, 3543–3548. doi:10.1111/j.1365-294X.2004.02334.x

Lidgard, D. C., Boness, D. J., Bowen, W. D., and McMillan, J. I. (2005). State-dependent male mating tactics in the grey seal: the importance of body size. *Behavioral Ecology* **16**, 541–549. doi:10.1093/beheco/ari023

Linklater, W. L., and Cameron, E. Z. (2000). Tests for cooperative behaviour between stallions. *Animal Behaviour* **60**, 731–743. doi:10.1006/anbe.2000.1525

Linklater, W. L., Cameron, E. Z., Minot, E. O., and Stafford, K. J. (1999). Stallion harassment and the mating system of horses. *Animal Behaviour* **58**, 295–306. doi:10.1006/anbe.1999.1155

Majluf, P., and Goebel, M. E. (1992). The capture and handling of female South American fur seals and their pups. *Marine Mammal Science* **8**, 187–190. doi:10.1111/j.1748-7692.1992.tb00382.x

Marshall, T. C., Slate, J., Kruuk, L. E., and Pemberton, J. M. (1998). Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* **7**, 639–655. doi:10.1046/j.1365-294x.1998.00374.x

Mattlin, R. H. (1978). Population biology, thermoregulation and site preference of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1828), on the Open Bay Islands, New Zealand. Ph.D. Thesis, University of Canterbury, Christchurch, New Zealand.

Maynard Smith, J. (1982). 'Evolution and the Theory of Games.' (Cambridge University Press: Cambridge.)

McCann, T. S. (1980). Territoriality and breeding behaviour of adult male antarctic fur seal, *Arctocephalus gazella. Journal of Zoology* **192**, 295–310. doi:10.1111/j.1469-7998.1980.tb04235.x

McConkey, S. D. (1999). Photographic identification of the New Zealand sea lion: a new technique. *New Zealand Journal of Marine and Freshwater Research* **33**, 63–66.

McLaren, J. A. (1967). Seals and group selection. *Ecology* **48**, 104–110. doi:10.2307/1933422

Miller, E. (1971). Social and thermoregulatory behaviour of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1828). M.Sc. Thesis, University of Canterbury, Christchurch, New Zealand.

Miller, E. H. (1974). Social behaviour between adult male and female New Zealand fur seals, *Arctocephalus forsteri* (Lesson) during the breeding season. *Australian Journal of Zoology* **22**, 155–173. doi:10.1071/ZO9740155

Miller, E. H. (1975). Social and evolutionary implications of territoriality in adult male New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1828), during the breeding season. *Rapports et Procés-verbaux des Réunions du Conseil International pour l'Exploration de la Mer* **169**, 170–187.

Negro, S. S., Cloots, R., and Gemmell, N. J. (2006). Cost-effective media for the rapid and high resolution of small DNA fragments using polyacrylamide-based electrophoresis. *Molecular Ecology Notes* **6**, 609–612. doi:10.1111/j.1471-8286.2006.01290.x

Oliveira, R. F., Taborsky, M., and Brockmann, H. J. (2008). 'Alternative Reproductive Tactics: an Integrative Approach.' (Cambridge University Press: Cambridge.)

Packer, C., Gilbert, D. A., Pusey, A. E., and O'Brien, S. J. (1991). A molecular genetic analysis of kinship and cooperation in African lions. *Nature* **351**, 562–565. doi:10.1038/351562a0

Paetkau, D., and Strobeck, C. (1994). Microsatellite analysis of genetic variation in black bear populations. *Molecular Ecology* **3**, 489–495. doi:10.1111/j.1365-294X.1994.tb00127.x

Peakall, R., and Smouse, P. E. (2006). GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. *Molecular Ecology Notes* **6**, 288–295. doi:10.1111/j.1471-8286.2005.01155.x

Queller, D. C., and Goodnight, K. F. (1989). Estimating relatedness using genetic markers. *Evolution* **43**, 258–275. doi:10.2307/2409206

Rasa, O. A. E. (1989). Helping in dwarf mongoose societies: an alternative reproductive strategy. In 'The Sociobiology of Sexual and Reproductive Strategies'. (Eds O. A. E. Rasa and C. Vogel.) pp. 61–73. (Croom Helm: Beckenham.)

Raymond, M., and Rousset, F. (1995). Genepop (Version 1.2) – population genetics software for exact tests of ecumenicism. *The Journal of Heredity* **86**, 248–249.

Riedman, M. (1990). 'The Pinnipeds: Seals, Sea Lions, and Walruses.' (University of California Press: Berkeley, CA.)

Robertson, B. C., and Gemmell, N. J. (2005). Microsatellite DNA markers for the study of population structure in the New Zealand fur seal (*Arctocephalus forsteri*). DOC Science Internal Series No. 196. Department of Conservation, Wellington, New Zealand.

Ryan, C. J., Hickling, G. J., and Wilson, K. J. (1997). Breeding habitat preferences of the New Zealand fur seal (*Arctocephalus forsteri*) on Banks Peninsula. *Wildlife Research* **24**, 225–235. doi:10.1071/WR95068

Shuster, S. M., and Wade, M. J. (2003). 'Mating Systems and Strategies.' (Princeton University Press: Princeton & Oxford.)

Sokal, R. R., and Rohlf, F. J. (1995). 'Biometry.' 3rd edn. (W.H. Freeman and Co.: New York.)

Soltis, J., Mitsunaga, F., Shimizu, K., Nozaki, M., Yanagihara, Y., Domingo-Roura, X., and Takenaka, O. (1997). Sexual selection in Japanese macaques. II: Female mate choice and male–male competition. *Animal Behaviour* **54**, 737–746. doi:10.1006/anbe.1997.0568

StatSoft (2005). STATISTICA (data analysis software system) version 7.1. *www.statsoft.fr*.

Stirling, I. (1970). Observations on the behaviour of the New Zealand fur seal (*Arctocephalus forsteri*). *Journal of Mammalogy* **51**, 766–778. doi:10.2307/1378300

Stirling, I. (1971). Studies on the behaviour of the South Australian fur seal, *Arctocephalus forsteri* (Lesson). II. Adult females and pups. *Australian Journal of Zoology* **19**, 267–273. doi:10.1071/ZO9710267

Tinker, M. T., Kovacs, K. M., and Hammill, M. O. (1995). The reproductive behavior and energetics of male gray seals (*Halichoerus grypus*) breeding on land-fast ice. *Behavioral Ecology and Sociobiology* **36**, 159–170. doi:10.1007/BF00177792

Tomkins, J. L., and Hazel, W. (2007). The status of the conditional evolutionarily stable strategy. *Trends in Ecology & Evolution* **22**, 522–528. doi:10.1016/j.tree.2007.09.002

Trivers, R. L. (1972). Parental investment and sexual selection. In 'Sexual Selection and the Descent of Man'. (Ed. B. G. Campbell.) pp. 136–179. (Aldine-Atherton: Chicago, IL.)

Twiss, S. D., Poland, V. F., Graves, J. A., and Pomeroy, P. P. (2006). Finding fathers: spatio-temporal analysis of paternity assignment in grey seals (*Halichoerus grypus*). *Molecular Ecology* **15**, 1939–1953. doi:10.1111/j.1365-294X.2006.02927.x

Twiss, S. D., Thomas, C., Poland, V., Graves, J. A., and Pomeroy, P. (2007). The impact of climatic variation on the opportunity for sexual selection. *Biology Letters* **3**, 12–15. doi:10.1098/rsbl.2006.0559

Van Parijs, S. M., Kovacs, K. M., and Lydersen, C. (2001). Spatial and temporal distribution of vocalising male bearded seals – implications for male mating strategies. *Behaviour* **138**, 905–922. doi:10.1163/156853901753172719

Van Parijs, S. M., Lydersen, C., and Kovacs, K. M. (2003). Vocalizations and movements suggest alternative mating tactics in male bearded seals. *Animal Behaviour* **65**, 273–283. doi:10.1006/anbe.2003.2048

Wainstein, M. D. (2000). Paternity in southern elephant seals (*Mirounga leonina*). Ph.D. Thesis, University of California, Santa Cruz, USA.

Walsh, P. S., Metzger, D. A., and Higuchi, R. (1991). Chelex 100 as a medium for the simple extraction of DNA for PCR-based typing from forensic material. *BioTechniques* **10**, 506–513.

Wishart, D. (2006). 'ClustanGraphics Primer. A Guide to Cluster Analysis.' 4th edn. (Clustan Ltd: Edinburgh & St Andrews.)

Worthington Wilmer, J., Allen, P. J., Pomeroy, P. P., Twiss, S. D., and Amos, W. (1999). Where have all the fathers gone? An extensive microsatellite analysis of paternity in the grey seal (*Halichoerus grypus*). *Molecular Ecology* **8**, 1417–1429. doi:10.1046/j.1365-294x.1999.00705.x

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