Mate choice among sympatric fur seals: female preference for conphenotypic males

Abstract When closely related species breed in sympatry, and where hybrids have lower fitness, reinforcement theory predicts that selection should favour mechanisms that reduce the probability of interspecific matings. If this situation arises among species that exhibit resource defence polygyny where males and females of different species reside in the same territories, there may be some conflict between mate choice based on territory-holding ability (sexual selection) and mate choice for correct species. We investigated this in a population of fur seals where three species are sympatric and where some females breed in the territories of heterospecific males, and where interspecific matings and hybrid pups are observed. The territorial status of males and the birthing sites of females were determined during daily observations, as were the movements of males and females, the location of matings and mating partners. DNA extracted from skin samples was used to determine paternities using DNA fingerprinting and the mtDNA genotype of individuals. Individuals were also classed on the basis of species-typical phenotype. We found that extra-territory inseminations (ETIs) were significantly more prevalent (67%) when territorial males and resident females were of different phenotype than when of similar phenotype (27%), but mtDNA genotype had no effect on the rate of ETIs. ETIs were probably by males with the same phenotype, as pups born to these females in the following season had the same phenotype as their mothers, suggesting they were not hybrids. These results suggest that within the resource defence polygynous mating system of these sympatric fur seals, female mate choice is more influenced by male phenotype than genotype. Contrary to our predictions, our study indicates that potential conflict between mate choice based on sexual selection and species recognition is unlikely, because females have some capacity to discriminate between males both within and between species on phenotypic traits additional to those under sexual selection. Although at least 25% of the pups born in this study were hybrid, this study can only support reinforcement theory if hybrids have reduced fitness. The fitness of hybrids among the species studied is currently unknown.

Key words Mate choice · Mating success · Hybridization · DNA fingerprinting · Mitochondrial DNA · Fur seal · Arctocephalus spp.

Introduction

An assumption often made for mammals exhibiting resource defence polygyny is that females choose breeding sites based on the resources of the sites and that females are then passive recipients of matings by the males in whose territories they reside (Emlen and Oring 1977). Females not only gain the direct benefits of the resources, but they might also gain indirect benefits, through sexual selection, of high-quality males who are able to compete successfully for the resources and access to oestrous females (Andersson 1994). However, when closely related species which exhibit resource defence polygyny breed sympatrichely, such that males and females of different species may reside in the same territories, there may be some conflict for females between choosing males on the basis of their territory-holding ability (sexual selection) versus their species status.

The selective benefits of species recognition have been suggested to be important in the evolution of mate choice and secondary sex traits (see Andersson 1994 for review). Where two divergent populations come into
contact, natural selection will favour assortative mating if hybrid progeny have lower fitness (Dobzhansky 1940; Butlin 1987, 1995). This theory, termed ‘reinforcement’, may complete speciation when post-zygotic barriers are incomplete (Butlin 1987, 1995; Rice and Hostert 1993; Rundle and Schluter 1998). Speciation by reinforcement requires strong selection against hybrids. However, two major processes may counter it: first, recombination, which may disrupt gene combinations that promote hybrid sterility or inviability, and secondly, gene flow from other non-sympatric populations, which may undermine the selection for assortative mating (Butlin 1995).

Whereas reinforcement is the evolutionary process whereby selection promotes recognition (and hence assortative mating) among species or divergent populations breeding sympatrically, reproductive character displacement is the selection of enhanced specific differences in traits, courtship or preference in areas of sympathy relative to areas of allopatry (Brown and Wilson 1956; Howard 1993). Most empirical studies of reinforcement have focused on the presence or absence of reproductive character displacement, which has been found in both experimental and field studies (Coyne and Orr 1989, 1993). Most empirical studies of reinforcement require strong selection against hybrids. However, two major processes may counter it: first, recombination, which may disrupt gene combinations that promote hybrid sterility or inviability, and secondly, gene flow from other non-sympatric populations, which may undermine the selection for assortative mating (Butlin 1995).

The congeneric fur seals in the genus Arctocephalus represent a recently radiated group of eight species which predominate in the southern hemisphere. Several of these species have ranges which overlap with other species, including Australian (A. pusillus doriferus) and New Zealand fur seals (A. forsteri) (Goldsworthy et al. 1997), Juan Fernandez (A. phillipii) and subantarctic fur seals (A. tropicalis) (J.M. Francis, personal communication), and Antarctic (A. gazella) and subantarctic fur seals (Condy 1978; Kerley and Robinson 1987; Shaughnessy et al. 1988). At Macquarie Island in the south-western Pacific Ocean, three fur seal species occur in sympatry: Antarctic, subantarctic and New Zealand fur seals (Shaughnessy and Goldsworthy 1993). Hybrids between Antarctic and subantarctic fur seals have been reported from two of the three islands where these species breed sympatrically; these have been inferred from individuals with intermediate external characteristics and skull morphometrics (Condy 1978; Kerley and Robinson 1987; Shaughnessy et al. 1988). At Macquarie Island, fur seal breeding is mixed species colonies where breeding territories may contain both male Antarctic and subantarctic fur seals, and territorial males of either species or New Zealand fur seals. Interspecific matings have been observed and phenotypic hybrid pups also occur (Shaughnessy et al. 1988).

The unique fur seal population at Macquarie Island provides a natural experiment enabling simultaneous investigation of the influence of species recognition and male resource-holding potential on female choice and male mating success. We compared the mating success of males holding territories comprised of conspecific and heterospecific females, and determined the discriminatory abilities of females by assessing the extent to which they obtained extra-territorial inseminations (ETIs) from DNA fingerprinting in relation to whether territorial males were of the same phenotype or mtDNA genotype. If females in territories of heterospecific males obtain more ETIs than females in territories with conspecific males, we infer this as evidence for assortative mating and species recognition.

**Methods**

**Study site**

Macquarie Island (54°S 159°E) is situated in the south-western Pacific Ocean, just north of the Antarctic Polar Front. The original fur seal population at Macquarie Island was exterminated by sealers by about 1820, and records indicate that prior to exploitation, the population numbered at least 190,000 individuals. However, the identity of the original species is unknown (Shaughnessy and Fletcher 1987). Fur seals did not breed on the island again until 1955, and since then the population has been increasing at a rate of 10.5% per annum (Shaughnessy and Goldsworthy 1993). Of the three species of fur seal that occur on the Island, Antarctic and subantarctic fur seal are the most numerous breeding species (Shaughnessy et al. 1988). The New Zealand fur seal population on the island consists of mostly non-breeding males, but males of this species occasionally hold breeding territories. The main concentration of breeding on the island occurs in two small bays (Secluded Beach and Goat Bay) on North Head Peninsula, on the northern tip of the island (Fig. 1). The study was conducted over three breeding seasons in the austral summers of 1991/1992–1993/1994. In these years, the total pup production for the island was 79, 86 and 96, respectively. This study was conducted at Secluded Beach where 86%, 90% and 91% of the pup births for the population occurred in the three seasons of the study, respectively.

**Species identification**

Species identification of individual seals was determined by both phenotypic and genetic differences among the species. Phenotypic differences among fur seal species include pelage colour and pattern, proportional differences in body and flipper shape, behaviour and vocalisations (Condy 1978; King 1983; Shaughnessy et al. 1988; Goldsworthy et al. 1997). The species identity of pups can also be readily determined by their phenotype, especially those of the Antarctic and subantarctic fur seal which differ markedly in the colouring and patterning of their natal pelage (Condy 1978; King 1983; Shaughnessy et al. 1988). On Macquarie Island, most individuals can be readily assigned to species based on such characteristics. The main species-specific characteristics used to assign a species phenotype to individual pups, females and males are summarised in Table 1. The characteristics of individual seals usually correlated well with the entire set of characteristics typical for that species, but some individuals shared characteristic of each species. We termed these individuals ‘phenotypic hybrids’, and they may be F1 hybrids or backcrosses (Condy 1978).

We also used mtDNA sequences to identify species-specific genotypes (Fig. 2) and in some cases hybrids. We amplified extracted DNA using the polymerase chain reaction (PCR), with oligonucleotide primers homologous to the tRNAs on either side of the mtDNA control region, 5'-TTCCCGGTCTGTGTAACCC-3' (T-Thr) and 5'-ATTTCAGTGCTGGTTTT-3' (T-Phe) following Hoelzel and Green (1992) and Hoelzel et al. (1993). DNA was amplified in 50-µl reactions containing 2 µl of 0.1–0.5 µg genomic DNA, 5 µl 10 x buffer (0.1 M Tris-HCl, pH 8.5, 0.025 M