

**BEHAVIOURAL THERMOREGULATION AND POLYGYNY  
IN THE NEW ZEALAND FUR SEAL**

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by

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*On the way the number of seals which we saw was quite astonishing: every bit of flat rock and parts of the beach were covered with them. They appeared to be of a loving disposition, and lay fast asleep, like so many pigs; but even pigs would have been ashamed of their dirt, and the foul smell which came from them.*

*Chuck Darwin, 1835*

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## ABSTRACT

The polygynous New Zealand fur seal, Arctocephalus forsteri, breeds in densely-packed colonies with males defending exclusive territories. The distribution of animals within a colony of these seals was monitored over three consecutive breeding seasons and behavioural thermoregulation was found to be an important factor influencing the site selection of both males and females. Three substrates were available to seals: rocks in the sun, rocks in the shade, and pools of standing water. The shaded areas and pools were used for cooling and use of these cooling substrates increased as rock surface temperature increased, resulting in a clumped distribution on hot days. Substrate preferences were tested experimentally by manipulating the availability of cooling substrates during two seasons. The number of females using an area increased significantly after shade or pools of water were added to that area. For males, pool additions resulted in increased use of those areas, while adding shade had no effect. Cooling substrates had a patchy distribution and could, therefore, be monopolised by territorial males.

The physical characteristics of territories were compared with the numbers of females per territory to determine if harem size was related to cooling substrate availability. Harem size was positively correlated with both shaded substrate area and total territory size, thus demonstrating that female thermoregulatory constraints are a major factor affecting male mating success. Substrate manipulation experiments also revealed that harem size varied in relation to changes in cooling substrate availability, both within the territory being measured and on sites adjacent to it. Harem size increased on two territories after shade was added to them, and also on two territories near sites from which cooling substrates were removed. Another two territories showed a decrease in harem size after cooling substrates were added to neighbouring areas. These results suggest that the quality of a territory (i.e. number of females on it) is directly related to its cooling potential.

The role of female aggression in the seals' social system was also investigated. Females defended small territories within male territories using displays and vocalisations not unlike those used by males during territorial disputes. Agonistic interactions occurred most often on shaded rocks, suggesting that this is a limited resource being contested. It is proposed that this competition for preferred microhabitats will limit harem size and, therefore, the mating success of territorial males. Resident females won significantly more conflicts than intruders, regardless of the type of substrate on which the interaction took place.

## GENERAL INTRODUCTION

An idea central to the theory of evolution by natural selection is that the reproductive success of each phenotype is measured relative to that of all other phenotypes in the population. With each phenotype in competition to maximise its reproductive success in the face of various environmental, physiological, and behavioural constraints, there is great potential for variability in the reproductive success of individuals. Characters that evolve by sexual selection account for some of the differences in individual reproductive success (Arnold 1983). Darwin (1871) proposed two types of sexual selection: intra- and intersexual. Intrasexual selection favours traits in males that allow them to better compete with other males for access to mates. The various fighting paraphernalia found in many male mammals (e.g. horns, tusks, antlers) and their combative behaviour during the breeding season are evidence of this selective pressure.

More controversial is intersexual selection (O'Donald 1983), which favours traits in one sex that are attractive to the other. This most commonly refers to male traits that females prefer and some of the skepticism surrounding this selective pressure has stemmed from doubts that females actively select mates. However, female mate choice has been demonstrated in several studies (e.g. Semler 1971; von Schantz et al. 1989). Another aspect of intersexual selection that has been criticised is female choice for males with "good genes". This assumes that there is genetic variation among males and that females can discern these differences. However, there is little empirical data that support this female choice (Parker 1983; but see Partridge 1980).

The intensity of sexual selection may vary between species and between populations within a species (Arnold 1983). This variance may be the result of some members of a population controlling other individuals' access to potential mates (Emlen & Oring 1977). Greater variance in reproductive success will result from greater control or monopolization of potential mates (Emlen & Oring 1977). This is true whether the control is direct, such as the physical exclusion of others of the same gender from mates, or indirect, such as controlling resources critical for successful reproduction. The degree to which resource monopolization can be achieved will also influence the type of mating system found in a species.

However, in addition to competition for control of mates, the differential investment that each sex makes toward raising the offspring will also affect the type of breeding system adopted by the population. In terms of gamete production, the cost of producing an ovum far outweighs the cost of producing

a sperm cell (Bateman 1948). A male can therefore afford to produce many more sperm than a female can produce ova, which, in terms of pre-zygotic investment, means that males can afford to produce more offspring than females. Stated another way, this means that each ovum represents a greater proportion of a female's reproductive potential than a sperm cell represents of a male's. It is this cost differential that supports the idea that where active mate choice does occur, it is usually the female that chooses the male; she has more to lose from a bad decision (Partridge & Halliday 1984).

But there is more to the successful rearing of offspring than producing a gamete. Guarding eggs or feeding young are examples of post-fertilization parental investment. Trivers (1972) defines parental investment as, "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring". Males and females may be in competition to minimise their own parental investment relative to that of the other sex, provided that the collective investment is sufficient for the offspring to survive to reproduce. Indeed, Trivers (1972) argues that the ways in which males and females maximise their reproductive success are seldom identical. In some insects, the parental investment of both sexes is limited to the metabolic cost of gamete production, while in many birds there is considerable additional investment in the form of incubation, guarding against predators, and feeding the young. However, once the eggs have been laid, both sexes are equally capable of performing these tasks and in many species males and females make similar post-fertilization investments. In eutherian mammals, females make a much greater investment than males because the offspring develops to an advanced state within the female's body, and the young are also nutritionally dependent on their mother's milk for some time after parturition.

It is not surprising that there are many different types of mating systems when one considers the different means by which males and females compete in producing offspring, and the many ecological constraints that operate on a species. Emlen & Oring (1977) refer to these ecological constraints as the Environmental Potential for Polygyny (EPP). Where the constraints are such that neither sex can monopolise additional mates or important resources, then EPP is low and the breeding is likely to be monogamous. Many woodland bird species exemplify this situation, i.e. nest sites are plentiful (not easily monopolised) while food is widely distributed and both parents are needed to ensure that the offspring receive adequate food. Monogamy is the most prevalent mating system found in birds (Lack 1968). When EPP is high, such as when various conditions result in the clumping of females, then polygyny is

likely to occur. This is common in many mammalian species (Eisenberg 1966).

### **The Evolution of Polygyny**

Polygyny occurs in many forms and is classified by the way in which males monopolise females. The different types of polygyny include: female-defense, resource-defense, and male dominance polygyny (Emlen & Oring 1977). In female-defense polygyny, males directly control access to females through herding or because of female gregariousness. In resource-defense polygyny, males monopolise critical resources and so are able to indirectly control access to females. Male dominance polygyny (i.e. leks and explosive breeding assemblages) occurs in species where mates or vital resources are not economically monopolisable and where females select mates from aggregations of males.

There have been six explanations put forward for the evolution of polygyny. The first of these suggests that polygyny is the by-product of an uneven sex ratio (Mayr 1939). This explanation is no longer widely accepted, and several contrary examples exist where polygamy occurs in populations with even sex-ratios, and monogamy occurs in populations with highly skewed sex ratios (Verner 1964). The second explanation suggests that polygyny evolved because it enables a male to monitor his reproductive activity so as to alter it when local population density changes (Wynne-Edwards 1962). For this idea to be valid, it must be demonstrated that males are voluntarily refusing to inseminate receptive females, yet there is no evidence from any species that this is the case (Orians 1969). Another suggestion is that polygyny is the result of female mate choice, e.g. a female will choose to mate polygynously with a male on a superior territory rather than monogamously with a male on a territory of lesser quality (Verner 1964; Verner & Willson 1966; Orians 1969). This is often referred to as the Polygyny Threshold Hypothesis and many studies provide evidence to support it (e.g. Carey & Nolan 1975; Pleszczyńska 1978; Trillmich 1983). Another model based on female mate choice is the "sexy son" hypothesis (Weatherhead & Robertson 1979, 1981). This suggests that females that mate with males possessing attractive traits, even if they are on inferior territories, will increase their fitness because those same traits will make their male offspring attractive to other females. Polygynous matings should occur if more than one female is attracted to the same traits. More recently, Lightbody & Weatherhead (1988) have proposed the Neutral Mate Choice Model which suggests that in situations where a female's mate choice will not affect her reproductive success, then she will make no choice at all. In the neutral

mate choice model, polygyny occurs because of the competitive ability of the males (Lightbody & Weatherhead 1987a). The final explanation is that polygyny is the result of fighting between males for exclusive access to females (Darwin 1871). This idea is also widely accepted (e.g. Bartholomew 1970; Jarman 1974; Southern 1964).

Excluding the uneven sex ratio and group selection arguments, the key differences between the models for the evolution of polygyny lie in the role of female mate choice. Both the polygyny threshold and sexy son hypotheses assume female mate choice, while both the neutral mate choice model and Darwin's explanation assume little or no mate choice by females. Instead, both of these place the emphasis on male competition. The neutral mate choice model requires, among other conditions, that females must be neither competitive nor cooperative, and that variations in territory features must be independent of variation in reproductive success or harem size (Lightbody & Weatherhead 1987a). In contrast, Darwin's hypothesis merely requires that males actively exclude other males from females, i.e. female or resource defense polygyny.

#### **Possible advantages of polygyny to each sex**

Although some exceptions are known (e.g. mormon crickets, Gwynne 1981), it is generally true that males can produce many gametes at little cost. Because a male has far more gametes available than he has females, female availability is often the limiting factor in maximising male reproductive success. Hence, polygyny is advantageous to males. This is particularly true for those species with internal fertilisation, since the number of ova per female here is often less than in species with external fertilisation. But for females, the advantages of sharing the same male are less obvious, and in some species monogamous mating would maximise a female's reproductive success (e.g. Downhower & Armitage 1971). This is especially true in species where male parental care is crucial to the successful rearing of the young, and where male help is unshareable (e.g. many bird species, Lack 1968). However, under certain ecological conditions, males can monopolise key resources such as food (Cronin & Sherman 1977) or sheltered areas (Rauch 1985). In these cases, females either have no choice but to mate polygynously, or the benefits they gain from access to these resources outweigh the cost of sharing the male.

Although resource-defense by males can strongly influence whether or not a female shares a mate, the role of the female as a member of a harem is not necessarily a passive one. Several studies of blackbirds (e.g. Nero & Emlen 1951; LaPrade & Graves 1982; Hurly & Robertson 1984, 1985; Lightbody &



Weatherhead 1987b) and rodents (e.g. Armitage 1965; Armitage & Downhower 1970; McLean 1984) have demonstrated that females attempt to repel additional females from a territory and that this may limit harem size. Hence, female behaviour may influence male reproductive success (see Chapter 3).

### **Pinnipeds and Polygyny**

All members of the Otariidae (fur seals and sea lions) are strikingly polygynous (Nutting 1891), sexually dimorphic, and some have enormous harems (up to 100 females per male in the northern fur seal, Bartholomew & Hoel 1953). The behaviour and ecology of most pinnipeds is well documented (see King 1983 for concise summaries and references). In addition to the many accounts of individual species, a model for the evolution of pinniped polygyny has also been proposed (Bartholomew 1970). Marine offshore feeding and terrestrial parturition are two characteristics unique to pinnipeds among mammals. Bartholomew argues that polygyny arose in pinnipeds from the interaction of these characteristics with several general mammalian attributes for polygyny (e.g. presence of stored fat as an energy source during fasting, one male can inseminate many females, males are very aggressive and this aggression is hormonally controlled, and males have no nutritional responsibility to pups (Bartholomew 1970). The fossil record suggests that polygyny has been present in pinnipeds since at least the mid to late Miocene (Mitchell 1966) and that pinnipeds of the late Miocene were very similar to present-day types (Downs 1956).

Otariids are excellent subjects for studies of polygyny and territoriality. Their large size and pronounced gregariousness make them easy to observe in large numbers, and their practice of feeding offshore, away from the breeding territories, removes the variable of food availability from studies of territory quality and mate choice. Otariids employ both resource-defense and female-defense polygyny. Fur seals defend territories that are well-defined portions of the rookery, whereas sea lions have less-rigid territories and instead defend a group of females. The South American sea lion shows evidence of using both systems, depending on topography (Campagna & LeBoeuf 1988).

In addition to sharing polygyny as a mating system, otariids also share the need to dissipate heat while ashore. The many adaptations that seals possess for life in a cold, aquatic environment (e.g. blubber, fur, high body volume to surface area ratio) become a hindrance on land at higher temperatures. Physiological means are seldom sufficient to dissipate excess heat and most otariids augment this with behavioural thermoregulation (Whittow et al. 1987). A variety of behaviours are used, including: exposing the less-insulated flippers

to the wind, immersing flippers in water or wet sand, flipping sand on top of the body, wetting the body with urine, resting in shaded areas, changing postures to expose or conceal more flipper area, or returning to the sea (Gentry 1973; Campagna & LeBoeuf 1988). The timing of breeding in summer, when the need to cool off is greatest, results in a strong link between behavioural thermoregulation and reproductive success (Gentry 1973; Mattlin 1978; Campagna & LeBoeuf 1988). In an Australian population of A. forsteri, Gentry (1973) found that males on territories where water was present gained twice as many copulations as males on dry territories who had to leave their stations in order to cool off. Campagna & LeBoeuf (1988) report a similar finding for Otaria byronia in Argentina. The relationship between thermoregulation and reproductive success is discussed further in Chapters 1 and 2.

### New Zealand Fur Seal

Like its congeners, the New Zealand fur seal breeds in densely-packed colonies on shores far removed from human disturbance. They breed on rocky beaches, backed by steep terrain and exposed to the prevailing winds (Crawley & Wilson 1976). As with other species of fur seal, A. forsteri was hunted to near extinction in the 19th Century and the population is only now recovering. Their range is restricted to New Zealand (predominantly South Island) and its subantarctic islands, with a small population in South Australia (Wilson 1981). The behavioural repertoire of this species has been described by Stirling (1970, 1971a, 1971b) and Miller (1971, 1974).

The breeding season starts in November with the arrival of adult males on the rookery. Males establish irregularly shaped and intensely defended territories, from which they attempt to exclude all other males. Females are not present during territory establishment but begin to arrive in late November and throughout December. They settle within a territory and give birth to a single pup two to three days after arrival (Miller 1975b). A female remains with her pup for c. 10 days before she makes her first feeding trip to sea. Oestrus lasts c. 24 hours and occurs about eight days post-partum (Miller 1975b). Oestrus occurs during the sedentary, post-parturition phase, and hence, females generally mate with the male in whose territory they give birth. Males maintain territories for up to two months, and they fast throughout this time (Miller 1975b). While most territorial males have abandoned their stations and left the rookery by mid-January, females and pups remain at the colony until September or October. The females alternate between feeding themselves at sea and nursing their pups on shore. The pups take milk up until the females abandon

the rookery in spring (c. nine months after being born).

### **Thesis Objectives**

The aims of this study were to investigate the microhabitat preferences of adult male and female A. fosteri during the breeding season, and to see how these preferences may have influenced mating success. The ability to cool off is important to seals on land and I modified the availability of shade and/or pools of water on three study sites to test microhabitat preferences. This is the first time manipulation experiments have been used to address the interrelationship between behavioural thermoregulation and mating success in pinnipeds. In addition to studying the resulting changes in female distribution, these manipulations also allowed me to investigate male territory quality. Chapters 1 and 2 deal with the issues of territory quality, microhabitat preference, and mating success. Chapter 3 explores the possible role that female aggression may play in limiting harem size, and thus, a male's mating success. This thesis presents evidence to suggest that both physiological constraints (i.e. the need to cool off) and behavioural constraints (aggression between females) are important factors in determining the mating success of male New Zealand fur seals.

## CHAPTER 1: Resource-defense polygyny: an experimental manipulation of cooling substrates.

### INTRODUCTION

Resource-defense polygyny occurs in species where males compete with one another for control of a resource that is vital to females (Emlen & Oring 1977). Any male whose territory contains a greater quantity or higher quality of the resource can be expected to mate with more females than a male whose territory is less well-endowed. Intersexual selection theory argues that traits which make males more attractive to females will be selected for (Darwin 1871; Fisher 1930; O'Donald 1977; Lande 1980; Kirkpatrick 1982). In resource-defense polygyny, intersexual selection may occur not because females actively choose a mate but, instead, because they select a site based on the material benefits that such a site provides (e.g. Halliday 1983). A number of studies have shown that males with higher quality or greater quantity of a resource in their territory, have access to more females (Armitage 1974; Howard 1978; Lenington 1980; Trillmich 1983). While a few workers have experimentally manipulated resource availability for some invertebrates (Thornhill 1981; Borgia 1982; Waage 1987; Alcock 1987), similar experiments on vertebrate species are all but unknown (but see Pleszczynska (1978) for an excellent exception).

Otariid seals are excellent subjects for studies of resource-defense polygyny. Although they feed and spend much of their time at sea, they come ashore to breed in large aggregations with easily defined territory boundaries. Because all feeding takes place at sea, food availability is not a complicating variable in analyses of site selection. Most fur seals breed on rocky beaches, backed by steep terrain and exposed to the prevailing winds (Crawley & Wilson 1976; Bester 1981). Suitable breeding habitat is therefore usually confined to a narrow strip between high tide and the slope behind the beach. The distribution of seals within this strip is further restricted because of the need to dissipate excess heat while ashore. With their dense fur and thick blubber layer, fur seals are highly vulnerable to heat stress while on land (Irving et al. 1962). Because the seals' physiological mechanisms for cooling off (McGinnis et al. 1970) are inadequate at very high temperatures, behavioural thermoregulation is necessary (see Vaz Ferreira & Palerm 1961; Gentry 1973; Limberger et al. 1986; Campagna & LeBoeuf 1988). Female New Zealand fur seals are known to prefer areas around

shade and pools of water (Mattlin 1978), and males attempt to monopolise these "cooling resources".

This paper describes the effects of manipulating the availability of cooling substrates on a beach used by breeding New Zealand fur seals. Male seals establish exclusive territories in November, prior to the arrival of females. Females each give birth to a single pup a few days after they return to the rookery in December, and enter oestrus about eight days post-partum (Miller 1975a). At this time, they are sedentary, and rarely stray more than a few metres from their pup and its birth site. The sedentary nature of sexually receptive females, combined with the exclusive nature of male territories, means that generally only the territory holder has access to females that give birth within his territory. I provide experimental evidence that the distribution of females is related to the availability of cooling substrates.

## METHODS

Seals were observed daily during three consecutive breeding seasons on Taumaka, the larger of the Open Bay Islands, New Zealand ( $43^{\circ}52'S$ ,  $168^{\circ}53'E$ ). During the breeding season, about 3500 fur seals inhabit the steeply sloping limestone coast of this 12-ha. island. For a detailed description of Taumaka, see Burrows (1972).

Seal locations were mapped daily between 1400 and 1500 hours on three study sites. This sampling time was chosen to coincide with the time at which thermal stress was maximal. In the first season (1984-1985), all study sites were left in their natural condition. Prior to the second (1985-1986) and third (1986-1987) seasons, the availability of cooling substrates was modified on two sites, while the third (site A) remained permanently unaltered as a control. Thermal stress conditions were measured by monitoring rock surface temperature ( $T_{rs}$ ) at each site, using diode thermometers attached to the substrate (six per site).

### Experiment 1: Shade addition

After two seasons of observations with only natural shaded areas present, one study site (site B) had shaded rock substrate added prior to the third season by erecting three separate "gazebos" on areas that were naturally devoid of shade or pools of water. These were erected without reference to territorial boundaries. Each gazebo consisted of a plywood sheet (1.2x2.4m) supported 1.5m off the ground, by steel posts that were bolted to the rock. The height was sufficient for either males or females to sit underneath, and

the shade provided was sufficient to accommodate up to three adult seals.

#### Experiment 2: Shade addition, then removal

Experiment 2 was similar to the shade addition experiment but, in this case, gazebos were erected prior to the second season and removed prior to the third (site C), permitting a comparison of seal distribution in relation to shade availability on a site that changed from natural to modified and back to natural conditions. Three gazebos, as described above, were erected to create shaded rock substrate for this experiment.

#### Experiment 3: Pool addition, then removal

Two pools were added to one study site (site B) prior to the second season, and were removed prior to the third. New pools were created, in areas that were naturally dry and unshaded, by building concrete dams in natural fissures to prevent the run-off of rainwater. Each pool had an approximate surface area of  $4\text{m}^2$ , but this fluctuated slightly depending on rainfall and evaporation.

The cooling substrate modifications for all experiments were located above the highest high tide and they were carried out in September, prior to the arrival of breeding males.

The effect of these modifications on seal distribution was assessed by inter-season comparisons of the number of seals in each experimental area. Because most seals are present on more than one day, many individuals are represented more than once in the total. Therefore, the units used to express the results are seal-days. For example, in experiment 1 (shade addition), the number of seals-days in the first and second seasons that used the specific area that would later be covered by a gazebo, were compared with the number using the same area after it had been shaded. For analysis, the total number of seal-days using the manipulated areas on all observation days, was compared with the similar number not using any cooling substrate. It is recognised that using seal-days as the units of analysis compromises the independence of the data. However, although there may be individual site preferences and the same seals present on more than one day, it should be noted that each day can be viewed as an independent unit. Thermal stress is not a problem at night, so seals begin each day independent of the previous day's weather - if they were too hot yesterday, they won't be at the start of today. Hence, a seal must make a new choice of substrate each day and this choice is based on the present day's weather. To compensate for the lack of complete independence between seal-days, only P values of 0.01 or lower were considered significant.

## RESULTS

Observations of the seal rookery during the unmodified first season revealed an uneven distribution of animals at varying temperatures. The most striking pattern was the preference shown by both females and males for cooling substrates (shaded rocks and pools of water) at higher temperatures (Fig.1). At  $T_{rs}$  below  $15^{\circ}\text{C}$ , 72% of females ( $N=130$ ) and 96% of males ( $N=90$ ) rested on rocks in the sun. As  $T_{rs}$  increased, the use of sunny rocks decreased so that at  $30\text{--}35^{\circ}\text{C}$ , only 47% of females ( $N=320$ ) and 43% of males ( $N=104$ ) used the non-cooling substrate ( $X^2=58.9$  and  $75.9$ , respectively,  $P<0.001$ ). At the highest substrate temperature recorded ( $40\text{--}45^{\circ}\text{C}$ ), these figures had fallen to 26% for females ( $N=41$ ) and 27% for males ( $N=19$ ) ( $X^2=26.2$   $P<0.001$ ,  $X^2=7.3$   $P<0.05$ , respectively). Of course, as the proportion of seal-days on the sunny rocks decreased, the proportion in shade and in pools of water increased. At  $30\text{--}35^{\circ}\text{C}$ , 25% of females ( $N=165$ ) used pools, while 28% ( $N=189$ ) were on shaded rocks. For males at this temperature, 47% ( $N=108$ ) were in pools while 10% ( $N=23$ ) made use of shaded rocks. This trend continued at the highest temperatures, where 34% of females ( $N=56$ ) used pools, and 40% ( $N=65$ ) were on shaded rocks. For males, 58% ( $N=41$ ) were in pools but only 15% ( $N=11$ ) used rocks in the shade. Thus, while the general trend of increasing use of cooling substrates at higher temperatures is the same for both sexes, females made more equitable use of both shade and pools, while males showed a preference for pools over shade. Even at the highest temperatures, a greater proportion of males was found on sunny rocks (27%) than on shaded rocks (15%). The maximum  $T_{rs}$  was  $> 30^{\circ}\text{C}$  on 46% of all days sampled.

### Experiment 1: Shade addition

This experiment further demonstrated the importance of shade to females, but not to males. After shade was added prior to the third season, 18% of females ( $N=25$ ) used the manipulated sites (Fig.2). This contrasted with only 2.2% ( $N=7$ ) and 1.9% ( $N=2$ ) of females on the same areas in the first and second seasons, prior to manipulation ( $X^2=25.2$ ,  $P<0.001$ ;  $X^2=9.6$ ,  $P<0.01$ , respectively). For males, 17% ( $N=13$ ) used the manipulated areas in the first season, and 15% ( $N=11$ ) in the second season. In the third season, after shade had been added, the proportion of males on the manipulated areas increased to 22% ( $N=15$ ), but this was not different from the proportions there prior to modification ( $X^2=0.047$ ,  $P>0.5$ ).

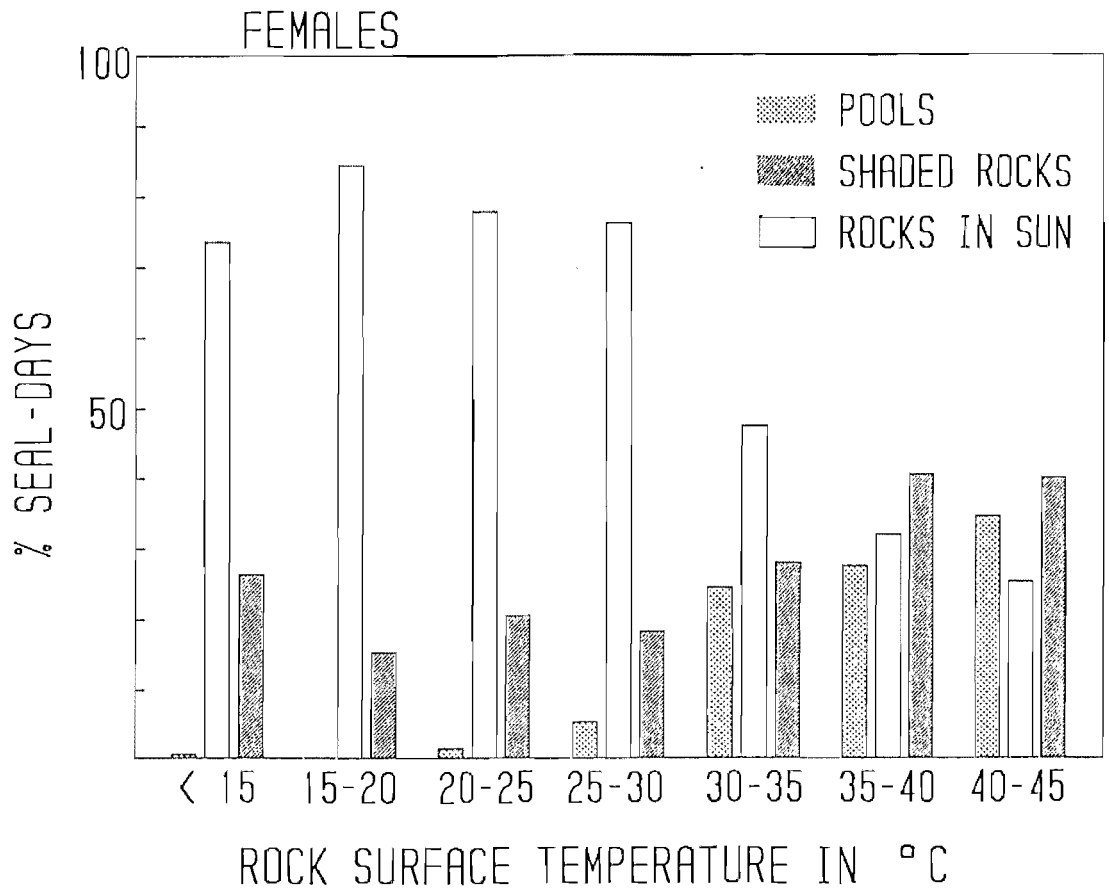
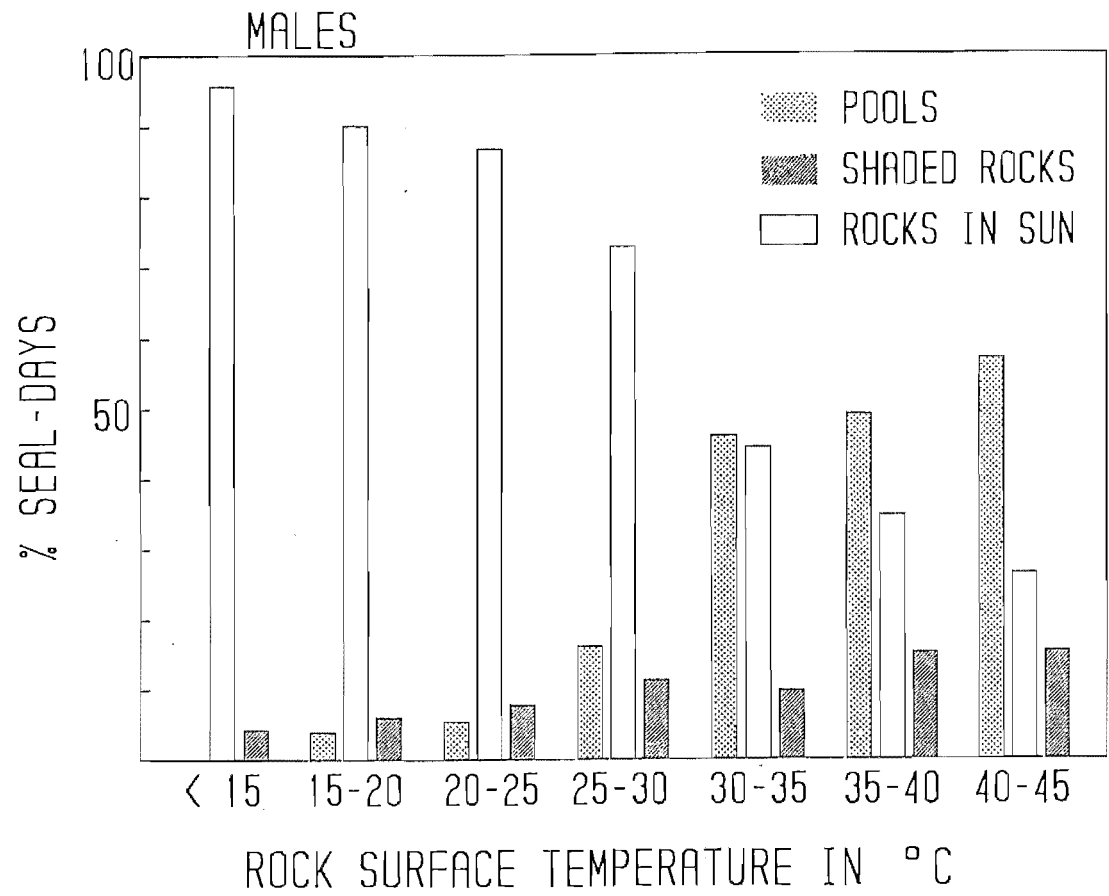


Figure 1. Substrate preferences. Proportions of males and females on each substrate type from all study sites combined, during season 1 (i.e. prior to any manipulation).



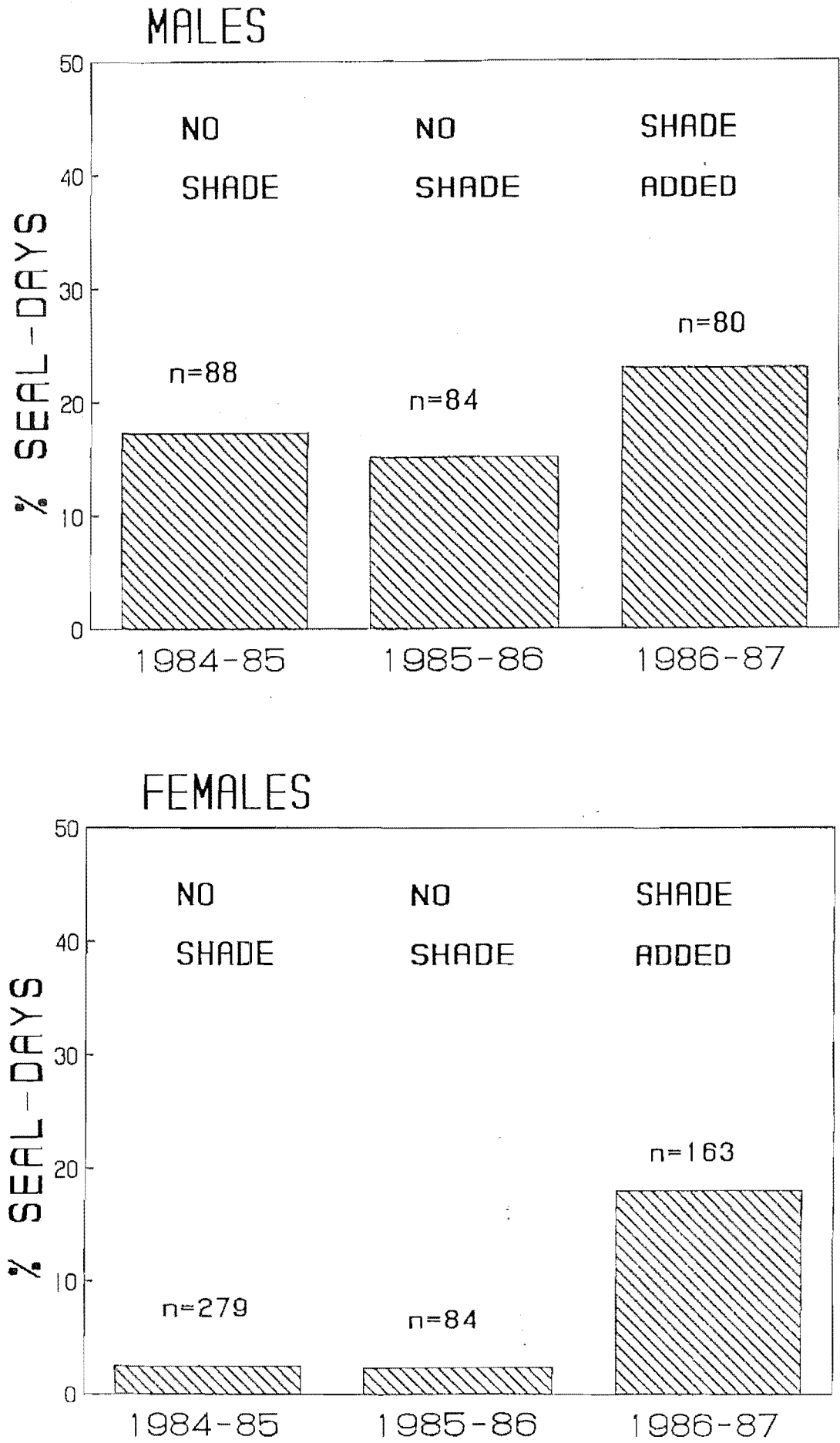


Figure 2. Shade addition experiment. Proportions of males and females on the manipulated areas, over three seasons.

### Experiment 2: Shade addition, then removal

The results of this second shade manipulation experiment corroborated those of the first (Fig.3). In the first season, under natural, unshaded conditions, only 4% of females (N=15) used the manipulated areas. With the introduction of shade for the second season, this figure jumped to 18.5% (N=12) ( $X^2=11.4$ ,  $P<0.001$ ). Shade was then removed prior to the third season, and the proportion of females which used the manipulated areas fell to 2% (1 animal) ( $X^2=6.7$ ,  $P<0.01$ ). The values for the first and third seasons are not significantly different from each other ( $X^2=0.0085$ ,  $P<0.36$ ).

### Experiment 3: Pool addition, then removal

Unlike shade manipulation, which only affected females, manipulating pool availability affected both female and male distributions (Fig.4). In the first season, the areas to be manipulated were in their naturally dry and unshaded state, and only 2% of females (N=5) were found there. However, the proportion of females in the areas after pools had been added (second season), jumped to 14% (N=12), ( $X^2=19.3$ ,  $P<0.001$ ). This value decreased back to 2% (N=3) after the pools were removed prior to the third season ( $X^2=10.7$ ,  $P<0.001$ ). The proportions of females using the experimental areas in seasons one and three, were not significantly different ( $X^2=0.005$ ,  $P<0.8$ ).

The trend for males in this experiment was the same, but even more pronounced than for females. In the first season, only 4% of the males (N=3) used the areas prior to manipulation but 29% (N=21) used the areas in the second season when pools were present ( $X^2=12.3$ ,  $P<0.001$ ). When pools were removed prior to the third season, only 3% (N=2) of the males used the manipulated areas ( $X^2=12.1$ ,  $P<0.001$ ). Again, the difference between the proportions of seals on the experimental areas in the first and third seasons, was not significant ( $X^2=0.008$ ,  $P<0.8$ ).

## **DISCUSSION**

The results support the prediction that female microhabitat selection is strongly influenced by thermoregulatory considerations. Changes in the availability of cooling substrates resulted in alterations of female distribution: females showed a significant preference for areas when they had been manipulated to provide improved cooling potential. Male distribution, while responding to changes made in pool availability, was not as responsive to shade manipulation as was female distribution. This is surprising when one considers that males are probably subjected to greater heat stress on land than females (on Taumaka, males do not enter the sea during the breeding

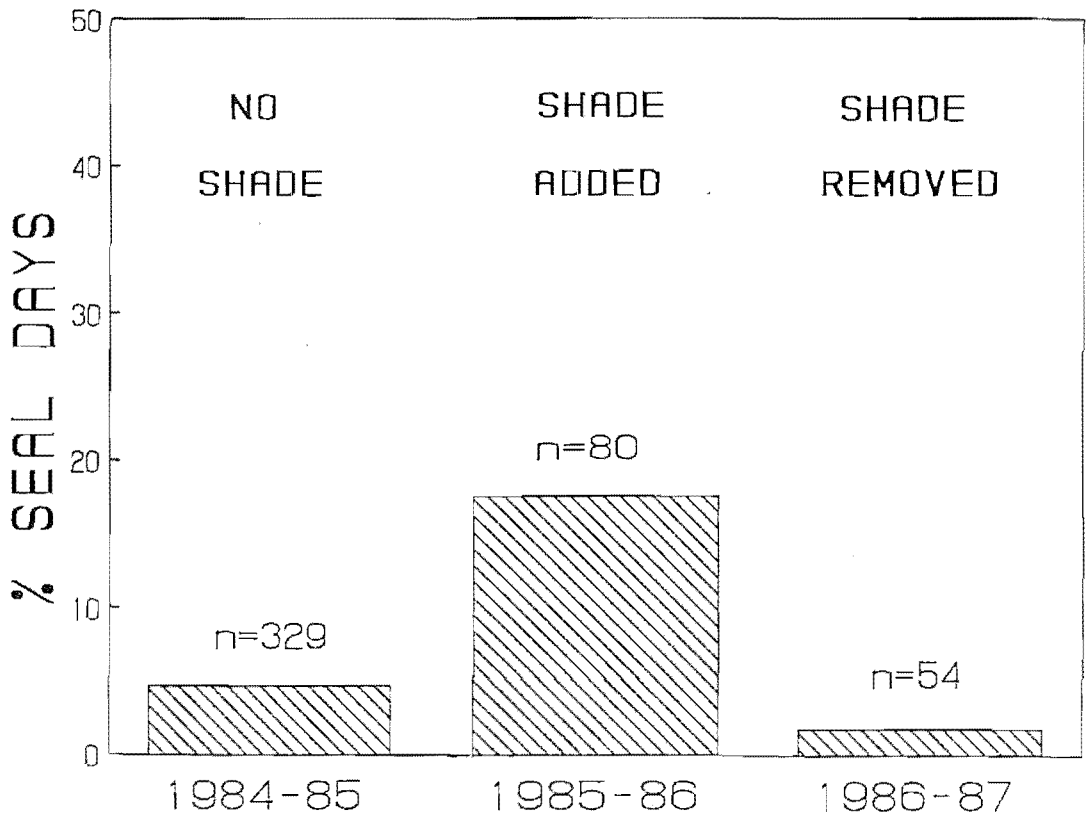
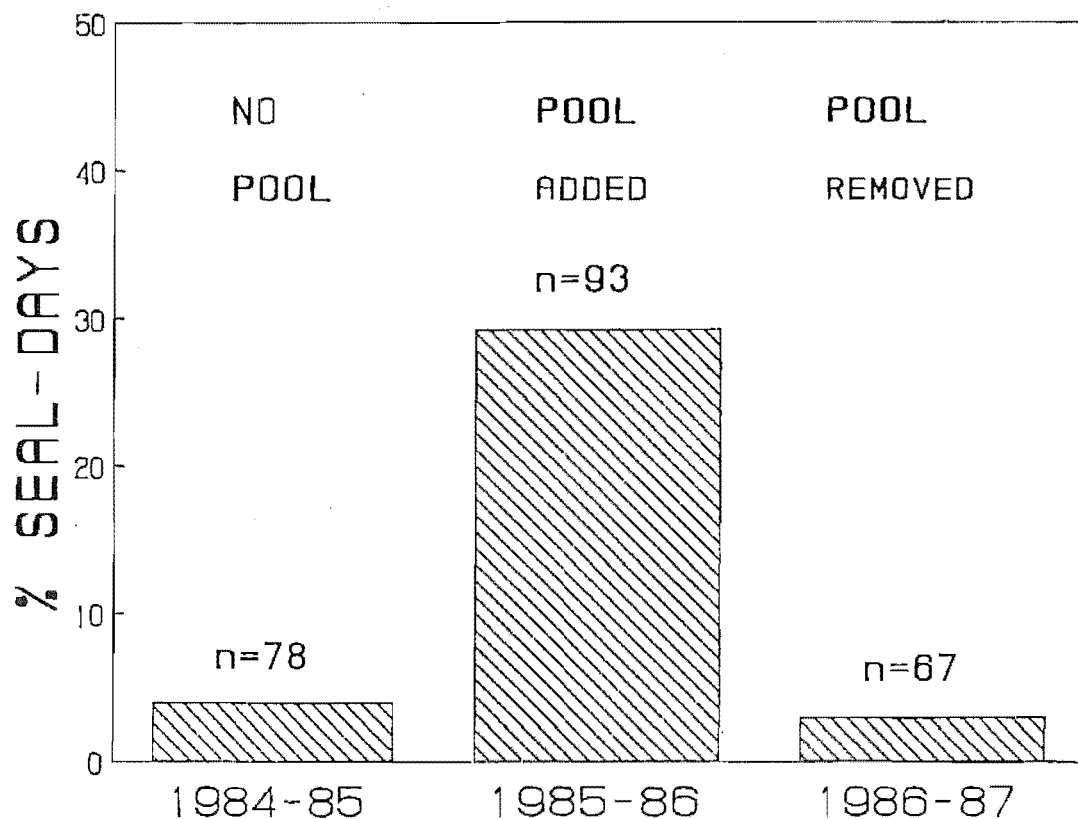


Figure 3. Shade added, then removed. Proportions of females on the manipulated areas, over three seasons.



FEMALES

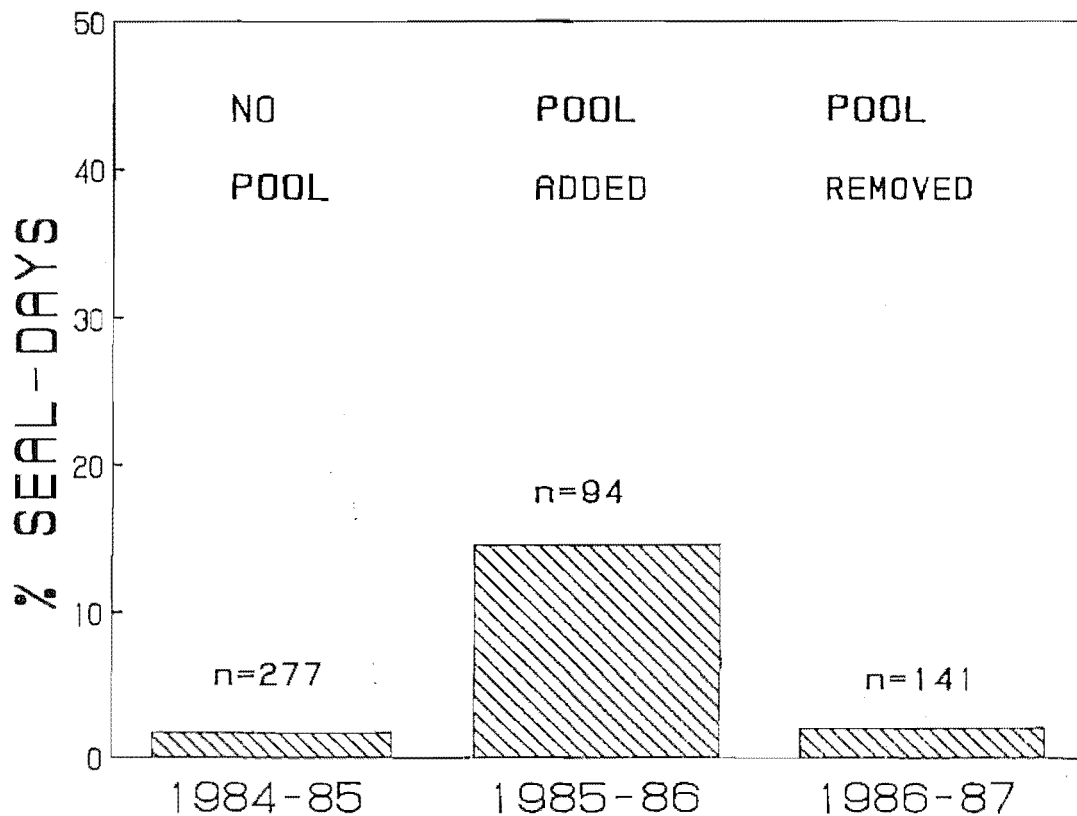


Figure 4. Pool added, then removed. Proportions of males and females on the manipulated areas, over three seasons.

season and have a greater volume to surface area ratio than females). However, the different behavioural constraints operating on males may account, at least in part, for this discrepancy. Although females are harassed and 'herded' by males (Miller 1974), they are more or less free to go where they wish on the rookery. Males, however, are restricted in their movements by the presence of neighbouring males. Therefore, the only males that could use manipulated substrates were those whose territories possessed them.

The limited use of shade by males, even at high temperatures, may also be a reflection of behavioural constraints. Territorial defense requires that a male be in a position to monitor the movements of other males onto his territory. Naturally-shaded substrate is produced by boulders and rock overhangs which can produce blind spots for the vigilant male. Also, the larger size of males may prohibit them from fitting into many shaded areas that can easily accommodate a female.

In resource-defense mating systems, it is important that the defending sex be able to identify and assess the quality and quantity of the important resource. This is particularly true for species like fur seals, where male territories are established in the absence of females. Male fur seals are subjected to problems of heat stress that are similar, though not identical, to those affecting females. Therefore, males should be able, to some degree, to assess the "attractiveness" of an area to females prior to the arrival of those females. Also, while male New Zealand fur seals are sexually mature at the age of 5 or 6 years, they do not hold territories successfully until 10 years of age (Mattlin 1978). In the years between sexual and social maturity, they attempt to establish territories and in doing so, they develop the fighting skills necessary for successful territory occupation. Breeding males (territory holders) will therefore have been around the rookery for several years as "social apprentices" before they are successful breeders and they may hold territories for several years after reaching social maturity. Thus, in addition to being able to assess what sites are attractive to females, males will have experience of what sites were inhabited by more females in previous seasons. Once identified, by self usage or experience of past female distribution, the discrete, patchy, nature of cooling substrates makes them an easy resource to monopolise.

Cooling substrates are also resources which are fixed both spatially and temporally and are therefore different from the more ephemeral resources defended by males of other polygynous species (e.g. food, orange-rumped honeyguides (Cronin & Sherman 1977), and oviposition sites, ragwort seed

bugs (McLain 1986)). Depressions in the rock which hold water or large overhangs which provide shade are much more permanent, and thus, past experience may reduce the need for constant reassessment.

Male New Zealand fur seals are controlling access to a resource that is important to females and their offspring, and not just for a brief period around copulation, but for several months. This suggests that an arriving female is selecting a site based on its physical characteristics, and not on the potential genetic contribution of the male that controls that site. The primary sexual selection force in this species is likely to be intrasexual, with males competing with one another for territories on the rookery, and particularly for those sites with greater cooling potential. This male competition results in only a small proportion of the total male population being responsible for the majority of female fertilisations (Bartholomew 1970). Hence, as long as a female settles on a territory and mates with a territory holder, it may not matter much to her which male inseminates her. Studies of other polygynous species have shown intense inter-male competition to render female mate choice superfluous (e.g. Cox & LeBoeuf 1977; Trillmich & Trillmich 1984). This point may be particularly valid at the present size of the New Zealand fur seal population, which is conservatively estimated as being one tenth the number of seals present before commercial exploitation began in the 18th century (Wilson 1981). Therefore, it is plausible to suggest that at today's population level, fewer seals may be relegated to more marginal breeding sites than would have been at higher, pre-exploitation population levels.

A potential difficulty with habitat modification experiments is that the result may be clouded by site fidelity. The degree of site fidelity in the New Zealand fur seal is unknown. One would expect that, if site fidelity was high, then only manipulations that made a site less tolerable, from a thermoregulatory point of view, would be effective in altering seal distributions. Those manipulations which merely enhanced the cooling potential of an area that was usually unoccupied would not be expected to overcome strong site fidelity. The results of this study suggest that site fidelity is not developed to such a degree that it prohibits short distance (c. 10m) movements on the rookery. Experiments 2 and 3 used manipulations that both enhanced and degraded the cooling potential of an area. Both experiments demonstrate that the seals are able to assess the varying cooling potential of the manipulated areas, and that these decisions can take precedence over site selection habits from previous seasons.

Mattlin (1978) suggested that accessibility to the sea was another factor determining female site preference, and further investigation will doubtless reveal others. However, it is clear that cooling substrate availability is an important proximate cue for female site selection, and that these cooling substrates are a vital resource that can be monopolised by polygynous males.

## CHAPTER 2: Male territory quality

### INTRODUCTION

In many polygynous species, males occupy exclusive territories and mate with the females that settle within these. Since for many species, males are occupying territories in the breeding areas before females arrive, female mate choice is the central issue in several models attempting to explain the evolution of polygyny (Altmann et al. 1977; Weatherhead & Robertson 1979; but see Lightbody & Weatherhead 1988).

In their polygyny-threshold model, Verner & Willson (1966) argued that a female would do better to mate with a previously mated male on a high quality territory, rather than with an unmated male on a territory of low quality. Studies of the breeding systems of many species have used this hypothesis to explain the occurrence of polygyny (e.g. Carey & Nolan 1975; Pleszczynska 1978; Searcy 1979; Lenington 1980; Trillmich 1983).

Although female mate choice is crucial to the understanding of polygyny, the cues used by females when selecting a mate are not always clear (e.g. O'Donald 1983). Some researchers support the idea that males are chosen (e.g. Verner & Willson 1966; Askenmo 1984; Dickinson & Lein 1987), while others argue that the physical characteristics of the territory are of primary importance in female choice (e.g. Bartholomew 1970; Miller 1975a; Rauch 1985; Warner 1987; Chapter 1). In addition, Yasukawa (1981) suggested that a complex interaction of male and territory quality may determine female choice. The issues are further clouded by the problem that in many species, it is the larger (and presumably highest quality) males which occupy the territories that researchers have defined as being of high quality (e.g. Davies 1978; Downhower & Brown 1980; Thornhill 1981). Territory quality is also difficult to assess because the human umwelt (*sensu* von Uexkull 1909) is usually thought to be different from that of the subject species. Nevertheless, attempts have been made to equate territory quality with such characteristics as "shady/shelter places" in lizards (Rauch 1985), downcurrent reef projections in fish (Warner 1987), nestbox attractiveness in birds (Askenmo 1984), the availability of oviposition substrate in damselflies (Alcock 1987) and food sources in birds (Cronin & Sherman 1977).

Otariid seals are excellent subjects for studies of territory quality because they breed in large aggregations and defend territories with



easily defined boundaries. All feeding takes place at sea and food availability is therefore not a complicating variable in analyses of territory quality and mating systems. Fur seals breed on rocky beaches backed by steep terrain and exposed to the prevailing winds (Bester 1981; Wilson 1981). Suitable breeding habitat is therefore usually confined to a narrow strip between high tide and the slope behind the beach.

The distribution of seals within this strip is further restricted because with their dense fur and thick blubber layer, fur seals are highly vulnerable to heat stress (Irving et al. 1962). Most seals need to dissipate excess heat while ashore, a problem which is exacerbated by the timing of breeding in summer. Although fur seals are known to possess some physiological mechanisms for cooling (McGinnis et al. 1970), these are inadequate at extreme temperatures and the use of behavioural thermoregulation becomes a necessity (Vaz Ferreira & Palerm 1961; Gentry 1973; Limberger et al. 1986; Campagna & LeBoeuf 1988).

New Zealand fur seals show a preference for areas around pools of water and shade (Mattlin 1978; Chapter 1). Male New Zealand fur seals, which are three times larger than females, establish territories in November prior to the arrival of the females. Females arrive and settle on a territory in December, give birth 2-3 days later, and enter oestrus and mate about eight days post-partum (Miller 1975b). At this time they rarely stray more than a few metres from their pup and its birth site. The sedentary nature of sexually-receptive females, combined with the exclusive nature of male territoriality, means that a territorial male generally has exclusive access to the females that give birth within his territory. In this study, I defined territory quality in terms of number of females available for mating. I investigated the relationship between the physical characteristics of territories and territory quality, by manipulating the availability of two substrates (shade and pools) used for cooling within male territories.

## METHODS

During the breeding season, about 3500 fur seals inhabit the steeply-sloping limestone coast of Taumaka, the larger of the Open Bay Islands, Westland, New Zealand ( $43^{\circ}52'S$ ,  $168^{\circ}53'E$ ). For a detailed description of Taumaka, see Burrows (1972). Seals were studied here by mapping seal locations twice daily on four noncontiguous study sites. Sampling times were chosen to coincide with the daylight times when

thermal stress was probably minimal (0600-0700), and maximal (1400-1500). In season 1 (1984-1985), all study sites were left in their natural condition. Prior to season 2 (1985-1986) and season 3 (1986-1987), the availability of cooling substrates was modified on three sites, while the fourth site (site A) served as a control and was left unaltered.

#### Cooling substrate manipulations

The timing and type of substrate manipulations for each study site are summarised in Table 1. Shade was added to a site by erecting three separate "gazebos" on areas that were naturally devoid of shade or pools of water. Gazebos were erected without reference to territorial boundaries. Each gazebo consisted of a plywood sheet (1.2 x 2.4 m) supported 1.5 m off the ground, by steel posts that were bolted to the rock. The height chosen was sufficient for seals of both sexes to sit up underneath, and each gazebo provided ample shade to accommodate as many as three adult seals.

The availability of pools of standing water was also modified. New pools were created in areas that were naturally dry and unshaded by building concrete dams in natural fissures to prevent run-off of rainwater. Each pool had a surface area of c. 4 m<sup>2</sup>, but this fluctuated slightly depending on rainfall and evaporation. Pools were effectively removed from an area by covering them with framed plywood. Local rocks were then placed on top of the plywood in order to remove any textural preference that the smooth wood might have on site selection. Prior to season 2, 20% of natural pools were removed. Another 54% were covered prior to season 3, resulting in a total of 74% of pools removed from this study site during the third season.

Modified cooling substrates were always located above the highest high tide and all modifications were made in September, prior to the arrival of breeding males.

Territory boundaries were determined by mapping the movements of territorial males and the locations of fights between neighbours. The areas of each territory and cooling substrate region (m<sup>2</sup>) were measured from aerial photographs using a Koizumi KP-27 polar-compensating planimeter. Where a territory boundary was uncertain, no territory area was computed. The total number of territories for all study sites combined was as follows: season 1 - 27, season 2 - 24, season 3 - 20. Simple and partial correlations were used to analyse the results where applicable. However, because small sample sizes precluded the use of statistical tests when comparing changes in the number of females per

## SUMMARY OF EXPERIMENTS

SITE	SEASON		
	1 (1984-85)	2 (1985-86)	3 (1986-87)
A	no modifications	no modifications	no modifications
B	no modifications	pools added	pools removed, shade added
C	no modifications	shade added	shade removed
D	no modifications	20% of pools removed	74% of pools removed

Table 1. Summary of experimental substrate manipulations for all study sites and seasons. See text for details of techniques used to modify substrates.

territory in response to manipulations, these data are presented descriptively.

Counts of females on each territory were available for early morning and mid-afternoon. For analysis, the number of females per territory was calculated by averaging the larger of these two daily counts, from all days that fell within that season's "Oestrus Period" (Oe.P.). The Oe.P. was defined as that period starting six days after the birth of the first pup on the study site and ending 12 days after the birth of the last pup there. This definition of Oe. P. was based on Miller's (1975b) report that females enter oestrus from 6-12 days post-partum. The Oe.P., therefore, spans the time of female presence that is most crucial to male reproductive success.

Comparisons of the number of females per territory were made between seasons to see what effect substrate manipulations had on male mating success. A territory was considered to be unaltered if none of its boundaries had shifted more than two metres from its position in the previous season. Only those territories whose boundaries remained unaltered or incorporated a complete neighbouring territory were used for inter-season comparisons. Boundary changes altered the size and location of many territories, and such perturbations made inter-season comparisons invalid. Because the total number of females on each study site varied between seasons, inter-season comparisons of the number of females per territory are presented as percentages of the total number of females on the entire study site.

There is a direct relationship between the number of females on a territory and the number of copulations that a territorial male achieves because oestrous females are sedentary and most mate exclusively with the male within whose territory they had their pups (Miller 1975a; Campagna & LeBoeuf 1988). A small number of females (only one observed in this study) may copulate with males in different territories, and some females may not copulate at all. However, the proportions of these females are likely to be similar in all territories. Thus, in the absence of directly observed copulation frequencies, females per territory was used as a measure of male mating success.

## RESULTS

The number of females per territory (harem size) ranged from zero to nine. There were more females on territories with more shade ( $r = 0.4507$ ,

$P < 0.001$ ; Fig. 1). The number of females on a territory was also positively correlated with the size of territories ( $r = 0.3464$ ,  $P < 0.05$ ; Fig. 2). A partial correlation between females and territory area showed this relationship held even when shade effects were removed ( $r = 0.2760$ ,  $P < 0.05$ ).

In contrast, pool area showed no significant correlation with number of females ( $r = 0.0563$ , NS). There was still no correlation even when variance contributed by shade and area were removed ( $r = 0.1450$ , NS).

#### Boundary Changes

The three seasons of observation allowed for two inter-season comparisons of territory boundaries. Boundary changes occurred between seasons at all study sites. There was no difference between the proportions of territories which changed on the manipulated sites and the proportion which changed on the control site ( $X^2$  test, N.S. Table 2). In all cases, the number of boundary alterations on manipulated study sites was little different from the natural reordering that occurred on the unmodified control site.

#### Effect of substrate manipulations on harem size

Although boundary changes limited the number of territories available for inter-season comparisons of harem size, all those that could be used suggest that site manipulations may affect the number of females on a territory. Shade was added to two territories that were not altered by boundary shifts. On both, the proportion of females using these territories (expressed as a percentage of all females on the study site) increased after the addition of shade, from 40.7% to 47.2%, and from 39.7% to 56.2% (Fig. 3). On unaltered territories at the control site (where no manipulations were made), female numbers fluctuated only slightly between seasons, with changes in the proportions from 15.7% to 16.5% between seasons 1 and 2, and from 20.4% to 19.2% between seasons 2 and 3 (Fig. 3).

Inter-season comparisons of four territories that were not directly manipulated also showed interesting changes in the numbers of females present. Territory 4, on site D, was  $\leq 10$  m from an area where a pool was removed prior to season 2. The proportion of females on this unaltered territory increased from 24.1% in season 1, to 39.7% in season 2 (Fig. 4a). Territory 1 on site C was  $\leq 10$  m from the area where gazebos were erected on that study site prior to season 2. On this unaltered territory, the proportion of females dropped from 19.2% to 5.2% (Fig. 4b). Finally, territories 2 and 3 of site B were  $\leq 6$  m from areas where shade was added prior to season 3. The proportions of females on these territories also declined, from 31.8% to 24.7%, and from 28.4% to 19.2%

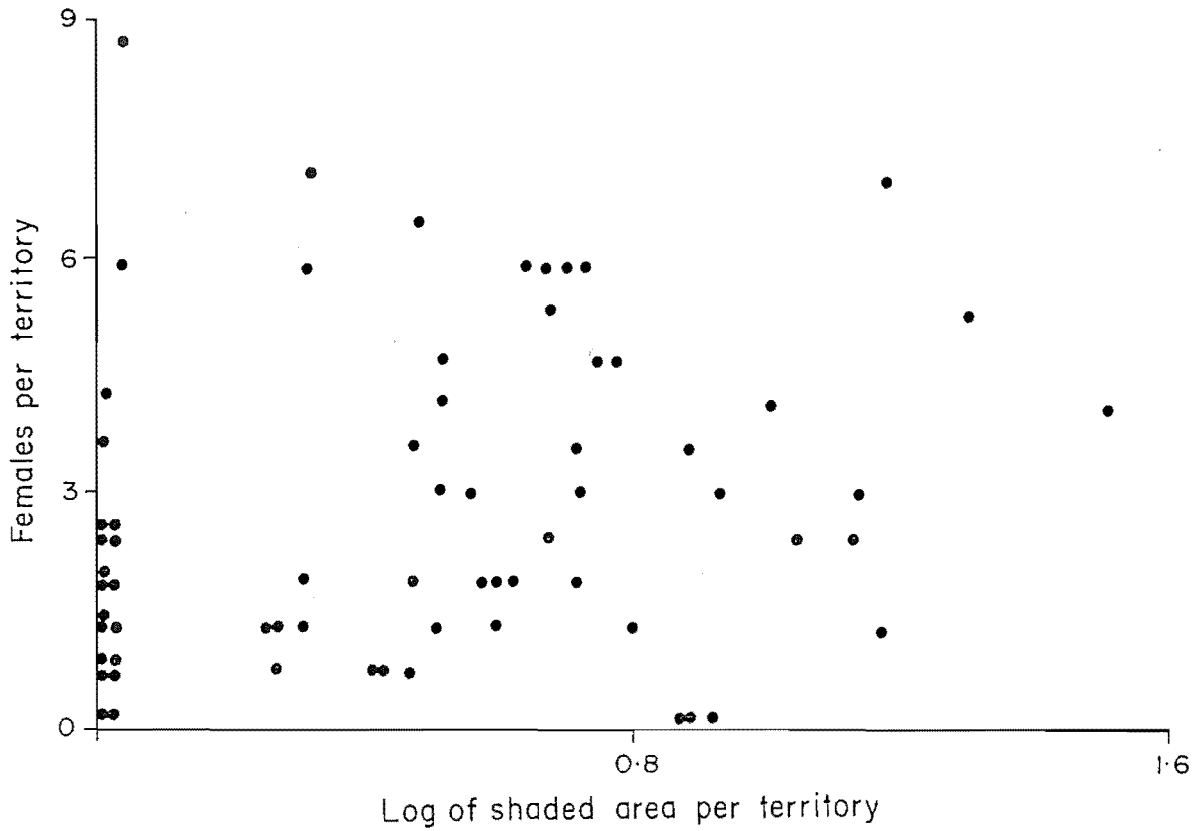


Figure 1. Scatter plot of harem size (females per territory) versus the log of the area of shaded substrate on a territory.

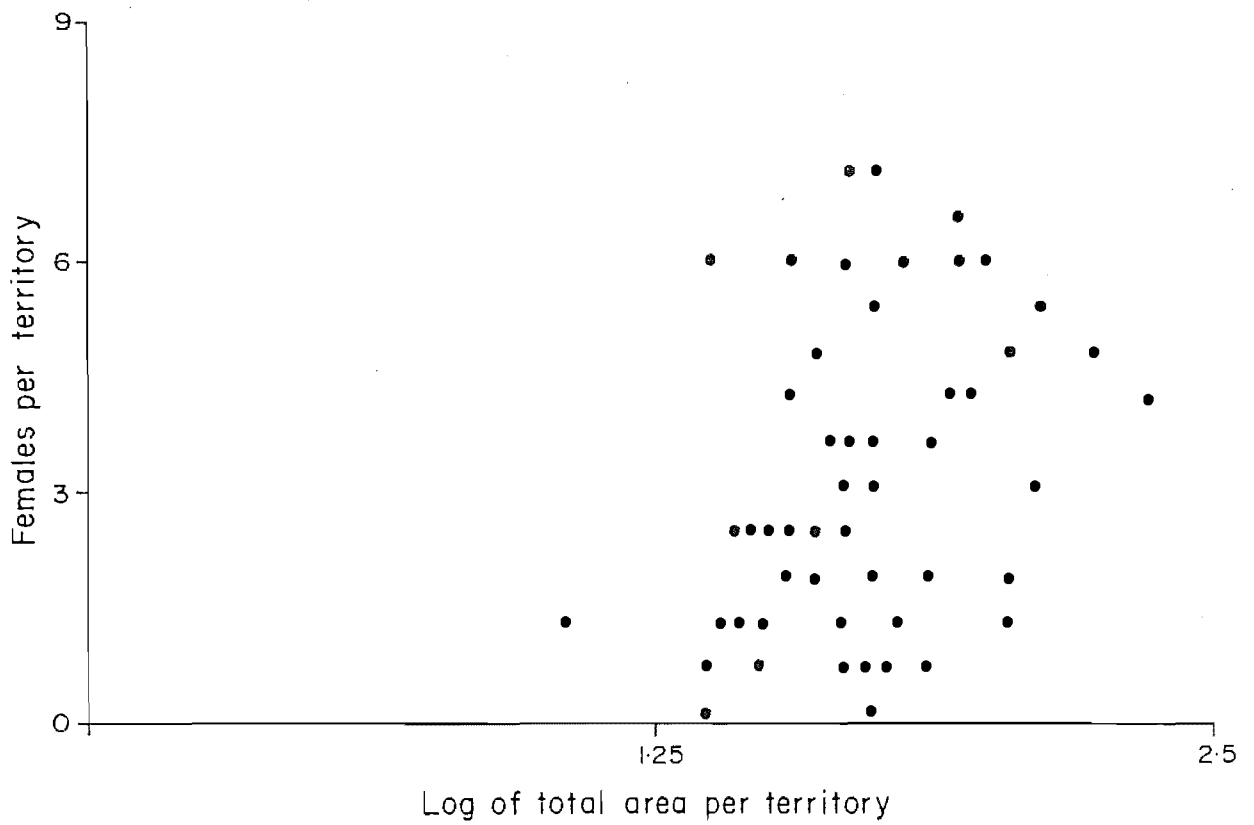


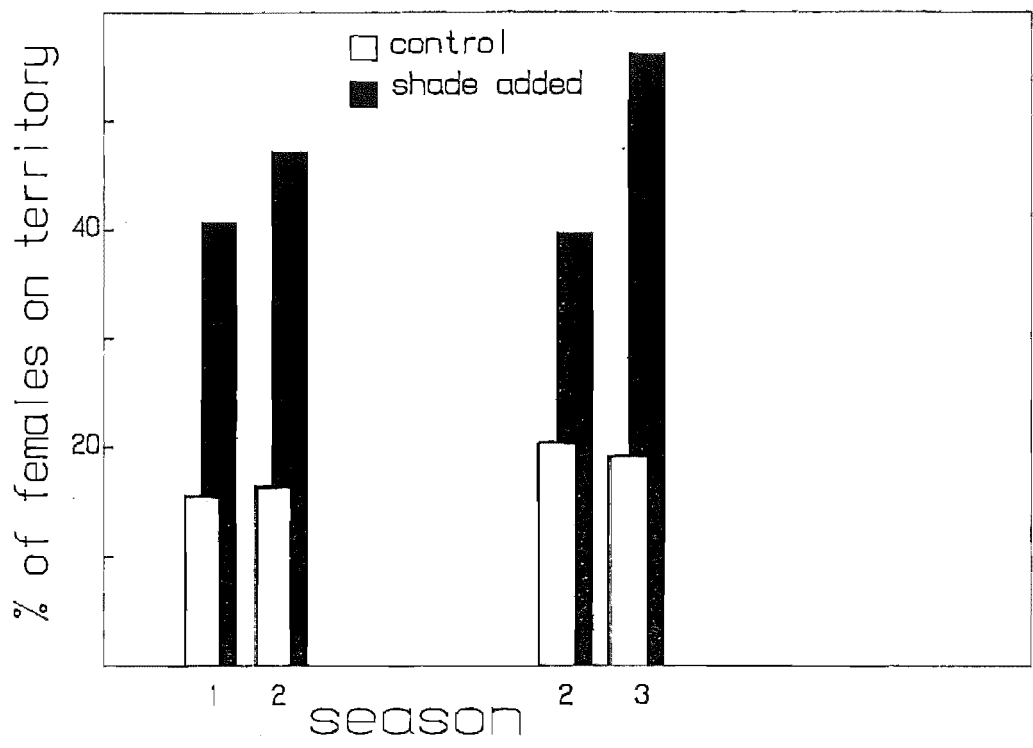
Figure 2. Scatter plot of harem size (females per territory) versus the log of the total area per territory.

## TERRITORY BOUNDARY CHANGES

SITE	BETWEEN SEASONS	BETWEEN SEASONS
	1 AND 2	2 AND 3
A	25.0 n = 8	37.5 n = 8
B	33.3 n = 6	33.3 n = 3
C	40.0 n = 5	33.3 n = 3
D	20.0 n = 5	66.7 n = 6

Table 2. Proportions (%) of territories whose boundaries changed between seasons. n = total number of territories on study site.





**Figure 3.** Effects of shade addition on harem size at two territories with unchanged boundaries on different study sites. Results are expressed as a percentage of all females on the study site because female population varied between seasons.

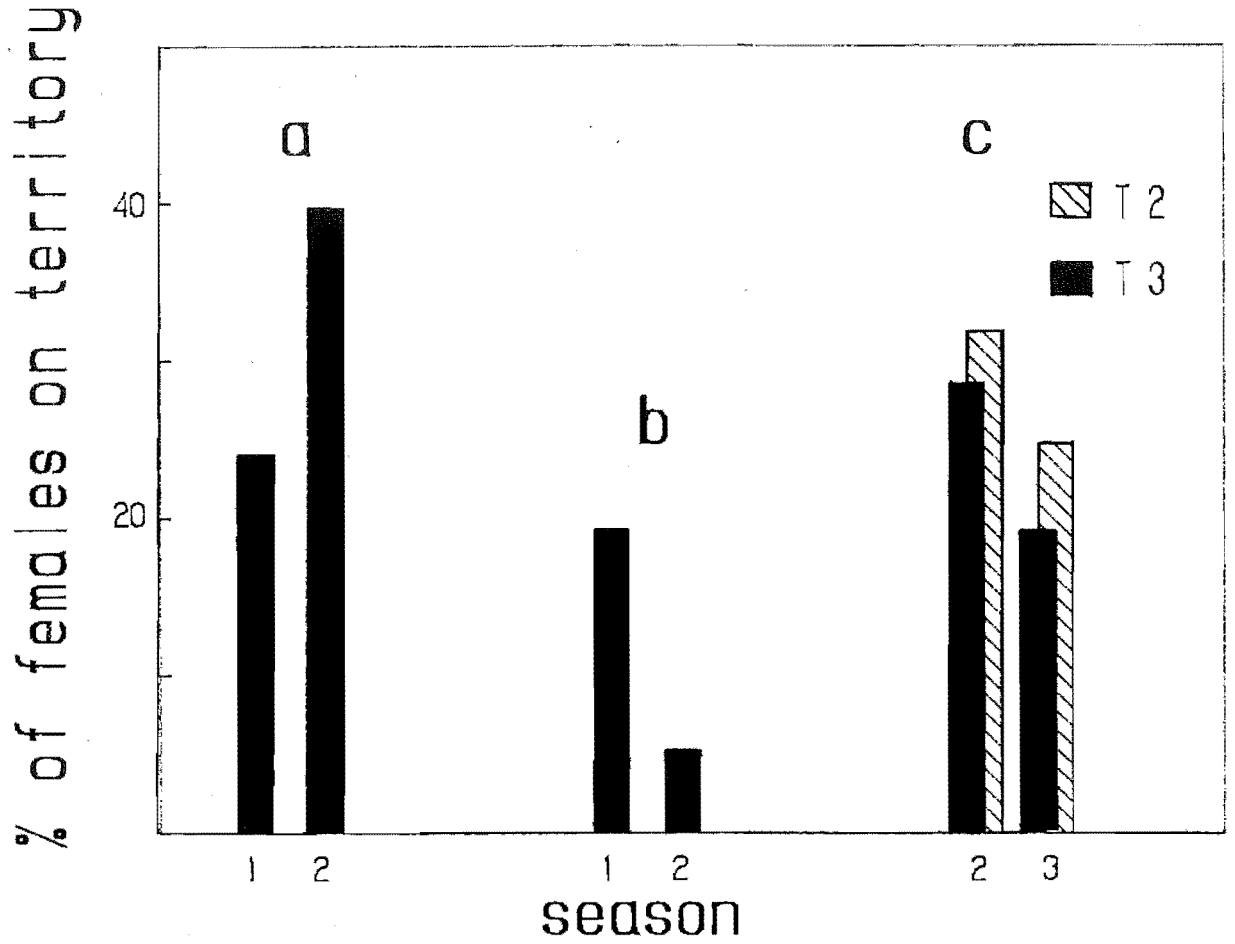


Figure 4. Effects of substrate manipulations on harem size at territories with unchanged boundaries that were adjacent to the manipulated areas. Substrates were not modified on the territories presented here. Results are expressed as a percentage of all females on the study site because female population varied between seasons.

(Fig. 4c). Boundary changes on all other territories adjacent to substrate manipulations precluded them from being used in this analysis.

## DISCUSSION

The results show that territories with more shade are populated with more females. This strong positive correlation between harem size and the amount of shade on a territory suggests that the area of shaded substrate on a territory can be used as an index of male territory quality, when territory quality is defined as the number of females that a male has access to. Although shade is important for seals as a place for cooling off while ashore (Mattlin 1978; Chapter 1), it is sparsely distributed on the breeding colony and is, therefore, a resource that is monopolisable by territorial males. The patchy distribution of shade results in variability in territory quality, which in turn begets differential male mating success.

Harem size is also positively correlated with total territory area and this is obviously important in terms of male mating success, because each female takes up space, and more area allows for more females. However, the amount of area that a male can successfully defend must be limited. Males on extremely large territories often have their holdings diminished with the arrival of additional males. Thus, there appears to be an energetic constraint on total territory area. Female behaviour also limits the number of females to which a male has access because female A. forsteri will not tolerate inter-individual distances of less than 1 m. This differs markedly from other female otariids, such as Stellar's sea lion Eumetopias jubatus (Gentry 1973), which rest in contact with one another.

Unlike shaded substrate, pool area was not correlated with harem size. This is surprising in light of experimental results (Chapter 1) which clearly showed that the number of females using an area increased significantly after pools were added to the area. The reason for this discrepancy is unknown, but it may reflect a preference for shade over pools by females needing to cool off. Females may use pools when they are available, but the presence of pools in the absence of shade may not be a sufficiently strong cue for female site selection. Pools may also be less preferred by females because they can evaporate and are therefore less stable than shaded substrate.

therefore less stable than shaded substrate.

Although limited, the data concerning the effects of substrate manipulation on harem size are biologically significant. In every available case, the results support the prediction that territories with greater cooling potential will also have larger harems. There were small fluctuations in harem sizes on territories at the control site, but these were smaller than the increases found at both shade-enhanced territories on manipulated study sites. In the absence of more territories with stable boundaries and manipulated substrates, the question to be asked is, "what, besides the addition of shaded substrate, could account for these increases in female numbers?". The possible options include: changes in environmental conditions, natural changes in physiography, or changes in the identity of resident males and/or females. None of these stand up to scrutiny. The different study sites are all within 300 m of one another so any changes in weather were likely to affect them all similarly. All four study sites showed similar thermal conditions. Also, there were no detectable changes in the physical characteristics at any study site, except where I carried out substrate manipulations. In order for changes in the identity of the resident male to be of consequence in accounting for the increase in females on a territory, one has to assume that females can assess the "quality" of a male. There is no evidence to suggest that female A. forsteri can assess male quality and, on the contrary, several studies of otariids suggest that male-male competition renders female mate choice superfluous (Bartholomew 1970; Miller 1975a; Trillmich & Trillmich 1984; Chapter 1). Obviously, changes occurred in the identities of the females present because additional females were on the modified territories. The extra females were either virgins returning to the rookery to breed for the first time, or they were experienced breeders that immigrated from other territories. If virgin females do not return to their natal territory to reproduce, then they must select a pupping site by the same means as any other female. However, if they are philopatric, then this could account for an increase in females per territory. Because there has been no long-term tagging programme for this species, it is not known if nulliparous females return to their birth site to breed. Results of site manipulation experiments suggest that females are not so "hard-wired" that they will not use areas that they previously left vacant (Chapter 1). Also, if the coincidental return of virgin females to these territories was responsible for the increased numbers of females present, one would expect similar increases at the control territories, proportionate to the number of pups weaned there. This was not the case. In summary, the most

likely explanation for the increase in the proportion of females on the shade-enhanced territories is that females can assess the cooling potential of an area and will move into that area from other territories.

Further support for this conclusion comes from examination of some of the territories adjacent to those that were manipulated. Again, the number of territories available for these inter-season comparisons was limited, but they do suggest that adjacent areas were influenced by substrate manipulations. Where the cooling potential of an area was reduced, a nearby unaltered territory showed an increase in the proportion of females there. Relative to other areas, this territory had been made more "attractive" as a site for cooling off. At the two study sites where shade was added, neighbouring territories showed a marked decline in the proportion of females present. These adjacent territories may have been made relatively less attractive because of shade addition elsewhere. Thus, the manipulation of cooling substrates seems to have an effect beyond the boundaries of the modified territories, and it appears that females are moving across territory borders to take advantage of these improvements in cooling substrates.

Males on territories with greater area of shaded substrate had access to greater numbers of females than males on less-endowed territories. In a South Australian population of A. forsteri, Gentry (1973) reported that the copulation frequency of males who had inland territories was only half that of males whose territories accessed water. Similarly, male South American fur seals A. australis, and southern sea lions Otaria byronia, on coastal territories had round-the-clock access to females, while landlocked and offshore males were left with vacant territories at different times of the day due to thermoregulatory constraints (Trillmich & Majluf 1981; Campagna & LeBoeuf 1988). One would expect male-male competition to be more intense where higher quality territories were at stake. Indeed, Miller (1971) showed that competition for shore territories was greater than that for inland territories.

There is insufficient evidence to suggest that males are altering territory boundaries to include areas of enhanced cooling substrate availability. While the experimental results showed that females made increased use of an area after its cooling potential had been improved (Chapter 1), male territory boundaries did not fluctuate in relation to these manipulations, i.e. the number of territory border changes on the manipulated sites was not significantly greater than that observed on the control site. Examination of the control site revealed that although

territory boundaries remained similar from one season to the next, they were not totally rigid and some natural discrepancies did occur. Such alterations probably reflect changes in the identities of the territorial males present. Like other otariids (Peterson 1965, Gentry 1970, as cited in Miller 1975a), some male A. forsteri hold territories in the same location for consecutive years and they are likely to delineate their stations by the same features in each year. Miller (1975a) showed that the rigidity of a territory boundary within a season "varied directly as a degree of topographical definition". However, the exact location and size of a territory is constrained by the fighting ability of a male's neighbours. Given the variability of the fighting skills of different males (Miller 1975a), a change of neighbour between seasons may result in a "weaker" opponent, and an increase in territory size, or in a "stronger" opponent, with a resulting reduction in territory size or the loss of preferred areas.

The relatively low number of boundary changes on the manipulated sites is puzzling in light of the experimental results (Chapter I), which showed that males made more use of an area after pools had been added. The results of this earlier study suggest that males are capable of assessing the cooling potential of a site, even without previous experience of cooling substrate on that site. Because males can identify new cooling substrates, one might expect that competition for such improved areas would be reflected by more changes in territory boundaries on manipulated study sites, than on the control site. This was not the case. Thus, while males can identify and make use of new cooling substrates, there is insufficient evidence to suggest that they are able to predict where females will settle after an area has been modified. This suggests that previous experience of female distribution may be important in determining male site selection.

Because male fur seals play no part in the rearing of pups, post-zygotic paternal investment is not likely to be a factor in female mate choice. However, males do control areas of cooling substrate, and Miller (1975a) has logically suggested that the regions where many females give birth can be considered an extension of male phenotype. Regardless of whether females are choosing males directly or simply selecting sites that males control, the polygyny-threshold hypothesis (Verner & Willson 1966) can be used to interpret the results of this study. A male is contributing only gametes and can inseminate many females during the same season. Hence, his contribution to reproducing and raising a pup is

shareable. A female that settles on a territory with much shaded substrate will be at an advantage over one that settles on a territory devoid of shade, regardless of whether the resident male has mated with other females. In addition, there is no trophic advantage to any particular territory because males fast during their territorial tenure, while females feed themselves at sea and suckle their young on milk. Space and proper microhabitat are the crucial factors defining a "good" territory for a female's own needs, the needs of her developing pup, and for maximising male mating success.

## CHAPTER 3. Female agonistic behaviour

### INTRODUCTION

The role of female aggression in the evolution of polygyny has recently received considerable attention (e.g. LaPrade & Graves 1982; Hurly & Robertson 1984,1985; McLean 1984; Davies 1985). Most researchers have interpreted their results within a framework that assumes female mate choice (see Altmann et al. 1977 and Weatherhead & Robertson 1979 for a description of female mate choice models). Several studies of redwinged blackbirds (Agelaius phoeniceus) have suggested that aggression between females can reduce harem size and, therefore, the reproductive success of territorial males (LaPrade & Graves 1982; Hurly & Robertson 1984,1985). These studies showed females defended small territories within a male's territory. Similar findings have also been reported for ground squirrels (e.g. Yeaton 1972; Festa-Bianchet & Boag 1982). This aggressive partitioning of resources contrasts with the expectation that females in harems should be tolerant of other females (Downhower & Armitage 1971).

Little attention has been paid to female aggression in species with resource-defense polygyny. In these species, female mate choice is minimal or non-existent, and males compete among themselves for exclusive access to females. The polygynous breeding system of the New Zealand fur seal is based on resource defense by males (Chapter 1) and this study presents evidence to suggest that females defend resources within a male's territory, and that this may limit harem size.

Male New Zealand fur seals establish exclusive territories in late November, before females arrive. Throughout December, females come ashore and settle within a territory. They give birth to a single pup a few days after arrival, and enter oestrus and mate c. 8 days post-partum (Miller 1975b). A fur seal's body is well insulated against the cold aquatic environment, but seals overheat easily when on land. Fur seals dissipate heat by sitting in pools of water or shaded areas. These "cooling substrates" are patchy in distribution and can be monopolised by males. The availability of cooling substrates is important physiologically, and possibly evolutionarily, because the number of females on a territory is positively correlated with the amount of shaded substrate present (Chapter 2).

Unlike some otariid seals, female New Zealand fur seals do not tolerate close neighbours and a minimum inter-individual distance of c. 1 m is maintained (Gentry 1973), often by means of agonistic behaviour. Various



postures and vocalisations are used by females in agonistic interactions and these encounters often attract the attention of the territorial male. Males exhibit "peacekeeping" behaviour and sometimes intervene and end female disputes (Miller 1974). This study investigated the location and seasonal timing of female conflicts in relation to the distribution of cooling substrates. Because shaded areas and pools of water are preferred substrates (Chapter 1), competition among females for use of these areas may be expected to limit harem size and affect male mating success.

## METHODS

Seals were studied daily during the breeding season on Taumaka, the larger of the Open Bay Islands, New Zealand ( $43^{\circ}52'S$ ,  $168^{\circ}53'E$ ). Approximately 3500 fur seals inhabit the steeply-sloping limestone coast of this 12-ha. island during the breeding season (Crawley & Wilson 1976). For a detailed description of Taumaka, see Burrows (1972).

Observations were made from a hide at a study site of c. 470 m<sup>2</sup>. This area supported up to 50 females within 8 territories. Entry to the hide was gained from the vegetation behind the rookery and observer presence seemed to have no effect on seal behaviour. Observation sessions lasted four hours and alternated daily between morning (0730-1130) and afternoon (1530-1930). "All-occurrence" sampling (Altmann 1974) was used to quantify female conflict behaviours. An interaction was recorded as a conflict if two females directed agonistic behaviours at one another. Incidents where a female appeared to ignore a "threat" display as she moved past the "threatening" female were not counted as conflicts. Air temperature (in the shade) and other weather conditions were recorded for each hour of each observation session. Females were considered to be either residents or intruders. A resident was defined as a female that occupied a site and was stationary. Intruders were females that moved toward a site and encroached on a resident. The victor of a conflict was defined as the individual that did not retreat from the conflict area and/or its opponent.

In order to compare how often there were conflicts on different substrates, values were standardised for both the number of females present and the area of each substrate type. The number of females was counted hourly during each observation period and the mean value for each session was used. Data presented in Figure 2 were smoothed by averaging the number of conflicts per female for consecutive two-day blocks. This combined the conflicts observed in a morning session with those from an

afternoon session. Total areas ( $m^2$ ) of each substrate type (measured from aerial photographs using a planimeter) were as follows: pools - 4.7; rocks in sun - 430.0; rocks in shade - 37.0. For analysis, a square root transformation was applied to the "conflicts per female per square metre" data in order to reduce the heterogeneity of the treatment variance. The distribution of conflicts throughout the season was also compared with the timing of pupping. The portion of the breeding season for which conflict data exists was divided into four-day blocks and the number of pups born in each of these was compared with the number of conflicts per female that occurred during the same intervals. The median pupping date was defined as the earliest date at which 50% of the maximum number of pups counted on the study area, were seen.

## RESULTS

### Conflict Description

Agonistic interactions between females were highly stereotyped (Stirling 1970). The following is a brief description of the behaviours observed during female conflicts. Names in parentheses are those used by Stirling (1970,1971a) in his original descriptions. Different names are used here so as to avoid subjectively attributing intentions or functions to these behaviours.

**Open mouth display (Open-mouth threat).** In this behaviour, the seal's head is oriented toward the opponent with the lower canines visible and the vibrissae pulled back. This display occurred in all conflicts.

**Lunge.** A lunge occurred when a female rapidly moved her head forward at an opponent but did not make contact.

**Snap.** This behaviour involved quick biting motions at the opponent's head and neck. The mouth snapped closed but always missed the opponent. Females may snap at each other while lunging or, if they are close together, without lunging.

**Neck waving.** This is a contact behaviour in which females push chest to chest while waving their necks asynchronously from side to side. Although rarely seen, neck waving usually occurred after all of the above behaviours had been used by both contestants.

**Chase.** Occasionally, a female would run after a retreating opponent. This generally occurred at the end of a lengthy interaction.

**Bite.** Biting is similar to snapping except that contact is made. Bites were accompanied by neck waving but were very rarely observed.

**Gape.** This display is similar to the open-mouth display except that the

seal opens its mouth c. 50% wider, orients its vibrissae forward, and averts its eyes from the opponent. A gaping animal usually retreated.

**Lowered-head posture (submissive posture).** In this display, the head and neck are lowered to minimise contact with the opponent (Stirling 1971a). This posture is usually assumed by retreating females, but also by most females when they are intruders approaching a resident.

**Female growl (female threat call).** This is a low guttural sound that may occur at any stage of the interaction and is usually accompanied by an open-mouth display.

**Scream (Submissive call).** This is a high-pitched squeal reminiscent of the sound heard after a chainsaw-wielding psychotic has run amok in a room full of puppies.

A typical conflict was initiated by a resident directing an open-mouth display at an approaching intruder. This was sometimes accompanied by a growl. If this proved insufficient to dissuade the intruder, the resident extended her displays to include a snap, a lunge, or neck waving, a contact behaviour. The intruder's response to each behaviour influenced the progression of the encounter and the degree of display repetition. A gape and retreat signalled the end of a conflict but, by using offensive displays in return, an intruder could prolong and sometimes win an encounter. Intruders usually approached in a lowered-head posture and seldom initiated open mouth displays (Miller 1971).

Contact behaviours (bite and neck wave) were rarely used ( $n = 13$ ). An examination of the proportion of conflicts that included contact behaviours showed that they were not used more often on any particular substrate - five percent of conflicts on sunny rocks and 3.2% of conflicts on shaded rocks included contact behaviours. No contact behaviours were observed in pools.

#### Location of conflicts

Conflicts took place more often in some parts of the study site than others (Fig. 1). There were greater numbers of conflicts around pools and shaded rocks, which is not surprising given that females prefer these substrates over rocks in the sun (Chapter 1). The two areas of sunny rock substrate that were the sites of many conflicts were both transit corridors. The first (point A, Fig. 1) is the main access way to the sea and is therefore an area where a female is more likely to encounter others. Point B (Fig. 1) is the area between two main cooling substrates and the conflicts that occurred there usually involved females already retreating from these neighbouring conflict zones.

The number and seasonal timing of conflicts varied on the three different substrates (Fig. 2). Almost twice as many conflicts (215) occurred

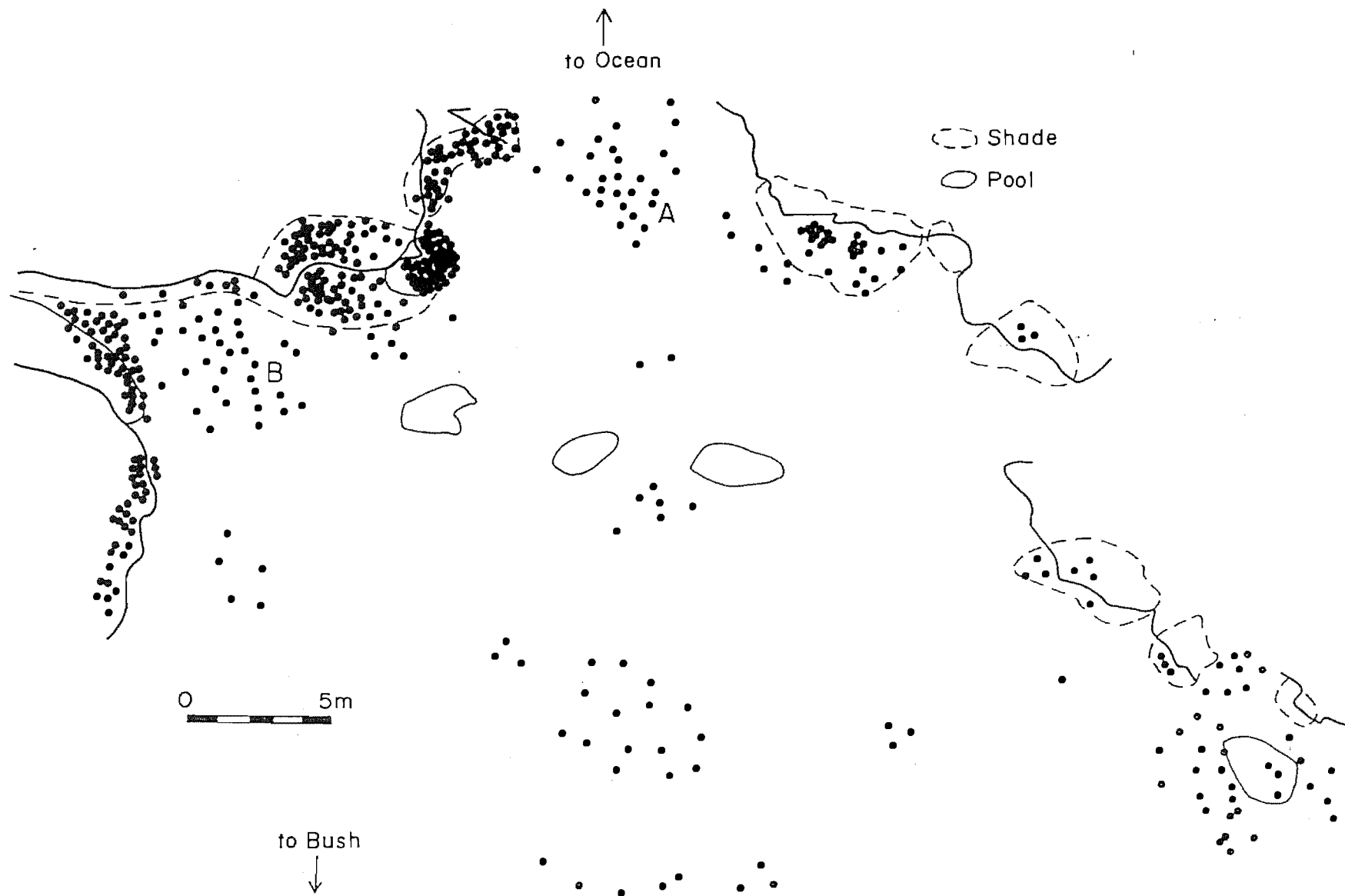


Figure 1. Schematic aerial view of main study site showing location of cooling substrates and all female-female conflicts. Each dot represents one conflict.

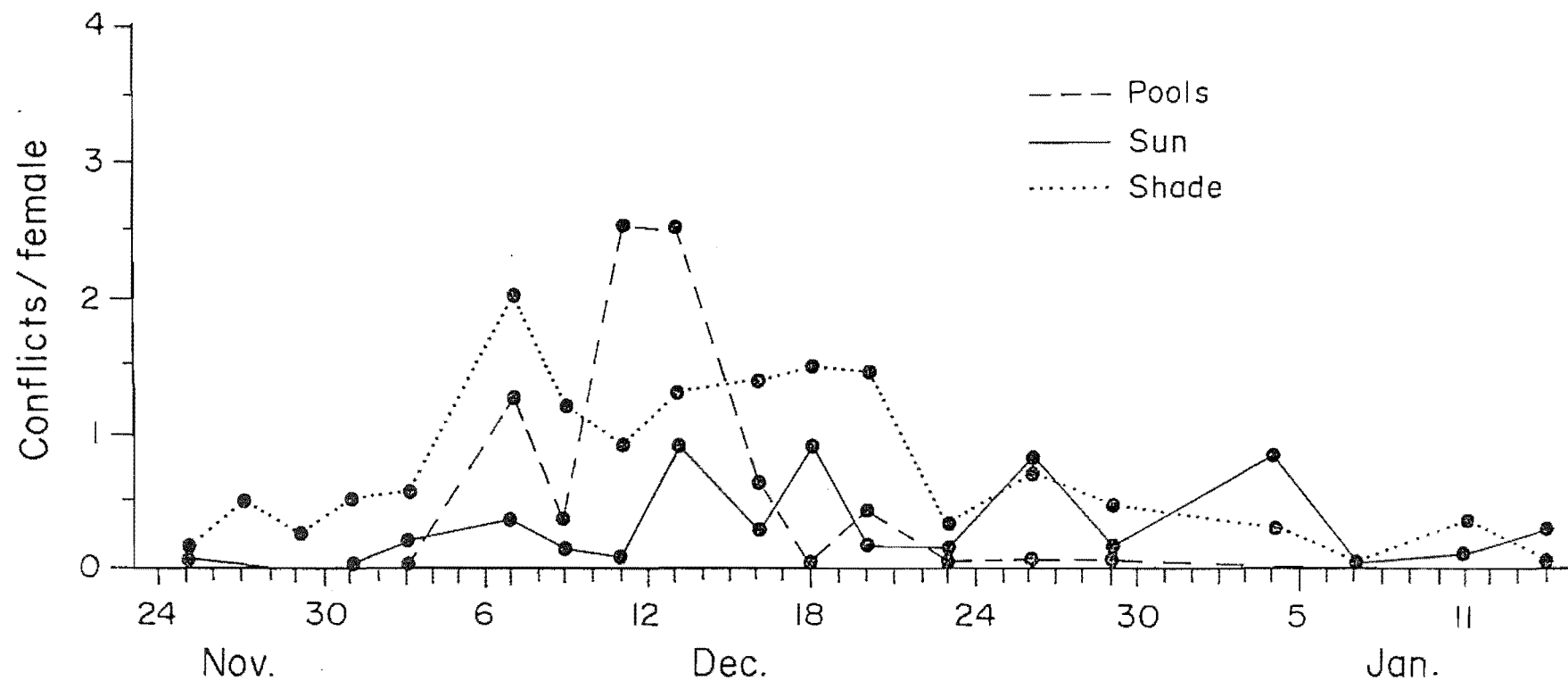


Figure 2. Number of conflicts per female for each substrate type throughout the breeding season.

on shaded rock than on either rocks in the sun (119) or in pools (104). On shaded rock substrate, the number of conflicts per female peaked on 7 December and remained relatively high until 20 December (Fig. 2). At pools, there was a sharp peak in conflicts per female from 11-13 December, and conflicts were almost non-existent after 23 December (Fig. 2). Unlike at the two cooling substrates, the number of conflicts per female on rocks in the sun showed four discrete peaks, on 13, 18, 26 December and 4 January (Fig. 2).

#### Factors influencing interaction rates

One would expect more conflicts to occur where more females are present. In addition, the density of females might be expected to influence conflict rates. In order to properly compare female aggression on different substrates, these factors must be controlled for. With this in mind, the number of conflicts per female per square metre was compared between substrates using one way ANOVA. Pools showed the greatest conflict density at 0.0910 conflicts/female/m<sup>2</sup>, followed by shaded rocks at 0.0198 c/f/m<sup>2</sup>, with sunny rocks two orders of magnitude lower, at 0.0006 c/f/m<sup>2</sup> ( $F = 8.53$ ,  $df = 2$ ,  $p < .001$ ). A Fisher's least significant difference test revealed the conflict density in pools and shade to be significantly higher than on sunny rocks.

Because cooling substrates were preferred by females and because greater numbers of conflicts occurred on cooling substrates when controlled for female density, one might expect that the number of conflicts would be greatest when temperatures were highest. However, a simple correlation between the number of conflicts per female (on all substrates) and the maximum air temperature from each observation session, revealed that this was not the case ( $r=0.3072$ ,  $P < .05$ ).

The timing of conflicts was also compared with the timing of pup production. A regression comparing the number of conflicts per female per day for all substrates combined, with the number of pups born per day failed to show a relationship between the two.

Examination of the outcomes of female agonistic interactions revealed that, on all substrates, the resident female was most commonly the victor in all conflicts which had a clear winner (Table 1). When an intruder was the victor, she settled on the spot vacated by the retreating resident. The data do not suggest that substrate type influenced an intruder's chance of winning. Intruders were seldom victorious on any substrate type (Table 1) and comparisons of each substrate against the others revealed no differences ( $X^2 = 2.43$ , NS). Of the 138 conflicts that had no victor, 105 of them involved

## CONFLICT OUTCOMES

	Pool	Sunny Rocks	Shaded Rocks	Total
resident wins	28	68	135	231
intruder wins	2	8	7	17
no winner	21	34	50	105
male intervenes, no winner	6	18	19	43

Table 1. Number of female-female conflicts and their outcomes on each substrate type.

displays and vocalisations that were exchanged between neighbouring residents with neither animal retreating. However, in 33 encounters, intervention by the territorial male ended the dispute without a clear victor. Male peacekeeping behaviour involved snaps and the physical separation of females by standing between them.

## DISCUSSION

Because seals come ashore only to rest and reproduce, there are few obvious reasons for female fur seals to interact agonistically (Miller 1971). The predominance of conflicts on cooling substrates suggests that female New Zealand fur seals are actively excluding others from these preferred areas. While it is true that greater numbers of females were found on these cooling substrates, this alone does not completely explain why there were more conflicts there. Even when female density was standardised, females showed a greater tendency to be aggressive in pools and shade than they did on sunny rocks. The need to cool off combined with the paucity of suitable space results in competition for cooling substrates.

Contests for space and/or favoured areas are known from other otariid females, e.g. California sea lion *Zalophus californianus wollebaeki* (Eibl Eibesfeldt 1955), and South African fur seal *A. p. pusillus* (Rand 1967). In my study, there were 430 m<sup>2</sup> of sunny rock substrate on the study site, but only 37 m<sup>2</sup> of shaded rocks, and just less than 5 m<sup>2</sup> of pools. Given the low tolerance that females have for close neighbours, it is clear that there is not enough cooling substrate to accommodate all females simultaneously. Some females abandon the rookery and go to sea when temperatures are high. Herding attempts by males appeared to stress these females as they attempted to leave (Miller 1974). Individuals may be leaving the rookery as a last resort when no suitable cooling opportunities exist on land.

Examination of the behaviours used by females during interactions also suggests that females compete for cooling substrates. Although the act of approaching may itself be considered to be aggressive, the type of displays which accompany the approach can also be interpreted as intensifying or minimising aggressive intention. The open mouth display is associated with aggression in both males and females, whereas the lowered-head posture is associated with submissive behaviour and is used by subordinates of all classes (Miller 1971). The approaching individual assumed a lowered-head posture in 88% of female interactions (Miller 1971). Residents responded to this posture with an open mouth display or other agonistic behaviours. Thus,



most conflicts arose when a resident female was defending her space rather than when an intruding female directly challenged the resident for it. The behaviour of intruders that were victorious also suggested that cooling substrates are a resource being contested. In every case where a resident retreated, the winning intruder occupied the location that the resident had just vacated.

The risks that an individual takes while contesting a resource might be expected to increase with increased resource value (Enquist et al. 1985; Waas 1989). Biting and neck waving are contact behaviours and, as such, their use in interactions places a seal at greater risk than any other agonistic behaviour. Hence, one would expect to find seals using contact behaviours more frequently on the more valuable cooling substrates. This was not the case in this study; biting and neck waving were uncommon on all substrates. This may suggest that few seals are willing to take greater risks when contesting the use of space, e.g. going to sea to cool off may be less costly (but see below).

It is surprising that variance in female interaction rates is not explained by environmental temperature or the timing of pupping. While there is a positive correlation between air temperature and conflict rate, the relationship is not strong. In addition, although it is well documented that mammals undergo dramatic changes in hormone levels with parturition (Turner 1966) and that levels of estrogen and progesterone have been shown to influence aggression (Michael 1969), the results do not show a strong relationship between conflict occurrence and pup production. The absence of marked individuals makes it difficult to more strongly demonstrate such a relationship.

Since females arrive on the rookery only a few days prior to giving birth to their pups (Miller 1975b), the high conflict rates of mid-December may also reflect the establishment of a dominance hierarchy among females, as has been reported for female Stellar sea lions Eumetopias jubatus (Sandegren 1970, as cited in Miller 1971). Extrapolating back from the median pupping date (13 December), we can consider 10-11 December to be the median arrival date of females. If females do establish a dominance hierarchy, then conflict levels would be expected to be highest during the initial stages, before stronger individuals and favoured areas were identified. (This is the case for male New Zealand fur seals (Miller 1975a).) Once these individuals and areas have been recognised, actual conflict numbers would be expected to drop as fewer challenges were made. Marked individuals were not available, but it would not be unexpected for a dominance hierarchy to be present in such a highly social species.

On rocks in the sun, two peaks in the number of conflicts per female were observed about a fortnight later than the corresponding peaks on the cooling substrates (26 December and 4 January for sunny rocks versus 7 December and 13 December for shaded rocks and pools, respectively). These differences may be because of the tendency for inland, sunny areas of the rookery to be used later in the season. Mattlin (1978) reported a shift to more inland areas by females as the season progressed.

Several studies have shown that female rodents and passerine birds behave aggressively toward conspecific females (Downhower & Armitage 1971; Michener 1979; LaPrade & Graves 1982; Yasukawa & Searcy 1982; Hurly & Robertson 1984,1985; McLean 1984). In polygynous species, the repulsion of additional females from a male's territory should be of benefit to females already present since it means resources and male parental care are shared between fewer individuals. This is particularly true in the above studies because, in those species, a male's territory provided food, cover and nest/burrow sites, and the males provided some parental care. All of these are resources that are, to a limited degree, shareable. But from the female point of view where monogamy maximises female reproductive success (Downhower & Armitage 1971), each additional female on a territory is a step further away from the optimal situation.

However, in fur seals the situation is somewhat different because for this species a territory only provides a female with resting space and the male contributes only gametes and protection from the harassment of other males. All feeding takes place at sea, there are no terrestrial predators, and males provide no care for the pups. Because of these conditions, there is no real advantage for females to mate monogamously. However, because of the limited space available on preferred substrates, an increase in harem size may decrease the reproductive success of some females. Once the number of females on a territory is sufficient to occupy all cooling substrate space on that territory, then the addition of extra females will be disadvantageous to females already present. When the available cooling substrates have reached saturation, additional females would do better to settle on a territory that was less-crowded relative to the availability of cooling substrates. This may explain why territories that were further inland and had little shade or pools, were occupied only later in the season.

When all cooling substrates are occupied, additional females must go to sea to cool off. (Only rarely were females observed to seek cooling substrates in territories other than their own and resident females were quick to repel them.) One certain cost of leaving the rookery is harassment by

territorial males, which attempt to "herd" any female trying to leave their territories (Miller 1974). Apart from minimising harassment, remaining on one's territory may also be advantageous by increasing attendance time with one's pup. Starvation is the major cause of pup mortality (Mattlin 1978) and a female that must always leave the rookery to cool off will have less time to suckle her pup than a female that does not leave.

Female New Zealand fur seals may not attempt to exclude other females from a male's territory per se, but rather from the cooling substrates within it. As such, they are defending an important, limited resource and in doing so they may be limiting the number of females that settle in that territory. This may in turn limit the number of mates available to the territorial male and reduce his mating success. If females are excluding others from preferred areas, then a positive correlation would be expected between harem size and area of preferred substrate. As shown in Chapter 2, shaded substrate area is positively correlated with the number of females on a territory.

As has been suggested for some bird species (Orians 1969; Lightbody & Weatherhead 1987b), polygyny may have evolved because it is advantageous to males and of neutral consequence to females, in species where territories do not provide food and nest sites. Polygyny is certainly advantageous to males (Bartholomew 1970), and should be neutral for females up to a certain harem size.

Therefore, male and female New Zealand fur seals should have different strategies for maximising their reproductive success. For the male, the more females he has on his territory the more copulations he can achieve and the greater his mating success. For females, however, too large a harem will lead to the exclusion of some females from sites advantageous for thermoregulation, and this may lead to a decrease in reproductive success for those individuals.

## GENERAL DISCUSSION

### Thesis Findings

In Chapter 1, I demonstrated the importance of behavioural thermoregulation to males and females during the breeding season. Blubber and fur, which are an asset to fur seals in their cold water environment, are a liability while on land because they make seals highly vulnerable to heat stress. Because physiological means alone are insufficient to dissipate excess heat, New Zealand fur seals choose to rest in pools of water or shaded areas when temperatures are high. I have shown that as rock surface temperature increased, so did the proportion of seals using pools and shaded rocks (cooling substrates). Although other researchers have documented behavioural thermoregulation in seals and sea lions (e.g. Gentry 1973), this study is the first to use experimental manipulations to highlight the social importance of the need to cool off.

By altering availability of cooling substrates, I demonstrated that female distribution was closely related to the distribution of shade and pools. My substrate manipulations resulted in modified female distribution: where shade or pools were added, female use of that area increased. In areas where cooling substrates were removed, female use declined.

In Chapter 2, I used substrate manipulation experiments to explore further the relationship between microhabitat preference and mating success. Comparisons of the number of females on a territory with the physical characteristics of that territory revealed that males on territories with more shaded substrate had larger harems. Harem size was also correlated with total territory area. Because the number of females per territory is a likely indicator of a male's mating success (Miller 1971; Campagna & LeBoeuf 1988), the correlation between harem size and shade availability seems to demonstrate an important link between a physiological constraint (the need to cool off) and an evolutionary process (selection for males able to monopolise cooling substrates).

Although males with more shade in their territories had greater mating success, males did not alter territory boundaries to include the manipulated cooling substrates. This suggests that although males are able to assess the changes in the cooling potential of an area (Chapter 1), other factors (e.g. past experience of female distribution) also play a role in the delineation of territories.

Experimental manipulations did affect harem size. On all six of the territories whose boundaries remained unchanged between seasons, the changes in the number of females supported the prediction that more females tended to go to territories with greater cooling potential. The number of females increased on two territories where shade was added, and the harem sizes in four territories adjacent to manipulated areas also changed as predicted, i.e. harem size decreased on territories near areas of enhanced cooling potential and increased on territories neighbouring sites where cooling potential was reduced. It appears that these changes in harem size are the result of female migration across territory boundaries.

There appear to be social implications for female agonistic behaviour (Chapter 3). Female *A. forsteri* defended small territories within a male's territory using a variety of displays. I suggest that these conflicts are contests for a limited resource, i.e. preferred substrate. Resident females won significantly more conflicts and were therefore more likely to retain their "territories" than be usurped by intruders. I also argue that the intolerance of close neighbours (c. 1 m minimum inter-individual distance, Gentry 1973) in combination with the competition for preferred resting spaces will limit the number of females on a territory and, therefore, the mating success of the territorial male.

### Sexual selection

The pronounced sexual dimorphism of the New Zealand fur seal is likely to be a product of intrasexual selection. With males fighting one another for access to females, there is a selective pressure for those with greater fighting abilities. Because they lack claws, long limbs, or structures such as antlers, fur seals have few weapons with which to fight. During aggressive interactions, males push chest to chest while trying to bite each other on the face, flippers, or other sensitive areas - body size and teeth are their only weapons. Larger seals are better able to manoeuvre their opponents into positions from which they can be bitten and, therefore, the victorious males are usually the larger males. Because only these larger males that have secured territories will have access to females, large body size should be selected for. This intense male-male competition is a part of intrasexual selection. Seals are sexually dimorphic because females are not under the same selection pressure for large body size, i.e. they do not fight for exclusive access

to mates. Note that body size is likely to be the result of sexual selection and not necessarily natural selection because large body size may not increase a male's chance of survival. Rather, it merely increases his reproductive success.

The operation of intrasexual selection on a species does not necessarily preclude the operation of intersexual selection. However, in A. forsteri the role of intersexual selection (if any) is not clearly evident. De-coupling the two is difficult because there is no assurance that the same traits that allow one male to better compete with another (e.g. body size) are not also favoured by female mate selection. However, I submit that intersexual selection is the lesser of the two sexual selection forces as there is no evidence to suggest that the identity of the territory holder influences where a female settles. Instead, I argue that female site selection is based on the physical characteristics of the territory, and this is supported by the finding that territories with greater cooling potential have more females (Chapter 2). Further evidence that females are selecting a site, not a male, comes from the results of my manipulation experiments which showed that females will move into formerly unoccupied areas, and cross territorial boundaries, after the cooling potential of those areas has been improved.

It is important to note that females that select a site and mate with whichever male controls that site, are still likely to be mating with males of high fitness. This is because male-male competition should not only result in the "fitter" males gaining territories, but also in those of greatest fitness occupying the best territories. Because of the number of years that males are associated with the rookery (both attempting to hold a territory and actually holding one), they are likely to have experience of areas preferred by females. Therefore, male competition for control of those areas is likely to result in the "best" males controlling the areas that are preferred by females. Hence, although there is no direct female mate choice, the result is the same - more females mate with higher quality males.

### **Parental investment**

The apparent lack of direct discrimination by females is consistent with current parental investment theory which suggests that in species where male help is crucial to the successful raising of offspring, females will be more choosy than in species requiring no paternal care (Parker

1983). Beyond insemination, male fur seals make no contribution to the rearing of pups. This lack of post-zygotic contribution makes a male's parental investment shareable among many females, which in turn, allows for polygynous mating.

In contrast, a female makes an enormous post-zygotic parental investment. Placental nurturing develops the pup to a relatively advanced state and the female continues to feed the pup with milk for c. nine months after parturition. The great disparity in male and female parental investment may also lead to great differences in the potential life-time reproductive success of the two sexes. Although the longevity of female New Zealand fur seals is unknown, studies of the congeneric Antarctic fur seal A. gazella show that females breed up to the age of 23 (Bonner 1979). Female A. forsteri have their first pup at five years (Mattlin 1978), which leaves an estimated breeding life of 18 years. Females usually produce a maximum of one pup per year, and assuming no mortality, a female could expect to produce about 18 pups in her life time. However, because a male has no paternal responsibilities, he can potentially produce many more offspring. If a male holds a territory for three seasons (the maximum known, but no study of more than three years has been made), and produces a pup by each female on his territory (30 is the largest harem reported, Miller 1971), he can produce as many as 90 pups in his life time. This does not include any opportunistic matings he may achieve prior to holding a territory. Hence, a male can potentially produce five times as many pups as a female. The larger harem sizes present at higher, pre-exploitation population levels would likely increase this discrepancy further.

While such a disparity might seem to disadvantage females, it should be noted that paternal care would not be expected to increase pup survivorship. Males can not feed pups, nor are there any predators from which to protect them during the breeding season. The evolutionary stability of polygyny in A. forsteri is likely to be the result of this breeding system being advantageous to males and neutral to females. Because males offer no help in raising pups, there is no disadvantage to females to share a male.

### Evolution of polygyny

The role of female mate choice is pivotal in many of the models of the evolution of polygyny. For female fur seals, direct choice of males is

unlikely, but choice of sites controlled by males can have the same consequences. As detailed in the General Introduction, six explanations for the evolution of polygyny have been put forward : uneven sex ratio, group selection, polygyny threshold, "sexy son", neutral mate choice, and male monopolisation of females. Of these six, only two are applicable to A. forsteri. I have discounted Mayr's (1939) model because there is no evidence that the sex ratio of this species is significantly different from 1:1. Wynne-Edwards' (1962) group selection argument is also unacceptable. I have never witnessed a male withhold copulation from a sexually receptive female. Indeed, males even attempted to copulate with females that were not receptive. Also, because gestation takes one year, a male is unlikely to know how many of his matings produced pups, and hence, he is in no position to regulate his reproductive output.

The sexy son hypothesis (Weatherhead & Robertson 1979) is not applicable to fur seals because it requires a female to choose a more "attractive" male on a territory of low quality. However, as discussed above, female A. forsteri do not appear to be choosing a mate based on his "attractiveness", but are selecting a site on its own merits. Besides, intense male-male competition for territories is likely to result in high quality territories held by attractive males.

In many respects, the neutral mate choice model (Lightbody & Weatherhead 1988) seems valid when applied to A. forsteri. This model emphasises the importance of male competition and argues that males on the largest territories will have the most mates. However, the neutral mate choice model also assumes that female reproductive success is not affected by the presence of other females or by variations in territory quality. Because variation in the quality of New Zealand fur seal territories is likely to be a major cause of variation in reproductive success (Chapter 2), this model does not apply to this species. In addition, this model also assumes that females are not competitive, whereas I have shown that they are (Chapter 3).

One way that polygyny in New Zealand fur seals may be explained is by the polygyny threshold model (Verner & Willson 1966). Because a male's reproductive contribution is shareable, a female that settles on a territory with high cooling potential will be at an advantage over one who settles on a territory devoid of cooling substrates, regardless of whether the resident male has mated with other females. The key to applying the polygyny threshold model to fur seals lies in the issue of female site choice - selection should favour those females which choose high quality



territories.

In addition, polygyny in A. forsteri can also be explained by Darwin's (1871) hypothesis that polygyny is the result of male competition for exclusive access to females (see next section). This hypothesis is generally the one used to explain the evolution of polygyny in pinnipeds (Bartholomew 1970). Although New Zealand fur seals are clearly an example of resource-defense polygyny, this does not exclude the applicability of the polygyny threshold model. Both explanations have their validity and, as with many other philosophical issues, the correct answer need not be "either/or" but may be a combination of the two.

### **New Zealand Fur Seals, Behavioural Thermoregulation, and Polygyny**

The type of breeding system used by a population is determined by the interaction of many different factors. Behavioural thermoregulation is one of the most important of these factors in the evolution of polygyny in A. forsteri.

Polygyny will occur only in populations where males can gain access to more than one female. The specific habitat requirements of species such as fur seals limit their distributions and therefore facilitate polygyny. In order to survive, fur seals must make use of two very different environments, i.e. they feed at sea and breed on land. Hence, breeding populations are concentrated along the interface of these two habitats (beaches). Distribution is further restricted to beaches with such characteristics as proximity to good feeding areas and those with offshore reefs to protect them from large waves (Wilson 1981). As a result of these general habitat requirements, New Zealand fur seals breed in densely-packed colonies. Because seals periodically need to rest in pools or shaded areas in order to prevent heat stress while ashore, needs for behavioural thermoregulation serve to further compress their distribution.

All of these factors produce a dense, but uneven, distribution of females which can be monopolised by a relatively small number of males. The importance of cooling off while ashore makes cooling substrates a valuable resource that, because of its uneven distribution, can be monopolised by the males. Hence, resource-defense polygyny is the breeding system found in this species. Stated another way, cooling substrates are the resources that bring females together at such densities that allow males to mate polygynously.

Cooling substrates are also a resource for which females compete among themselves. These contests over preferred areas emphasize the importance of behavioural thermoregulation in the social system of this species - it is a resource worth fighting for. For a male, winning control of the resource leads to exclusive access to any females that come to use it and this may increase his reproductive success. For females, winning control of the resource allows them to rest in a more beneficial environment, which may in turn affect their own reproductive success. Therefore, although males and females use different "strategies" to maximise their reproductive success (Chapter 3), access to cooling substrates is crucial to both sexes.

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