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INFLUENCES OF SOCIAL AND HABITAT FEATURES ON SELECTION AND USE OF BREEDING HABITAT AND PUP SURVIVAL IN SOUTH AMERICAN FUR SEALS

BY

MONICA ANNE STEVENS
B.A., Illinois Wesleyan University 1992
M.S., Frostburg State University 1997

DISSERTATION

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In

Zoology

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August 9, 2002
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ABSTRACT

INFLUENCES OF SOCIAL AND HABITAT FEATURES ON SELECTION AND USE OF BREEDING HABITAT AND PUP SURVIVAL IN SOUTH AMERICAN FUR SEALS

by

Monica Anne Stevens

University of New Hampshire, September 2002

Quantitative information is lacking about how fur seals use habitat and how this use influences fitness. Such information is important for understanding the prospects for recovery of declining populations like those of South American fur seals (Arctocephalus australis) in Peru. In this study I examined the influences of habitat features and human disturbance on selection of breeding habitat by female fur seals in Peru; and I examined how mortality of pups was influenced by habitat features, female behavior, and the social environment on the beach.

Arctocephalus australis in Peru have declined gradually over the past decade, and declined dramatically (72%) due to low food availability during the severe El Niño in 1997-98. Pup mortality has been greater for fur seals in Peru than in other populations of fur seals due to pups becoming injured or separated from their mother when high densities of aggressive females move to limited water-access sites to avoid overheating. In 1999, the seals abandoned some historically important breeding beaches, and did not colonize new beaches.
I found that currently used breeding beaches were less likely to have human disturbance and more likely to have offshore islands, stacked rocks, tide pools, and abundant shade than abandoned or unused beaches. At low population numbers, females seemed to select habitat that maximized thermoregulation and minimized disturbance, but was detrimental to survival of pups.

Pup mortality remained high (20-46%) following the population decline, despite population densities one third those prior to the decline. Pup mortality was greater at rugged, rocky beaches exposed to heavy surf than at flat, open beaches with abundant tide pools. Females whose pups survived for ≥ 20 days spent less time exposed to heavy surf and suckling a yearling, and more time suckling their pup than females whose pups died. High percentages (23-52%) of females continued to suckle yearlings, possibly stemming from low food availability.

Birth sites and thermoregulatory sites were farther apart at the rugged beach than at the flat beach. This separation was associated with higher rates of movement and pup mortality. Population density did not differ between the two beaches (~0.3-0.4 females/m²).
INTRODUCTION

Of the many ways humans negatively impact wildlife, overexploitation and destruction of habitat are two of the most important (Meffe and Carroll 1997). Overexploitation of fur seals for their fur and blubber decimated most populations during the late 1700s through the mid 1900s (Busch 1985). Although some populations recovered (e.g., Antarctic fur seals, Arctocephalus gazella) (Riedman 1990), others like South American fur seals (A. australis) in Peru are now limited to small fractions of their former numbers and distributions (Bonavia 1982, Arias-Schreiber and Rivas 1998). Hundreds of thousands fur seals bred in Peru during the 1800s, but were nearly extinct by the mid 1900s (Bonavia 1982; Fig. I-1). By 1980, populations had recovered to a limited extent, but declined again due to low food availability during severe El Niño events in 1983-1984 and 1997-1998 (Fig. I-1, Arias-Schreiber and Rivas 1998). Major population declines are widely understood to be a key factor in the risk of extinction (Gerber and Hilborn 2001). A. australis was listed as in danger of extinction in Peru in 1998 (Decreto Supremo N° 013-99-AG).

Compounding the problem of population declines due to overexploitation and limited food availability, fur seals in Peru also have limited available habitat. Seals need terrestrial breeding sites that are protected from human disturbance, and in Peru A. australis breed only in reserves or extremely remote areas (Majluf 1992). The distribution of fur seals in Peru was further restricted in 1998 after the population decline when seals abandoned some historically important breeding beaches. This is alarming
because fur seals rarely abandon breeding beaches (Gentry 1998) and new sites in Peru were not colonized.

High densities of fur seals breeding at limited beaches has resulted in high mortality rates for pups. Females must make frequent movements to limited access points to water where they go to cool; this exposes pups to aggressive females on the breeding beach, and leads to pups being injured or starving when they become separated from their mother (Majluf 1992). Reproductive success in the form of high offspring survival rates is necessary for recovery of otariid populations (Gerber and Hilborn 2001). One of the most important factors influencing reproductive success of females is selection of reproductive sites (Bartholomew 1970, Emlen and Oring 1977). Information is lacking about how selection of breeding habitat influences mortality of pups in fur seals.

Between 1998 and 2001 I examined factors influencing breeding habitat selection and pup mortality for *A. australis* in Peru. In this chapter I first review the general theories of habitat selection and female reproductive success, relating each to the breeding behavior and ecology of pinnipeds in general and *A. australis* in particular. Then I identify information that is lacking in the literature and is essential to understanding breeding ecology of fur seals. Finally I summarize my overall objectives and hypotheses.
Figure 1. Population numbers of South American fur seals in Peru between 1900 and 2000 (Bonavia 1982, Arias-Schreiber and Rivas 1998, M. Arias-Schreiber, Instituto del Mar del Peru [IMARPE], unpub. data).

**Habitat Selection**

A ‘habitat’ is any place where an organism is able to colonize and live, and is an essentially homogeneous unit with respect to the physical and biological features most relevant to the behavior and survival of the organism (Fretwell and Lucas 1970). Habitats are heterogeneous in time and space and have different suitabilities for an organism in terms of its reproductive success; so natural selection should favor individuals that are able to select their optimal habitat (Fretwell and Lucas 1970). Factors that contribute to the suitability of a habitat include the abundance of food and shelter, opportunities for reproduction, avoidance of predators, and physical features complementary to the locomotor restrictions of an organism (Hildén 1965).
Habitat selection is a hierarchical process in which organisms first select a general area in which to live based on stimuli encountered (Hildén 1965). It is important for researchers to examine habitat selection on a variety of scales, including both 'macro' (e.g., home range or larger area – or a breeding beach for fur seals) and 'micro' (e.g., features of the environment in the immediate vicinity of an animal) (McIntyre 1997). The initial decision by an animal about whether to explore a habitat is often made quickly and with incomplete information; and then subsequent opportunities to refine decisions may be possible to various degrees depending on the organism and environment (Orians and Wittenberger 1991). The process of settling in a habitat can also be constrained by social pressures. For example, better habitats are likely to be occupied earlier than poorer ones, and resident individuals may defend their area more aggressively than transients or recent settlers do; so early settlers likely maximize habitat quality and minimize aggressive confrontations (Orians and Wittenberger 1991).

Factors influencing habitat selection can be divided into 'ultimate' and 'proximate' factors (Baker 1938). Ultimate factors are those that affect natural selection of the behavior (e.g., food, requirements imposed by structural characteristics of an individual, and shelter from predators or environmental factors (Hildén 1965, Orians and Wittenberger 1991). The presence of mates may also be considered an ultimate factor. Proximate factors are cues that trigger settlement behavior, and may or may not have biological significance to the animal (Hildén 1965). Examples of proximate factors in habitat selection include landscape features or the presence of conspecifics (Hildén 1965).
The presence or density of animals in a given habitat does not necessarily indicate that the habitat is of high quality for that species (Van Horne 1983, Orians and Wittenburg 1991). Animals could be abundant in an area for other reasons, such as the presence of proximate factors that previously indicated optimal habitat, their optimal habitat no longer exists or is inaccessible; they are avoiding another habitat; or the habitat is a 'sink' habitat (i.e., to which animals immigrate, but where local mortality is greater than local reproduction; Pulliam 1988). It is therefore important for researchers to measure reproductive success when assessing habitat quality.

Because the suite of resources needed by an organism is unlikely to be uniformly distributed in space (Lacher and Mares 1996), selection of sites for different purposes (e.g., parturition, copulation, and feeding) may be independent, with the distribution of the most restrictive resource exerting the strongest influence on habitat selection by an organism (Orians and Wittenburg 1991). Because parturition sites are critical to most organisms and usually limit movement for some time period, selection of parturition sites is often the most influential component of habitat selection (Orians and Wittenburg 1991).

**Selection of Breeding Habitat by Pinnipeds**

The order Pinnipedia is divided into three families: the Phocidae (true seals), the Odobenidae (the walrus), and the Otariidae (the eared seals – fur seals and sea lions. The geographic distribution of pinnipeds ranges from the Arctic to the Antarctic, with the phocids and the walrus being more associated with extreme polar regions than the otariids. Some phocids and otariids are found in tropical or subtropical areas where there are cold, nutrient-rich upwelling systems. Pinnipeds evolved from terrestrial arctoid (or
bearlike ancestors, but because of their adaptations for foraging at sea they are inefficient at moving on land. Pinnipeds must come ashore to give birth, so they must select habitat that minimizes their vulnerability to terrestrial predators. This habitat includes land (usually islands or remote areas), pack ice, or fast ice. Otariids breed only on land in aggregations of individuals.

The otariids are divided into two subfamilies: the Otariinae (sea lions) and the Arctocephalinae (fur seals). Within the Arctocephalinae there is one species in the genus Callorhinus (the northern fur seal) and eight species in the genus Arctocephalus. At the largest geographic scale, habitat selection by marine mammals is critically influenced by water temperature, which may indirectly influence marine mammal distribution though influences on prey distribution (Martin and Reeves 2002). After female otariids give birth, they alternate between nursing their pup on land and foraging at sea, and habitat used for parturition must have a rich food source nearby.

The Arctocephalus species are very similar in terms of morphology, behavior, and ecology (Gentry & Kooyman 1986), and there has been confusion about the taxonomic status of the individual species (Repenning et al. 1971). Arctocephalus spp. tend to breed on rocky beaches, often rugged and exposed to heavy surf (Subantarctic fur seal, A. tropicalis, Bester 1982; Galapagos fur seal, A. galapagoensis, Trillmich 1986). Other populations breed on less rugged beaches buffered from heavy surf (Juan Fernández seals, A. philippii, Francis and Boness 1991; Antarctic fur seals, A. gazella, Boyd 1993), or on flat, open beaches (A. gazella, Bonner 1968, and Budd 1972; Cape fur seals, A. pusillus, Shaughnessy 1984). Fur seals have physical adaptations for fasting and foraging in cold waters (e.g., blubber and underfur) that make them susceptible to overheating on
land (Limberger et al. 1986), so *Arctocephalus* spp. that breed at low latitudes where they are susceptible to heat stress must select habitat features that enable them to thermoregulate (e.g., water [tide pools, shoreline, sea spray], shade [caves, rocky crevasses, overhangs], and wind). (Bester 1982, Majluf 1987a, Vaz-Ferreira and Ponce de Leon 1987, Francis and Boness 1991).

**Habitat Selection and Breeding Behavior of *Arctocephalus australis***

*Arctocephalus australis* breed predominantly on offshore islands from Tierra del Fuego in the south to southern Brazil and southern Peru in the north (Gentry and Kooyman 1986). Their presence in Peru at such low latitudes (15-18°) is linked to the Peruvian (or Humboldt) current along the coast that brings cold, nutrient rich water, and anchovies (*Engraulis ringens*) – the seals’ main food source (Idyll 1973, Majluf 1987a).

The breeding season of *A. australis* in Peru corresponds with the maximum availability of anchovies (Majluf 1987a). Majluf (1987) described in depth the reproductive ecology of female fur seals at Punta San Juan (PSJ), Peru. Adult territorial males are present on the breeding beach only during the breeding season; the first arrive in September and the last leave by November. A few subadult males are always holding ‘territories’ around the breeding area during the rest of the year, until they are displaced by territorial males in October.

Adult females are present year-round at the breeding beach; however, the proportion of time they spend ashore and their use of beaches changes with season. Before arriving during the breeding season females forage at sea for about 7 days (Harcourt 1992), and return to the breeding beach 0-2 days before giving birth. Parturition generally takes place from early September to late December each year.
Ninety percent of births occur within a 40-day period, with a peak in mid-November. The perinatal attendance period occurs from birth until 8-10 days later when the mother copulates and makes her first foraging trip. For the first 3-4 days after birth mothers and pups remain in close contact. Later in the perinatal period pups become more mobile and start spending more time away from their mothers (<30 m from their suckling site).

Young at PSJ may be weaned between 9-36 months (Majluf 1991), whereas offspring in other species of fur seals and populations of *A. australis* are generally weaned within a year (Vaz Ferreira 1956, Bonner 1994). Flexibility in lactation duration is probably an adaptation to unpredictable seasonal and annual food supplies (Majluf 1987a; Trillmich 1987). Every 2-7 years an El Niño event disrupts the upwelling system on which the fur seals depend (Cane 1983); and sea surface temperatures increase, causing primary productivity to decrease and anchovies to die or migrate to greater depths (Majluf 1987a). Foraging becomes more energy intensive for the seals and poor health follows, indicated by lower breeding population sizes, poor physical condition, and high mortality of pups (Trillmich et al. 1986). Food shortages can also result in abortion or failure of the blastocyst to implant (Boyd 1984).

In addition to considering the need for a nearby food supply when selecting a breeding beach, *A. australis* must also consider thermoregulatory needs, avoiding human disturbance, and avoiding predation by Southern sea lions (*Otaria flavescens*). Learning and previous experience also play a role in selection of breeding habitat by *A. australis*. Females may use a different birth site the year after they were unsuccessful at reproduction (Majluf 1996).
Habitat associated with thermoregulation is especially important for Peruvian populations of *A. australis*, which are exceptional among *Arctocephalus* species in that only they and *A. galapagoensis* breed on or near the equator (Bonner 1994). Male territories must contain water, and females must go to the shore or tidepools daily to avoid overheating (Majluf 1987a).

Habitat where human disturbance is minimized is also important for fur seals. Fur seals in Peru were exploited by the ancient Peruvians as far back as 2000 B.C. (Bonavia 1982), and populations were nearly extirpated by indiscriminate commercial hunting from the early 1900s until 1946. In 1959 sealing in Peru was totally banned, but some authorized killing occurred up to 1977 (IMARPE), and poaching continues to occur (Majluf 1987b; M. Araujo, [Ministerio de Agricultura Projecto Especial de Promocion del Aprovechamiento de Abonos Provencientes de Aves Marinas – PROABONOS – pers. comm.]). Fur seals at PSJ breed at high densities (0.5-1.4 females/m²), reportedly because of the risk of poaching faced by seals outside protected areas (Majluf 1992).

Southern sea lions prey upon fur seal pups, and occasionally juveniles and adult females at PSJ (Majluf 1987a). Sea lions kill 0.2%-13% of pups at PSJ (Harcourt 1992).

Although colonial breeding is common in wide-ranging species that need to come together to mate (reviewed by Danchin and Wagner 1997), *A. australis* in Peru breed at greater densities than can be explained this need or by habitat limitation. Habitat that is apparently suitable or has been used in the past is often empty of seals, while nearby beaches are densely populated.

Instead of dense breeding aggregations being a result of habitat limitations or insuring mating opportunities, it has also been hypothesized that seals actively select
densely populated microhabitats on a beach, and might gain reproductive benefits from such locations. Benefits potentially gained by a female in the center of a dense cluster include protection from harassment by males (Trillmich and Trillmich 1984, Boness 1991), avoidance of mating with suboptimal peripheral males (McLaren 1967; Bartholomew 1970), increased vigilance to detect predators (Terhune 1985; da Silva and Terhune 1988), and decreased probability of being taken by a predator (Hamilton 1961). Male *A. australis* also prevent male sea lions and subadult male fur seals from entering their territories, so females located near a territorial male might experience less harassment and predation. The combination of dense breeding aggregations, limited thermoregulatory sites, and daily movements by females to thermoregulatory sites has important implications for survival of pups.

**Female Reproductive Success**

Reproductive success can be defined as the number of offspring an individual produces that survive and reproduce. Variation in reproductive success among females in polygynous breeding systems has been considered to be substantially lower than variation among males; this is thought to stem from unequal investment in gametes between the sexes, with females investing considerably more time and energy into each egg than males put into each sperm (Trivers 1972). In a polygynous mating system, a low percentage of males can fertilize most females, so male mating success is highly skewed. Alternatively, all females tend to be inseminated (Parker 1970). Variation in female reproductive success is now known to be greater than previously thought (Clutton-Brock 1988). Female reproductive success in a variety of taxa is most commonly influenced by five phenotypic characteristics: age, body size,
dominance rank, mate choice, and early development (Clutton-Brock 1988). Also potentially important are environmental factors such as temperature, population density, and food availability (Clutton-Brock 1988). In many birds and mammals, offspring survival is the variable that most influences variation in reproductive success (Clutton-Brock 1988). This has also been found for pinnipeds (Le Boeuf and Reiter 1988, Lunn et al. 1994, Wickens and York 1997, Durant 1998). Offspring survival is largely dependent on female condition, so decisions related to food acquisition are very important for females. Females also need to make decisions about how much energy to put into a given offspring when that effort could negatively affect her future reproductive success (Winkler 1987).

All female pinnipeds invest considerably in the single pup to which they give birth each year – they have a long period of gestation, intensive maternal care, and give birth only annually or biennially (Riedman 1990). Males provide no parental care, and therefore the male with which a female mates does not influence her reproductive success, unless the male’s genes provide benefits to her offspring (reviewed by Andersson 1994). This is not likely to be a critical factor influencing variation in reproductive success in female otariids because competition among males likely minimizes the ability of suboptimal males to access females. Factors that contribute to variation in pup survival in otariids include female experience; food availability; breeding habitat; and environmental stochasticity, such as storms. More experienced females are more likely to successfully wean their pup. Particularly high early pup mortality in pinnipeds has been associated with the combination of heavy surf and high density (Reiter et al. 1981), high rates of movement through the colony to and from the shore.
(Baker 1984), and heat stress resulting from reduced wind and breeding habitat far from water (De Villiers and Roux 1992).

A successful mother must be able to protect her pup, deter other pups from stealing her milk, defend her breeding space from other females, and be able to find her pup after returning from foraging at sea (Riedman 1990). The combination of high breeding density, limited thermoregulatory sites, and the need to make thermoregulatory movements has resulted in remarkably high pup mortality rates for *A. australis* in Peru. Pup mortality during the first month of life varies between 15 and 49% (Harcourt 1992; Majluf 1992), and is usually much higher than the maximum of 20% in other populations of *A. australis* and species of fur seals (see review in Harcourt 1992). Disturbances created by movements and aggressive interactions among females result in mothers and pups being separated during the critical bond-formation period, and pups subsequently dying of starvation or injury (Majluf 1992).

**Objectives and Hypotheses**

Fur seal habitat has been qualitatively described for all species of fur seals (summarized above), but why fur seals select some beaches for breeding, while leaving apparently similar beaches unused is poorly understood. Despite the common recognition that limited breeding habitat free from human disturbance negatively impacts seals, quantitative evidence of this is lacking. In Chapter 11 I examine how macrohabitat features and human disturbance influenced whether sites were currently used, abandoned, or apparently not used in the past by fur seals for breeding. I hypothesized that currently used beaches would be associated with thermoregulatory features (e.g., shade, tide pools,
shoreline), inaccessibility to humans (e.g., steep slopes at rear of beach and shoreline), and safety for pups (e.g., gradual-sloping access points to calm water).

In Chapter II I examine factors associated with use of microhabitat (sites of births and copulations, and movements on the breeding beach), and I compare microhabitat and movement between two beaches with different topographies – a flat, open beach with abundant tide pools vs. a rugged beach exposed to heavy surf. I hypothesized that females at the flat beach with abundant tide pools would have less competition for safe thermoregulatory habitat, and therefore move less than females at the rugged beach.

Although high rates of movement by females within breeding colonies have been implicated as contributing to high pup mortality rates, movements by female fur seals have not been quantitatively studied. No studies have examined how use of habitat influences fitness in fur seals. In Chapter III I examine how social and habitat features on the breeding beach influence early pup mortality rates. I compared mortality rates at high vs. low breeding densities using data from 1990-1993 provided by P. Majluf, and data I collected in 1999 at Punta San Juan, and in 2000 at Punta Coles. I expected my results to confirm that high rates of movement are driven by thermoregulatory needs. I further hypothesized that pup mortality would be density-dependent, and therefore lower following the dramatic population decline. I expected this because decreased population density would likely result in fewer female-female encounters, and therefore fewer aggressive acts toward pups. I also hypothesized that pup mortality would be lower at the flat beach than at the rugged beach. At the latter beach I expected pups to be more likely to fall and/or be washed away.
Finally, I summarize the main conclusions of this study and report management implications of my findings.
CHAPTER I

INFLUENCES OF HABITAT FEATURES AND HUMAN DISTURBANCE ON USE OF BREEDING BEACHES BY SOUTH AMERICAN FUR SEALS

INTRODUCTION

Major population declines are widely understood to be a key factor in the risk of extinction (Gerber and Hilborn 2001). In taxa such as pinnipeds, which require specific habitat for breeding on land but are constrained by adaptations for feeding at sea (Limberger et al. 1986), understanding the factors important to selection of breeding habitat is particularly key to assessing prospects for recovery of small populations.

Between 1996 and 1998, populations of South American fur seals (Arctocephalus australis) in Peru declined 72% due to low food availability during the severe El Niño in 1997-1998 (M. Arias-Schreiber, Instituto del Mar del Peru [IMARPE], unpub. data). As a result, A. australis is now classified as in danger of extinction in Peru (Decreto Supremo N° 013-99-AG). This drastic decline followed an unexplained gradual decline of the same population over the past decade. The overall number of A. australis in Peru declined at least 10% between 1992 and 1996; however, northern populations (13°-15° latitude) tended to decrease in numbers, while southern populations (16°-17° latitude) increased (Arias-Schreiber and Rivas 1998). Hypotheses proposed to explain population declines and shifts in geographic distribution of A. australis include: changes in sea temperatures and distribution of prey, disturbance by shellfishermen and researchers,
competition with Southern seal lions (*Otaria flavescens*) for space or food, and predation by *O. flavescens* on fur seal pups (Arias-Schreiber and Rivas 1998).

Concurrent with the recent extreme population decline, fur seals in Peru abandoned a number of historically important breeding beaches (S. Insley, P. Majluf and D. Boness, unpub. obs.). Abandonment of breeding beaches is particularly alarming because new beaches were not colonized. Besides extirpations of fur seal colonies due to large-scale killing or disturbance, abandonment of major breeding sites by otariids is an extraordinary event. After the 1982-83 El Niño, *A. australis* were reported to have immigrated to new breeding sites in Peru and northern Chile (Guerra and Portflitt 1991, Majluf 1991); however, previously used sites were not abandoned.

Abandonment of breeding beaches also is of concern because *A. australis*, like all otariids, tend to show a high degree of breeding-site fidelity (Majluf 1987a, Majluf et al. 1996). Site fidelity is important for males and females to locate one another to mate, and for females to find and nurse their dependent pups after foraging trips (e.g., Riedman 1990, Majluf 1987a).

At Punta San Juan (PSJ), Peru in 1999, fur seals previously marked at the abandoned primary breeding beach bred in more rugged areas (e.g., steep cliffs, large jagged rocks exposed to heavy surf). Some females gave birth on isolated ledges along steep cliffs, and lost their pups due to falls (pers. obs.). High pup mortality at low population numbers would be of particular concern for *A. australis* in Peru, which reportedly have higher pup mortality than other populations of fur seals (15–49% during the first month of life; Majluf 1987a, Harcourt 1992) and may suffer 100% pup mortality during severe El Niño events (S. Insley, P. Majluf, D. Boness, and M. Stevens, unpub.).
Most of this high mortality has stemmed from density-dependent factors. Pups are frequently injured or separated from their mothers when high densities of exceptionally aggressive females make long-distance movements to limited thermoregulatory sites (Majluf 1987a, Harcourt 1992, Majluf et al. 1996). Pups are also killed by attacks from aggressive female fur seals, or when they fall from cliffs and are washed away by heavy surf. A non density-dependent cause of pup mortality – predation by Southern sea lions on breeding beaches (Majluf 1987a, Harcourt 1992) – has been important at one reserve, PSJ, where 0.2-8.3% of pups were killed by subadult male sea lions (Harcourt 1992). Sea lions have not been reported to kill fur seals at other sites in Peru. There are no other important terrestrial or aquatic predators of fur seals in Peru, except for humans (Majluf 1987b).

Little research has investigated what factors might influence selection and abandonment of breeding beaches (i.e., macrohabitat) by fur seals. The objective of my study was to determine how habitat features and human disturbance influenced whether beaches were currently used, abandoned, or apparently not used in the past by fur seals for breeding.

**METHODS**

**Study Areas**

My three study areas were protected guano reserves that contain breeding beaches for the majority of fur seals in Peru: PSJ (15°22'S, 75°12'W), Punta Atico (Atico) (16°14'S, 75°12'W) and Punta Coles (Coles) (17°42'S, 71°22'W). Mean air temperatures during the breeding season of 2000 were 19.5°C and 19.3°C for PSJ and
Coles respectively; and mean sea surface temperatures were 13.9°C and 15.3°C (Ministerio de Agricultura Proyecto Especial de Promoción del Aprovechamiento de Abonos Provenientes de Aves Marinas [PROABONOS], unpub. data). Air and sea surface temperatures were not available for Atico. PSJ has 3 km of coastline, and Atico and Coles have 5 km and 6 km respectively.

Annual precipitation at all three areas is <10 cm (Geelan and Lewis 1992). Breeding macrohabitats available to *A. australis* include flat, open beaches comprised of sand and/or pebbles and stones, beaches with a single layer of rocks, stones, and boulders; beaches with stacked rocks; rocky platforms; and offshore islands. Slopes at the back of beaches range from shallow to vertical, but in all cases there is no vegetation. I considered the entire coasts of all three reserves to be potential breeding areas. To divide each coastline into different potential breeding beaches, I designated boundaries using geographic features that clearly separated stretches of beach (e.g., peninsulas or inlets) or appeared difficult for fur seals to access (e.g., extremely steep shore). By interviewing current and former guards and biologists who had worked at the reserves, beaches were identified as currently used, abandoned, or unused (apparently not used for breeding within the past two decades). Beaches were only reported to have been abandoned following the 1997-98 El Niño. Abandonment of breeding beaches most likely occurred in the past when the species was almost extirpated in Peru, but detailed information about fur seal distribution does not exist from that time. This study addresses a single abandonment event that occurred and persisted after the dramatic population decline following the 1997-98 El Niño.
Characterization of Breeding Beaches

Between January and July 2001 I recorded 14 variables (Table 1-1) related to habitat and human disturbance at 70 potential fur seal breeding beaches (17 beaches at PSJ [5 abandoned, 6 currently used, and 6 unused], 36 at Atico [5 abandoned, 9 currently used, and 22 unused], and 17 at Coles [1 abandoned, 8 currently used, 8 unused]). I also included 'reserve' as a variable (i.e., PSJ, Atico, or Coles). Many variables were binary due either to the nature of the variable, or my inability to access beaches to perform precise measurements. It was requisite to select variables that could be classified from a distance because some fur seals are present at breeding beaches year round and I did not want to disturb these seals. The variables are a comprehensive composite of factors I believed to be most critical to fur seals in selecting and continuing to use breeding beaches.
Table 1-1. Variables recorded at 70 potential fur seal breeding beaches in Peru.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Units measured</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aspect of the beach</strong>&lt;br&gt;North- or south-facing?&lt;br&gt;(North=N, NW, or NE; South=S, SW, or SE)</td>
<td>North=1, South=0</td>
</tr>
<tr>
<td><strong>East- or west-facing?</strong>&lt;br&gt;(East=E, NE, or SE; West=W, NW, or SW)</td>
<td>East=1, West=0</td>
</tr>
<tr>
<td><strong>Lowest slope at shore</strong></td>
<td>&lt;10° or ≥ 10° Degrees</td>
</tr>
<tr>
<td><strong>Lowest slope at rear of beach</strong></td>
<td></td>
</tr>
<tr>
<td><strong>Whether human disturbance was known to have occurred at the beach</strong></td>
<td>Present=1, Absent=0</td>
</tr>
<tr>
<td>(e.g., by shellfishermen or researchers)</td>
<td></td>
</tr>
<tr>
<td><strong>Whether offshore islands existed perpendicular to the beach</strong>&lt;br&gt;(island/s large enough not to be inundated at high tides and rough seas, with flat areas apparently suitable for a female to give birth)</td>
<td>Present=1, Absent=0</td>
</tr>
<tr>
<td><strong>Whether various substrates were present at the shore</strong>&lt;br&gt;(four variables)</td>
<td></td>
</tr>
<tr>
<td>Sand/gravel (substrate comprised predominantly of particles the size of sand to small stones [&lt;3 cm³]; stones 3 cm³–0.07 m³ were often present, and occasionally individual rocks or boulders – but not to the extent as to change the essential open character of the substrate)</td>
<td>Present=1, Absent=0</td>
</tr>
<tr>
<td>A single layer of rocks, stones, and boulders (substrate comprised of rocks and stones &gt;0.07 m³–0.4 m³ in contact with the bottom substrate and not stacked on top of each other; isolated rocks or boulders 0.4 m³–7 m³ that were not stacked may have been present)</td>
<td>Present=1, Absent=0</td>
</tr>
<tr>
<td>Stacked rocks (large, angular rocks [0.4 m³–7 m³] stacked on top of one another forming sheltered areas and irregular contours, sometimes interspersed with large boulders [&gt;0.07 m³–0.4 m³], and rocks &gt;7 m³)</td>
<td>Present=1, Absent=0</td>
</tr>
<tr>
<td>Solid rocks (continuous rock that could not obviously be divided into individual rocks [e.g., cliffs meeting the sea at very steep angles, solid rock platforms]; large rocks [&gt;7 m³] may have been present to a limited extent)</td>
<td>Present=1, Absent=0</td>
</tr>
<tr>
<td><strong>Whether opportunities for abundant shade existed</strong></td>
<td>Present=1, Absent=0</td>
</tr>
<tr>
<td><strong>Whether tide pools were present</strong></td>
<td>Present=1, Absent=0</td>
</tr>
<tr>
<td><strong>Whether spray from waves occurred</strong></td>
<td>Present=1, Absent=0</td>
</tr>
<tr>
<td><strong>Whether the area was bordered on both sides by peninsulas</strong></td>
<td>Present=1, Absent=0</td>
</tr>
</tbody>
</table>
To define substrates, I modified Bester’s (1982) definitions for categorizing beaches used by *A. tropicalis*. ‘Boulders’ refer to water-worn, rounded stones, whereas ‘rocks’ refer to rough, angular stones. Because it is important to quantify topography at a spatial grain relevant to decisions of individual animals (Twiss et al. 2000), I recorded presence or absence of various substrate types at potential breeding beaches instead of categorizing entire beaches. This enabled me to account for habitat that might seem negligible, but may be important to decisions made by seals. For example, if a shore was comprised primarily of stacked rocks, but also had a narrow area of sand/gravel, I recorded the presence of both substrates and did not just categorize the shore as stacked rocks. The small sand/gravel area could be important because it could enable sea lions or humans to enter the beach. Slope at the rear of the beach could be important for habitat selection because steep rear slopes should prevent human access by land; however, steep slopes could also prevent pups from escaping high seas. Aspect of the beach affects exposure to sun and wind, and could influence thermoregulation.

I interviewed current and former guards and biologists who had worked at the reserves to determine where human disturbance had occurred and where sea spray occurred. Although guards and biologists do not have infallible knowledge about these variables, the guards usually walk the entire coastlines of the reserves at least once each day, so I am confident that human disturbance is at least minimal at beaches I considered not to have human disturbance.
Analysis

To distinguish among variables associated with active and abandoned breeding beaches, and those not used by seals for breeding, I performed discriminant analysis (DA) (SYSTAT® 9 Statistics I, SPSS, Inc., Chicago, IL). I used interactive backward stepping to remove variables that contributed least to distinguishing groups (i.e., had the lowest F-to-remove values), and stopped at the point when percent classified correctly in the jackknifed analysis was maximized, indicating the model was most stable with respect to removal of beaches.

Although DA theoretically requires explanatory variables to meet the assumptions of joint normality and equality of covariance matrices, DA is "remarkably robust to violations of assumptions in terms of error rates, as long as interactions among explanatory variables do not affect the response" (Knoke 1982). Error rates were low, and variables were unlikely to have biologically significant interactions that would confound interpretation of results. Others have used binary variables in discriminant analysis and have produced useful predictive models (Daudin 1986, Vlachonikolis and Marriott 1982, Titterington et al. 1981). Ecological significance of models is supported if DA models have an ecologically meaningful and consistent interpretation (Green 1974). Unequal covariance matrices do not affect the validity of differences found among group centroids; however, unequal covariance matrices can distort the representation of entities (e.g., beaches) in canonical space, so ellipses may not reliably reflect overlap among groups (McGarigal et al. 2000). I chose DA over other classification methods such as classification or regression trees because DA has the capability of using different
combinations and weights of the same variables to distinguish groups, which I believe produces the most realistic and useful model.

RESULTS

Characterization of Breeding Beaches

Discriminant analysis revealed significant multivariate differences among beaches currently used for breeding and those abandoned or unused (F=5.97, U=0.46, P<0.00001, n=70). After removing variables that contributed least to the model, all remaining variables were important to the model and were intercorrelated. Variables used in the final model, which included all 70 beaches, were human disturbance, offshore islands, stacked rocks, abundant shade, and tide pools (Table 1-2). The model classified 74% of beaches correctly among the three categories.

Separate discriminant analyses of PSJ, Atico, and Coles included some additional variables (Table 1-2). Stacked rocks were important features to all four models, while human disturbance, offshore islands, tide pools, and abundant shade were important in three out of the four models.
Table 1-2. Canonical discriminant functions (standardized by within variances) for variables comprising discriminant analysis models that distinguish currently used breeding beaches from those abandoned or unused by *A. australis*. Four were produced – for all three reserves (Punta San Juan, Punta Atico, and Punta Coles, Peru) combined, and for each reserve separately.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Reserve/s</th>
<th>Canonical discriminant functions for Factor 1</th>
<th>Canonical discriminant functions for Factor 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Human disturbance</td>
<td>All combined</td>
<td>0.727</td>
<td>0.144</td>
</tr>
<tr>
<td>Offshore islands</td>
<td>All combined</td>
<td>-0.580</td>
<td>0.588</td>
</tr>
<tr>
<td>Stacked rocks at shore</td>
<td>All combined</td>
<td>-0.470</td>
<td>-0.871</td>
</tr>
<tr>
<td>Tide pools</td>
<td>All combined</td>
<td>-0.437</td>
<td>-0.282</td>
</tr>
<tr>
<td>Abundant shade</td>
<td>All combined</td>
<td>-0.283</td>
<td>0.362</td>
</tr>
<tr>
<td>Human disturbance</td>
<td>PSJ</td>
<td>3.278</td>
<td>0.455</td>
</tr>
<tr>
<td>Rear slope of beach</td>
<td>PSJ</td>
<td>2.740</td>
<td>0.185</td>
</tr>
<tr>
<td>Offshore islands</td>
<td>PSJ</td>
<td>-2.185</td>
<td>-1.126</td>
</tr>
<tr>
<td>Abundant shade</td>
<td>PSJ</td>
<td>1.489</td>
<td>1.363</td>
</tr>
<tr>
<td>Solid rock at shore</td>
<td>PSJ</td>
<td>-1.433</td>
<td>-0.281</td>
</tr>
<tr>
<td>Sea spray</td>
<td>PSJ</td>
<td>1.326</td>
<td>1.420</td>
</tr>
<tr>
<td>Stacked rocks at shore</td>
<td>PSJ</td>
<td>-1.103</td>
<td>-0.305</td>
</tr>
<tr>
<td>Stacked rocks at shore</td>
<td>Atico</td>
<td>0.807</td>
<td>0.639</td>
</tr>
<tr>
<td>Bordered by peninsulas</td>
<td>Atico</td>
<td>-0.640</td>
<td>0.549</td>
</tr>
<tr>
<td>Tide pools</td>
<td>Atico</td>
<td>0.580</td>
<td>-0.058</td>
</tr>
<tr>
<td>Abundant shade</td>
<td>Atico</td>
<td>0.422</td>
<td>-0.697</td>
</tr>
<tr>
<td>Offshore islands</td>
<td>Coles</td>
<td>-2.400</td>
<td>0.137</td>
</tr>
<tr>
<td>Stacked rocks at shore</td>
<td>Coles</td>
<td>-2.054</td>
<td>-0.617</td>
</tr>
<tr>
<td>Beach facing north</td>
<td>Coles</td>
<td>2.048</td>
<td>1.444</td>
</tr>
<tr>
<td>Human disturbance</td>
<td>Coles</td>
<td>1.847</td>
<td>0.445</td>
</tr>
<tr>
<td>Single layer rocks/stones/boulders at shore</td>
<td>Coles</td>
<td>-0.291</td>
<td>-0.921</td>
</tr>
<tr>
<td>Tide pools</td>
<td>Coles</td>
<td>-0.071</td>
<td>0.781</td>
</tr>
</tbody>
</table>

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In Fig. 1-1, Factor 1 (the x-axis) is the first canonical discriminant function, which is the linear combination of variables that has the highest possible multiple correlation with the three groups (currently used, abandoned, or unused beaches). Factor 2 (the y-axis) is the second canonical discriminant function, which is the linear combination of variables that is not correlated with Factor 1 that has the highest possible multivariate correlation with the groups. Variables with the highest absolute values are the most influential to the function.

Currently used beaches were distinguished from abandoned or unused beaches by Factor 1 (Fig. 1-1a). Human disturbance was associated with abandoned and unused beaches, and offshore islands, stacked rocks, abundant shade, and tide pools were associated with currently used beaches (Table 1-2). Abandoned and unused beaches were separated by Factor 2 (Fig. 1-1a). Abandoned beaches were more likely to have stacked rocks at the shore (Table 1-2).

Although the variable reserve did not contribute significantly to distinguishing beaches, I present discriminant analyses for each reserve. These models also revealed significant differences among beaches currently used for breeding and those abandoned or unused (PSJ: F=4.32, U=0.44, P=0.003, n=17; Atico: F=3.70, U=0.44, P<0.002, n=36; Coles: F=7.36, U=0.03, P<0.0001, n=17). Models classified 100% of beaches correctly for Coles, 94% for PSJ, and 66% for Atico. At Atico, human disturbance occurred at all potential breeding beaches and was not useful for the model in distinguishing beaches.
Figure 1-1. Plots of canonical scores for all potential fur seal breeding beaches sampled at (a) Punta San Juan, Punta Atico, and Punta Coles, Peru; (b) only Punta San Juan; (c) only Punta Atico; and (d) only Punta Coles. Discriminant analysis revealed significant multivariate differences (P<0.001) among the groups (beaches currently used by fur seals for breeding [white circles], abandoned beaches [striped ovals], and unused beaches [black circles] for all four analyses. Larger symbols indicate group means. Arrows point to variables driving the corresponding factor in that direction.
Factor 1
(Fig. 1-1c)

More - borders
Less - stacked rocks
- shade
- pools

Factor 2
(Fig. 1-1d)

More - north
- human disturbance
Less - stacked rocks
- islands
At PSJ, like in the overall model, Factor 1 distinguished currently used beaches from those abandoned or unused (Fig. 1-1b, Table 1-2). Human disturbance at PSJ was also associated with abandoned or unused beaches, as were steep rear slopes. Offshore islands were associated with currently used beaches. Factor 2 distinguished abandoned from unused beaches - abundant shade and sea spray were associated with abandoned beaches.

At Atico, Factor 1 distinguished currently used and abandoned beaches from unused beaches (Fig. 1-1c, Table 1-2). Stacked rocks, tide pools, and shade were associated with currently used and abandoned beaches. Beaches bordered by peninsulas were associated with unused beaches.

At Coles, Factor 1 distinguished currently used beaches from those abandoned or unused (Fig. 1-1d, Table 1-2). Offshore islands and stacked rocks were associated with currently used beaches, and human disturbance and north-facing beaches were associated with abandoned and unused beaches.

Results of the discriminant analysis model are supported by descriptive statistics, which also demonstrate clearly how human disturbance, offshore islands, stacked rocks, abundant shade, tide pools, and sea spray are important for distinguishing among currently used, abandoned, and unused beaches (Table 1-3). As indicated by the discriminant analysis, mean shore and rear slopes do not apparently distinguish among beaches. Mean rear slopes (degrees) ± SD for currently used, abandoned, and unused beaches were 19.5±17.2, 31.8±26.1, and 18.7±16.5 respectively; and mean shore slopes were 7.6±7.6, 6.0±2.9, and 16.4±4.0 respectively.
Table 1-3. Percentages of currently used, abandoned, and unused fur seal breeding beaches that had categorical habitat and disturbance variables (Table 1) present at the beach. All sampled beaches (n=70) from Punta San Juan, Punta Atico, and Punta Coles, Peru are included. In bold are variables for which discriminant analysis revealed significant differences among currently used, abandoned, and unused beaches. Higher percentages of abandoned and unused beaches had human disturbance. Higher percentages of currently used beaches had offshore islands, abundant shade, and tide pools. Lower percentages of unused beaches had stacked rocks at the shore and sea spray.

<table>
<thead>
<tr>
<th></th>
<th>Currently used (%)</th>
<th>Abandoned (%)</th>
<th>Unused (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Human disturbance</td>
<td>73.9</td>
<td>90.9</td>
<td>98.2</td>
</tr>
<tr>
<td>Sea lion predation</td>
<td>26.1</td>
<td>45.5</td>
<td>16.7</td>
</tr>
<tr>
<td>Offshore islands</td>
<td>47.8</td>
<td>0.0</td>
<td>5.6</td>
</tr>
<tr>
<td>Sand/gravel at shore</td>
<td>34.8</td>
<td>27.3</td>
<td>25.0</td>
</tr>
<tr>
<td>Single layer rocks/stones/boulders at shore</td>
<td>78.3</td>
<td>72.7</td>
<td>91.7</td>
</tr>
<tr>
<td>Stacked rocks at shore</td>
<td>65.2</td>
<td>72.7</td>
<td>27.8</td>
</tr>
<tr>
<td>Solid rock at shore</td>
<td>87.0</td>
<td>63.6</td>
<td>77.8</td>
</tr>
<tr>
<td>Abundant shade</td>
<td>82.6</td>
<td>18.2</td>
<td>13.9</td>
</tr>
<tr>
<td>Tide pools</td>
<td>60.1</td>
<td>36.4</td>
<td>30.6</td>
</tr>
<tr>
<td>Sea spray</td>
<td>95.7</td>
<td>90.1</td>
<td>13.9</td>
</tr>
<tr>
<td>Bordered by peninsulas</td>
<td>69.6</td>
<td>63.6</td>
<td>75.0</td>
</tr>
</tbody>
</table>
DISCUSSION

Fur seals breeding in a hot environment where they are exposed to human disturbance must make trade-offs among maximizing their environment for thermoregulation, safety of pups, and avoiding disturbance. My results suggest that at low population levels, South American fur seals in Peru selected breeding beaches (macrohabitat) where access by humans was difficult, but where thermoregulatory behavior by mothers proved potentially dangerous to pups (e.g., giving birth at steep, rocky shorelines with heavy surf where pups could easily fall or be washed away, or have more difficulty escaping from aggressive females). In other pinnipeds, changes in breeding habitat selection have coincided with population declines (Budd 1972, Gentry 1998) and in response to human disturbance (Kenyon 1972, Gerrodette and Gilmartin 1990). Guadalupe fur seals (*A. townsendi*) apparently used open beaches before sealing occurred, but only occurred at the base of steep cliffs after sealing began (Peterson et al. 1968). *A. australis* has previously been reported to breed in macrohabitats where human disturbance was minimized (i.e., reserves and extremely remote areas (Majluf and Trillmich 1981). This study demonstrates selection of particular beaches within reserves with topography that is least accessible to humans.

After the 1997-98 El Niño, when the fur seal population declined dramatically in Peru, seals abandoned some of their former primary breeding beaches, but continued breeding at adjacent beaches that were more rugged. Abandoned and unused beaches were more likely to have human disturbance than currently used beaches. Offshore islands were associated with currently used beaches, which may also indicate avoidance of disturbance because the islands are difficult for humans to access. Fur seals in Peru
have been exploited by humans since around 2000 B.C. (Bonavia 1982), and populations were nearly extirpated by indiscriminate commercial hunting from the early 1900s until 1946. In 1959 sealing in Peru was totally banned, but some authorized killing occurred up to 1977 (IMARPE, unpub. report), and poaching continues to occur (Majluf 1987b, M. Araujo, guard at Punta Coles for PROABONOS, pers. comm.).

I also found that thermoregulatory features (shade, tide pools, and stacked rocks, which provide shade and create tide pools) were more associated with currently used than abandoned or unused beaches. *Arctocephalus* spp. that breed where they are susceptible to heat stress must select habitat features that enable them to thermoregulate. *A. tropicalis* at Gough Island use wind and sea spray (Bester 1982), *A. australis* in Uruguay use the shoreline, pools, or shade from inland rocks (Vaz-Ferreira and Ponce de Leon 1987), *A. philippii* use shade from cliffs (Francis and Boness 1991), and *A. galapagoensis* pups use damp shade under rocks (Limberger et al. 1986). Carey (1991) showed experimentally that *A. forsteri* preferred breeding areas where shade or tide pools were added. Fur seals must thermoregulate behaviorally because of their physical adaptations for fasting and foraging in cold waters (e.g., blubber and underfur) (Stirling 1983, Limberger et al. 1986). Peru is at the northern limit of the geographic range of *A. australis*, so habitat associated with cooling is especially important for Peruvian populations. Females carry their pup in their mouth as they make daily movements between dry, ‘pup-safe’ areas, and the water where they go to cool.

Several macrohabitat variables were important for distinguishing beaches at one reserve, but not others. At PSJ abandoned and unused beaches tended to have steeper rear slopes than currently used beaches. Steep rear slopes might make it difficult for
females to bring pups to higher ground to avoid high seas. At Atico, currently used and abandoned beaches were less likely to be bordered by peninsulas. Such borders buffer rough seas and make beaches more accessible for shellfishermen approaching from the water (which is common at Atico). At Coles, currently used beaches were more likely to face north. North-facing beaches are the closest beaches to a military base adjacent to the reserve, so avoidance of those beaches was probably also a response to human disturbance.

The importance of stacked rocks in the breeding habitat of South American fur seals is unclear. Breeding beaches of *A. forsteri* were found to be steeper and contain more ledges and crevices (i.e., conditions created by stacked rocks) than non-breeding beaches (Bradshaw et al. 1999, Ryan et al. 1997). Selection of stacked rocks by seals may reflect the dual advantages of this substrate – cool spaces for thermoregulation, and lower accessibility to humans. A tradeoff to the benefits of stacked rocks may be greater risks to newborn pups when maneuvering on this substrate. This is supported by high pup mortality rates in years after breeding beaches were abandoned when population density was low (discussed in detail in Chapter III). At PSJ in 1999, pup mortality within the first month of life was 45% at the rugged beach adjacent to the former primary breeding beach (S. Insley, P. Majluf, and D. Boness, unpub. data). This is at the high end of the range of first-month mortality observed at the former primary breeding beach (49% in 1987, 31% in 1998, and 24-35% between 1990 and 1993 (Chapter III). At a similar beach at Coles in 2000 pup mortality was also high, 32% (Chapter III). While such mortality data are not available for Coles from other years, in other *Arctocephalus* spp.,
early pup mortality ranges from 3-28%, but does not generally exceed 20% (reviewed by Harcourt 1992).

In other pinnipeds, topography of breeding areas has been suggested to influence fitness. Steep topography makes it difficult for northern elephant seal pups (*Mirounga angustirostris*) to escape high seas (Le Boeuf and Briggs 1977). For grey seals (*Halichoerus grypus*), pupping success was lower at a beach that lacked low-elevation land adjacent to the main access points from the sea and had less availability of pools (Twiss et al. 2000). Anderson and Harwood (1985) found that differences in terrain were associated with different percentages of time resting (i.e., farther from water, less time resting) for *H. grypus*.

Habitat that minimizes human access may be especially important to seals in small populations that may increase vigilant behavior in a large, open habitat. In large groups, the vulnerability of individuals to predators is often reduced by ‘the dilution effect’ (e.g., Pulliam 1988). In harbor seals (*Phoca vitulina*), breeding within a larger group resulted in lower energy expenditure per individual on vigilance, and faster detection of predators (Terhune 1985, da Silva and Terhune 1988). South American fur seals might select microhabitat with three-dimensional structures that prevent direct access to them – microhabitat selection is examined in Chapter II. In addition to limiting disturbance by predators or humans, such microhabitat would also limit harassment of females by male fur seals. In polygynous pinnipeds, females tend to prefer to be near other females to reduce harassment by males (Trillmich and Trillmich 1984, Boness 1991, Boness et al. 1995).
Allee suggested that habitat suitability can vary with population density (Allee et al. 1949, Stephens et al. 1999). This study suggests that fur seals in Peru might assess habitat suitability differently at low densities. It is possible that due to 'selfish herd' or 'dilution' effects on predation/disturbance, seals find open, low-relief habitat unfavorable at low densities.

Use of marginal quality habitat (Eberhardt and Siniff 1977), and high pup mortality (Congdon 1997, Durant 1998) are two important indicators of poor condition of a population. Population increases are not to be expected unless immature survival is quite high or adult survival is particularly high. Pup mortality is consistently high in Peruvian *A. australis*, and adult mortality is relatively high (50% of adult mortality is fisheries-related (M. Arias, pers. comm.), and El Niño events occur regularly (e.g., Trillmich and Ono 1991). If El Niño events and human disturbance continue at current levels, prospects for population growth in Peruvian *A. australis* may be poor.

Information about habitats selected and avoided by seals, and about habitats that are beneficial to pup survival are important for management of the species. Such information can be used to help mitigate factors causing seals to abandon areas, and to prioritize protection of beaches with respect to current and possible future population sizes.
CHAPTER II

USE OF MICROHABITAT BY FEMALE SOUTH AMERICAN FUR SEALS DURING THE BREEDING SEASON: INFLUENCES OF TOPOGRAPHY, THERMOREGULATION, POPULATION DENSITY, AND HARASSMENT BY MALES

INTRODUCTION

The study of movements and spatial patterns of individuals is important to understand the environmental features animals select or avoid (Stevick et al. 2002). Selection of reproductive sites is one of the most important factors influencing reproductive success of females (Bartholomew 1970, Emlen and Oring 1977). Ideal reproductive sites have a climate suitable for homeostasis, maximal food availability, and minimal risks such as predation and inter- or intra-specific disturbance. Variables associated with reproductive sites can be examined on a variety of spatial scales, from a large-landscape scale to the fine-scale immediate surroundings of an individual.

Few studies have quantitatively examined factors influencing use of fine-scale breeding habitat (e.g., birth sites and movement within a colony) by pinnipeds (e.g., Pomeroy et al. 1994, Twiss, 2000). For Arctocephalus spp., habitat at the scale of the breeding beach has been qualitatively described as being difficult for humans to access, with habitat ranging from sandy beaches to rugged, rocky shorelines (reviewed in Chapter I). Quantitative analysis of microhabitat use by New Zealand fur seals (A. forsteri) showed that the area of cooling substrate (shade or tide pools) in males’ territories was correlated...
with the number of females in the territory (Carey 1991). Fur seals breeding at low latitudes are vulnerable to heat stress while on land because of their thick underfur and blubber (Limberger et al. 1986). Majluf and Trillmich (1981) first described breeding beaches for South American fur seals (*Arctocephalus australis*) in Peru as steep, rocky slopes or more level rock with areas of vertical structure that provide shade. Some historically important breeding beaches were recently abandoned after the population declined 72% during the severe El Niño in 1997-98. Following the decline, the seals tended to use more rugged breeding beaches than they had prior to the decline (discussed in Chapter I). Females appeared to minimize human disturbance and maximize thermoregulation (i.e., habitat for 'cooling off') while putting their pups at risk of injuries from falls (Chapter III). This is of concern because *A. australis* in Peru have higher rates of early pup mortality than any other population of fur seals (15-49% within the first month of life – Majluf 1987a, Majluf 1992, Harcourt 1992) (reviewed by Harcourt 1992, and Wickens and York 1997). These high rates have stemmed from high densities of aggressive females making daily movements to limited thermoregulatory sites (e.g., tide pools, shoreline), during which pups risk becoming injured by aggressive females or separated from their mother (Majluf 1987a, Harcourt 1992). Although I had hypothesized that pup mortality rates would be lower following the decline, pup mortality remained high because at low population numbers females selected habitat that apparently minimized human disturbance and maximized thermoregulation, but had topography dangerous for newborn pups (Chapter I). Offspring mortality must be low for small populations of pinnipeds to recover (Congdon 1997, Durant 1998, Gerber and
Hilborn 2001). It is therefore important to understand breeding habitat features important to *A. australis* in Peru, and how habitat use influences mortality of pups.

In this chapter I examine factors associated with how female *A. australis* in Peru use microhabitat on the breeding beach. I compare characteristics of sites used for births, copulations, and by randomly selected females; and I examine factors influencing movements by females. Key factors driving use of microhabitat likely include physical topography (e.g., safety for pups, accessibility to humans), thermoregulation (e.g., proximity to tide pools or the shoreline), density of females, and harassment by males. Although high population density poses risks to pups, dense aggregations might also provide various benefits including less harassment by males (Trillmich and Trillmich 1984, Boness 1991), a lower probability of being preyed upon (Hamilton 1961), increased overall vigilance, and decreased energy expenditure per individual on vigilance (Terhune 1985, da Silva and Terhune 1988).

I compare microhabitat used at a flat, open breeding beach with abundant tide pools (the type of beach that was more likely to be abandoned – Chapter I) to microhabitat used at a steep, rugged beach exposed to heavy surf. I hypothesized that females at the flat beach would spend more time near thermoregulatory sites than at the rugged beach because tide pools are safer for pups than a rugged shoreline. I quantified movements at the two breeding beaches and compared factors influencing movements. I hypothesized that females at the flat beach would move less than females at the rugged beach. Females at the flat beach with abundant tide pools should need to move less to thermoregulate than females using a rugged shoreline because of less competition for thermoregulatory sites in the former habitat. Also, females using tide pools for

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thermoregulation should need to move less often to safer spots for their pups than females using a rugged shoreline.

METHODS

Study species

The breeding biology of South American fur seals in Peru was described in detail by Majluf (1987a). The seals come ashore to breed during the austral spring (October-December). Males defend small territories that must contain water. Females give birth on land to a single pup. The perinatal attendance period occurs from birth until 8-10 days later when the mother copulates and makes her first foraging trip. For the first 3-4 days after birth mother and pup remain in close contact. A female will carry her pup in her mouth during thermoregulatory movements. Later in the perinatal period pups become more mobile and start spending more time away from their mothers (<30 m from their suckling site). Young may be weaned between 9-36 months (Majluf 1991). Female *A. australis* in Peru move freely through the colony without being herded by males, and also reportedly choose with whom they mate - sometimes copulating outside their normal range (Majluf et al. 1996).

Study sites

Punta Coles (Coles), Ilo, Peru (17°42'S, 71°22'W) is a protected guano reserve that comprises about 6 km of coastline, and is one of the most important breeding areas for fur seals in Peru (Arias-Schrieber and Rivas 1998). I selected two study beaches that represented the two general types of breeding topographies used by fur seals at Coles – a rugged rocky beach named ‘north-facing-9’ (N9), and a flat, open beach named ‘south-facing-12’ (S12). The beaches are about 0.5 km apart. N9 has about 75 m of shoreline, is backed by a 2-5 m cliff, and has approximately 5-25 m of beach between the shoreline and cliff. The beach
consists primarily of stacked rocks, particularly at the shoreline, and is exposed to heavy surf during high tides and rough seas. Smaller sections of N9 have gradual-sloping, broad, flat rocks with tide pools. Overhangs and crevices at the rear of the beach provide some shade.

S12 is a flat, open beach comprised of a single layer of rocks interspersed with tide pools, and has sand (no cliffs) at the rear. I delineated the study site as a 175 m-long section of beach that could be observed clearly. The beach is not exposed to heavy surf and has almost no shade. Neither beach in this study has sufficient shade for more than a few individuals to be in the shade for an entire day, so the most important thermoregulatory features were the shoreline and tide pools.

Censuses

Censuses of the populations at N9 and S12 were performed every other day between 6:00 and 9:30 (usually before 8:00) from 11 October to 17 December 2000. Total numbers of adult females, territorial males, and pups were recorded.

Movements

To examine factors driving movements of females on the breeding beach, I performed behavioral observations at N9 and S12. At N9 observations were made from a cliff-top blind about 12 m from the rear of the colony, and at S12 observations were made from a 4 m wooden tower with a blind constructed about 15 m from the rear of the colony.

To identify individual females at N9 I squirted them on the back with hair dye using a 100 cc syringe, or hitting them with a dye-filled egg (Clairol Born Blonde®) from behind a blind or natural barrier. Detailed drawings of seals and their dye marks were used to make positive identifications. I was unable to mark females at S12 because the
flat, open nature of the beach did not allow seals to be approached without disturbing them.

Observations were conducted during all daylight hours during the seals' breeding season in October-December 2000. Thirty-minute focal observations (Martin and Bateson 1993) of marked females were performed daily by two observers during two 3-4 h periods, with all times equally represented. When more than one marked female was present I randomly selected which to observe. Random marked females were selected by dividing the beach in half and tossing a coin to eliminate one half of the beach until one marked female was isolated. During focal observations, all movements by focal females were recorded and classified according to definitions presented in Table 2-1.
Table 2-1. Variables recorded during 30-min focal observations of female fur seals (focal female = FF, BL = Body length of female). Date, substrate, density, and distances to water and territorial males were also recorded for births and copulations.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>30 Oct. = 1, 31 Oct. = 2, etc.</td>
</tr>
<tr>
<td>Substrate</td>
<td>Water, sand/gravel, solid rock, or stacked rocks ('stacked rocks' have sufficient 3-D structure to potentially provide shade within 1 BL of FF)</td>
</tr>
<tr>
<td>Number of movements</td>
<td>FF moves &gt; 1 BL. Separate movements distinguished if FF rested between movements (e.g., lying down, not looking around, eyes closed)</td>
</tr>
<tr>
<td>Types of movements by FF</td>
<td></td>
</tr>
<tr>
<td>Avoid female</td>
<td>Response to an approach by another female</td>
</tr>
<tr>
<td>Avoid territorial male</td>
<td>Response to an approach by a male that holds a territory or is the same size as territory holders</td>
</tr>
<tr>
<td>Avoid subadult male</td>
<td>Response to an approach by a non-territorial male that is smaller than territory holders</td>
</tr>
<tr>
<td>Avoid water</td>
<td>In response to waves or surf hitting her</td>
</tr>
<tr>
<td>Thermoregulatory</td>
<td>Toward the shore, a tide pool, or shade</td>
</tr>
<tr>
<td>Toward pup</td>
<td></td>
</tr>
<tr>
<td>Number of approaches (App) by females</td>
<td>Other female approaches FF within 1 BL</td>
</tr>
<tr>
<td>Number App by subadult males (SA male)</td>
<td>SA male approaches FF within 1 BL</td>
</tr>
<tr>
<td>Number App by territorial males (T male)</td>
<td>Territorial male approaches FF within 1 BL</td>
</tr>
<tr>
<td>Number of females within 2 BLs (density of females)</td>
<td>Number of heads of other females within 2 BL of head of FF (A female is more likely to threaten a female near her head than near her tail, and is more likely to threaten another female whose head is near her head than one whose tail is near her head.)</td>
</tr>
<tr>
<td>Distance to water</td>
<td>Distance (BL) from a FF to shore or tide pool</td>
</tr>
<tr>
<td>Distance to T male</td>
<td>Distance (BL) from a FF to a T male</td>
</tr>
<tr>
<td>Whether female in tucked posture</td>
<td>All four flippers pressed against body (minimizes surface area and heat loss – Fay and Ray 1968)</td>
</tr>
</tbody>
</table>
When no marked females were present, random females were selected to observe using the method described above. Focal observations were performed at S12 using the same methods as for N9, except that only random females were observed. Hours of the day observations were performed and environmental conditions were the same for N9 and S12. Each day approximately two observer hours were spent at N9 for every one at S12. At N9 and S12, 746 and 353 focal observations were performed respectively. Twenty-two marked females were followed throughout the season, with 2-14 h of observation per female for a total of 237 h of observation for identified females.

**Microhabitat**

I characterized microhabitat for births, copulations, and random samples of focal females; and compared substrate, density of females, and distances to the nearest water and territorial male among these sites and between females at N9 vs. S12. Focal observations were performed as described above. All variables except movements and approaches were recorded at the start of the focal period (i.e., data were not adjusted if the female moved during the observation period). Density of females was measured by determining the number of females within 2 body lengths of focal females.

To facilitate the comparison of density with estimates reported in the literature, I also counted the number of females within a 5 m x 5 m quadrat in the center of the colony where density was maximal. Area of the quadrat was estimated using 1 BL = 1.5 m.

For all births and copulations, the same microhabitat variables were recorded as for focal observations. For copulations I recorded which sex initiated the interaction (i.e., one sex approached the other, or the female displayed her underside to the male) to gain understanding about the relationship between male harassment, movement by females, and copulations.
Thermoregulation

To examine the association between body temperature and movement by females, I conducted specialized focal observations on females at N9 that were near enough (within approximately 15 m) that I could measure their flipper temperatures using the non-contact infrared thermometer. Flippers of seals (as well as other marine mammals) have a countercurrent vascular heat exchange arrangement through which they are able either to conserve or dissipate heat (Tarasoff and Fisher 1970). Flipper surface temperatures approaching core body temperature could signify that seals are using vasodilation to release heat into the environment (Worthy 1991). I conducted observations during eight periods between 16 November and 11 December – four from 8:30 – 10:00, and four from 17:00-18:30 – all on clear days with calm seas. These were the times when I expected seals to make transitions between thermoneutrality and stress from heat (in the morning) and possible stress to pups from cold (in the evening). Pups have not yet developed their insulating blubber layer (Blix et al. 1979). Before each observation period, five identified females were selected. Then at the start of each period, and at half-hour intervals, flipper and substrate temperatures were recorded for each female. I recorded all movements by females, events (if any) that preceded the movement (e.g., approach by another seal), and the substrate to which she moved.

Analysis

For all statistical analyses using data from both study sites, I first examined whether the data differed statistically between sites (i.e., N9 and S12), and only combined results when there was no difference. To compare count data I used chi square contingency-table tests - eliminating the highest f_{ij} value after each test and performing
subsequent tests with the remaining values until a nonsignificant chi-square value was obtained (Zar 1984). Distances from focal females, copulations, and births to nearest water and the nearest territorial male were categorized as <1, 1-2, 3-5, and >5 BL. Prior to using parametric tests I performed square root transformations on binomially distributed data and arcsine transformations on percentage data (Zar 1984). When multiple tests were performed, Bonferroni corrections (SYSTAT® 9.0, SPSS, Inc., Chicago, IL) were used.

RESULTS

Census

At N9 the maximum number of females was 95, and the maximum number of males was 10. At S12 the maximum numbers of females and males were 204 and 25 respectively.

Movements

The distribution of movement types did not differ between the rugged beach (N9) and the flat beach (S12) ($X^2=5.15$, $p=0.27$, Fig. 2-1). Significantly more movements per observation period occurred at N9 than at S12 (295 movements/745 focal observations at N9 [0.40 per observation] vs. 92 movements/353 focal observations at S12 [0.26 per observation] $X^2=12.45$, $p=0.0004$). The majority of movements by females (63%) were thermoregulatory (See Table 2-1 for definitions of movement types). Eighteen percent of movements were toward pups; these usually occurred following a movement by a female away from her pup and toward water. Very few movements were caused by approaches by subadult males (only 2%) – fewer than those that resulted from approaches by females
(6%) or territorial males (15%). Three percent of movements were in response to water hitting the female.

![Graph](image)

Figure 2-1. Numbers of different types of movements (defined in Table 2-1) by females during focal observations at (a) beach N9, and (b) beach S12. Numbers for each category are the numbers of movements of that type per 745 half-hour focal observations. There were totals of 745 focal observations at N9 and 353 at S12, so numbers for N9 are actual values and numbers for S12 are adjusted to the scale for N9.

**Microhabitat**

The percentages of births, copulations, and randomly selected focal females that were observed on various substrates (water, sand/gravel, solid rock, and stacked rock) are presented in Table 2-2. No births, copulations, or randomly selected females were
observed on sand/gravel. Neither beach N9 nor S12 was comprised of a heterogeneous matrix of sand/gravel and rock; rather, N9 had sandy beach adjacent to the study area, and S12 had sand/gravel to the rear. Only copulations were observed in water. Although females used water for thermoregulation, females in open water were not selected for focal observations, and for any female partially submerged in a tide pool I recorded the adjacent substrate because no tide pools were large enough to contain an entire female.

This analysis examines whether solid rock and stacked rocks were used in equal numbers for birth sites and copulation sites vs. focal females, and for birth sites at N9 vs. S12. At N9, birth sites were more likely to be on stacked rocks than focal females (Table 2-2), however this tendency was marginally nonsignificant ($X^2=3.33$, df=1, $p=0.068$). At S12, birth sites and focal females were equally likely to be on stacked rock (Table 2-2; $X^2=0.556$, df=1, $p=0.456$). Copulations and focal females at N9 and S12 were equally likely to be observed on solid rock and stacked rock (Table 2-2; $X^2=0.916$, df=1, $p=0.338$ for N9; and $X^2=0.365$, df=1, $p=0.546$ for S12). Birth sites at N9 were more likely to be on stacked rocks than birth sites at S12 (Table 2-2), however this tendency was marginally nonsignificant ($X^2=3.37$, df=1, $p=0.066$).

Birth sites at N9 were significantly less likely to be adjacent to water (<1 BL) and more likely to be far from water (>5 BL) than copulation sites and sites of focal females ($X^2=19.97$, $p<0.001$, df=3; Table 2-3). Birth sites at S12 did not differ from locations of focal females in general in distance to water ($X^2=7.54$, $p=0.10$, df=4), but were less likely to be adjacent to water (<1 BL) and more likely to be far from water (>5 BL) than copulation sites ($X^2=13.16$, $p=0.04$, df=6). Birth sites and focal females were both less
likely to be adjacent to water at the rugged beach than at the flat beach ($X^2=15.29$, $p=0.004$, df=4 for births; $X^2=35.88$, $p<0.0001$, df=4 for focal females; Table 2-3).

Density of females was significantly greater for birth sites at N9 than for focal females and copulation sites ($F=5.282$, $p=0.029$; Tukey's post hoc test, $p=0.024$; Table 2-3). Density of females did not differ between birth sites, focal females, and copulation sites at S12 ($F=0.473$, $p=0.623$; Table 2-3). Mean density of females was greater for focal females at S12 than at N9 ($F=5.28$, $p=0.022$; Table 2-3). Mean density of females did not differ between birth sites at N9 and S12 ($t=0.372$, $p=0.713$). Maximum density was 0.4 females/m² at S12, and 0.3 females/m² at N9.

Birth sites at N9 and S12 did not differ in distance to the nearest territorial male ($X^2=5.65$, $p=0.226$, df=4; Table 2-3). Distance to the nearest territorial male did not differ between focal females and birth sites ($X^2=1.38 =, p=0.71$, df=4; Table 2-3).
Table 2-2. Percentages of births, copulations, and randomly selected females that were observed on various substrates.

<table>
<thead>
<tr>
<th>Site type</th>
<th>Beach</th>
<th>n</th>
<th>Water</th>
<th>Sand/gravel</th>
<th>Solid rock</th>
<th>Stacked rock</th>
</tr>
</thead>
<tbody>
<tr>
<td>Births</td>
<td>N9</td>
<td>59</td>
<td>0</td>
<td>0</td>
<td>13.6</td>
<td>86.4</td>
</tr>
<tr>
<td></td>
<td>S12</td>
<td>63</td>
<td>0</td>
<td>0</td>
<td>27.0</td>
<td>73.0</td>
</tr>
<tr>
<td>Copulations</td>
<td>N9</td>
<td>13</td>
<td>7.7</td>
<td>0</td>
<td>0</td>
<td>92.3</td>
</tr>
<tr>
<td></td>
<td>S12</td>
<td>33</td>
<td>18.2</td>
<td>0</td>
<td>9.1</td>
<td>75.8</td>
</tr>
<tr>
<td>Focal females</td>
<td>N9</td>
<td>738</td>
<td>†</td>
<td>0</td>
<td>7.0</td>
<td>93.0</td>
</tr>
<tr>
<td></td>
<td>S12</td>
<td>349</td>
<td>†</td>
<td>0</td>
<td>29.2</td>
<td>70.8</td>
</tr>
</tbody>
</table>

† Females in open water were not selected for focal observations, and for any female partially submerged in a tide pool I recorded the adjacent substrate because no tide pools were large enough to contain an entire female.

Table 2-3. Mean density and mode distance to the nearest water and territorial male for birth sites, copulation sites, and randomly selected females.

<table>
<thead>
<tr>
<th>Site type</th>
<th>Beach</th>
<th>Mean (±SE) number females within 2 BLs</th>
<th>Mode distance to water (BLs)</th>
<th>Mode distance to Tmale (BLs)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Births</td>
<td>N9</td>
<td>3.13 (0.29)</td>
<td>1</td>
<td>3-5</td>
<td>59</td>
</tr>
<tr>
<td></td>
<td>S12</td>
<td>3.12 (0.21)</td>
<td>0</td>
<td>3-5</td>
<td>63</td>
</tr>
<tr>
<td>Copulations</td>
<td>N9</td>
<td>2.00 (0.49)</td>
<td>0</td>
<td>3-5</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>S12</td>
<td>3.06 (0.40)</td>
<td>0</td>
<td>3-5</td>
<td>33</td>
</tr>
<tr>
<td>Focal females</td>
<td>N9</td>
<td>2.46 (0.09)</td>
<td>1</td>
<td>3-5</td>
<td>738</td>
</tr>
<tr>
<td></td>
<td>S12</td>
<td>3.00 (0.16)</td>
<td>0</td>
<td>3-5</td>
<td>349</td>
</tr>
</tbody>
</table>
Of 46 observed copulations, the beginnings of 22 were observed. Of those, the male initiated 5, the female initiated 9, and 8 were equally initiated by both. Copulations were more likely to be in water than locations of focal females ($X^2 = 16.13$, $p = 0.002$, df = 3).

Severe harassment of females by males (i.e., biting, preventing them from moving) was not characteristic of fur seal breeding behavior in this study. During all observations at both beaches, only one incidence of a male preventing a female from moving was observed. The female was sleeping in a crevasse and a large male jumped on top of her and forced a copulation. The female moved rapidly into the water afterwards, but had no observable injuries. No males were observed to injure females.

Territorial males did not prevent harassment of females by subadult males. Females that were closer to a territorial male (<3 BL) were equally likely to be approached by a subadult male as females that were farther (>3 BL) from a territorial male ($X^2 = 0.38$, $p = 0.538$).

**Thermoregulation**

During specialized thermoregulatory observations at N9, more female movements per observation period occurred during mid-morning (8:30-10:00) than in the evening (17:00-18:30) (24/42 during mid-morning, and 0/28 in the evening, $X^2 = 35.63$, $p < 0.001$, df = 1; Figs. 2-2a, 2-2b). During mid-morning, all movements were toward water, and there were no apparent external stimuli preceding the movements. All females moved to the water before 10:00. All females whose flipper temperature reached 38°C moved to water shortly thereafter (Fig. 2-2a). Core body temperature is not known for South American fur seals, but has been determined to be 38°C for South African fur seals.
(Arctocephalus pusillus pusillus) (DeVilliers and Roux 1992). Core body temperature is likely similar in *A. australis*. Greater percentages of females were in tucked postures when there was no sunlight hitting the beach (Fig. 2-3).

Air temperature remained at about 20°C throughout the daylight hours. This relatively low temperature likely results from cool winds coming from the sea (mean wind speed = 6.7±3.41 SD km/h, mean sea surface temperature = 15.5°C – Ministerio de Agricultura Projecto Especial de Promocion del Aprovechamiento de Abonos Provencientes de Aves Marinas, [PROABONOS]). Surface temperature of rocks on N9 ranged from 24±0.5°C at 7:00 to 35 ±0.9°C at 12:00 (Fig. 2-2). Mean (±sd) surface temperatures are presented in Table 2-4 for sand with no shade, rock with no shade, and shaded rock.
Figure 2-2. Numbers of females that moved and numbers of those that did not move at various flipper temperatures during observations of focal females (a) from 8:30-10:00 and (b) from 17:00-18:30 at N9.
Figure 2-3. Percentages of focal females that were in tucked postures (black bars), and mean substrate temperatures (solid line) ± SE for focal females at different times of day. Sunlight first hits the beach at 8:00 on a clear day, and the last sunlight hits the beach at 15:50 on a clear day.

Table 2-4. Mean surface temperatures for various substrates (sand with no shade, rock with no shade, and shaded rock) between 07:00 and 08:00, and between 12:00 and 13:00.

<table>
<thead>
<tr>
<th>Substrate</th>
<th>Mean temperature (°C ± sd)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>7:00-8:00</td>
</tr>
<tr>
<td>Sand (no shade)</td>
<td>29.3 ± 4.9</td>
</tr>
<tr>
<td>Rock (no shade)</td>
<td>25.3 ± 3.3</td>
</tr>
<tr>
<td>Rock (shade)</td>
<td>20.3 ± 1.75</td>
</tr>
</tbody>
</table>
DISCUSSION

Sixty-three percent of movements by focal females were thermoregulatory; the percentage of movements caused by thermoregulatory needs is likely higher because most of the 18% of movements toward pups occurred after females had left their pups to enter the water. Further evidence for the importance of thermoregulatory movements is the fact that all focal females in the special thermoregulatory observations moved to water as substrate temperature increased in the morning. Many females' flipper temperatures approached their core body temperature (Fig. 2-2a). Sand/gravel substrate was not used for births, copulations, or randomly selected females — possibly because this substrate reaches very high temperatures and is more accessible to humans, and rocky substrate (especially in the shade) is cooler throughout the day (Table 2-4). Births and copulations were equally likely to occur on stacked rocks as randomly selected females; however, births had a greater, but nonsignificant tendency to occur on stacked rock than random females at N9 or births and random females at S12. At N9, solid rock tended to occur at the shoreline, so giving birth on stacked rocks rather than solid rocks might have stemmed from females avoiding heavy surf.

Very few movements (2%) resulted from approaches by subadult males, but a higher percentage (15%) resulted from approaches by territorial males (Fig. 1). Proximity to water and other females seemed more important to females in their selection of microhabitat than proximity to a territorial male. Females were most often >3 BLs from territorial males, but were rarely that far from another female or water (Table 2-2).

Females seem to select birth sites that are as near to water as possible because of their need to thermoregulate, but farther from water when it is associated with rugged...
topography and heavy surf. Female fur seals in this study tended to use locations on the beach that were adjacent to water when tide pools among flat rocks were available. This trend was true for both focal females in general, and for birth sites. However, on the rugged beach (N9) with heavy surf and few tide pools, females — and particularly birth sites — were farther from the water. Because seals need to go to the water regularly to thermoregulate, and because copulations are usually in water (tide pools or at the shoreline), this can result in a spatial separation between microhabitat used for birth sites vs. thermoregulation and copulation. These results support earlier claims by Majluf (1987a) that the interaction of females using ‘pup safe’ topography and their need to thermoregulate in the water results in high rates of female movement on breeding beaches in Peru.

Birth sites near thermoregulatory sites at rugged beaches like N9 likely increase the risk to pups of falls and being washed away by heavy surf. Pups might also risk heat loss at such beaches; females at N9 assumed tucked postures in the evening, indicating that they were minimizing heat loss. Selection by females of a rugged breeding beach like N9 might be indicative of females trading safety of pups for an environment that is more difficult for humans to access (discussed in Chapter II).

Females at the flat, open beach (S12) had a greater pup survival rate (Chapter IV), and a lower rate of movement than females at N9. High rates of movement on the breeding beach were more associated with pup mortality than high density.

An important characteristic used by females in selecting a breeding beach is likely a group of females with a particular density. Females in my study of a small population bred at maximum densities of 0.3 females/m². This estimate might represent a minimum
density for the core of a fur seal breeding colony. Selection by females of terrain occupied by other seals might result from the benefits of increased vigilance and protection against male harassment discussed earlier. All births were within 3 BL of another female, but many stretches of shoreline were unused by females, despite being used in previous years or having habitat that appeared similar to currently used sites.

The primary factors influencing microhabitat use and high rates of movement by female *A. australis* in Peru appear to be the interaction of (1) females selecting either rugged or very high-density breeding beaches with limited thermoregulatory sites that are safe for pups (e.g., tide pools, shore without heavy surf, low density of seals), (2) females selecting birth sites away from water when rugged sites are used or when density is high, and (3) the need for females to move to water for thermoregulation and copulation. My results are consistent with those of Twiss et al. (2000), who found that female grey seals (*Halichoerus grypus*) preferred breeding close to water, and that lack of low-elevation land adjacent to the main access points to the sea was associated with more costly behavior (e.g., more time in locomotion and away from their pups).
CHAPTER III

INFLUENCES OF SOCIAL AND HABITAT FEATURES AND FEMALE BEHAVIOR ON PUP MORTALITY IN SOUTH AMERICAN FUR SEALS

INTRODUCTION

Offspring survival is one of the most important factors influencing variation in female reproductive success (Clutton-Brock 1988) and population growth rate (Congdon 1997). For pinnipeds, changes in offspring survival rate affect population growth rate more than other demographic factors such as natality, age at first reproduction (Eberhardt and Siniff 1977, LeBoeuf and Reiter 1988, Wickens and York 1997, Durant 1998, Galimberti et al. 2001) or inbreeding (Stewart et al. 1994). Populations of otariids (fur seals and sea lions) are capable of recovering from extremely low population numbers if survival rates are high (Gerber and Hilborn 2001), but high pup mortality rates pose a serious threat to recovery. Information on early pup mortality rates and factors influencing these rates is therefore essential to understanding the prospects for recovery of small otariid populations like those of South American fur seals (Arctocephalus australis) in Peru.

Recent estimates indicate that populations of A. australis in Peru declined 72% between 1996 and 1998 due to low food availability during a severe El Niño event in 1997-98 (M. Arias-Schreiber, Instituto del Mar del Peru [IMARPE], unpub. data). The species is now listed as in danger of extinction in Peru (Decreto Supremo N° 013-99-AG). Even prior to this extreme decline, populations had been undergoing an unexplained gradual decline and
southerly shift in geographic distribution (Arias-Schreiber and Rivas 1998). *A. australis* in Peru also have higher pup mortality rates than other populations of fur seals (reviewed by Harcourt 1992, and Wickens and York 1997). Pup mortality ranges from 15-49% within the first month of life (Majluf 1987a, Harcourt 1992), and up to 100% during severe El Niño events (S. Insley, P. Majluf, D. Boness, and M. Stevens, unpub. obs.).

Among the factors that most likely affect pup mortality in *A. australis* are competition for thermoregulatory sites, predators, availability of food resources and human disturbance, some of which may be density dependent. A primary cause of pup mortality in Peru has been pups becoming injured or separated from their mother when high densities of exceptionally aggressive females make long-distance movements to limited thermoregulatory sites (Majluf 1987a, Harcourt 1992, Majluf et. al. 1996). Females give birth to a single pup between October-December, mate about a week later, and then begin to alternate between time nursing pups on land and foraging at sea. Pups are weaned after 5-36 months, depending on available food resources (Majluf 1992). Suitable fur seal breeding habitat that is protected from human disturbance is limited in Peru, so seals there have bred in exceptionally dense colonies. Peru is at the northern limit of the geographic range of the species, so these seals are exposed to high levels of solar radiation, making them susceptible to overheating while on land during the breeding season (Limberger et al. 1986). Pups may also be killed by falls from cliffs, being washed away by heavy surf, or predation by Southern sea lions (*Otaria flavescens*). Although predation by sea lions on breeding beaches has been important at one site, Punta San Juan (PSJ), where 0.2-8.3% of pups were killed by subadult male sea lions (Majluf 1987a, Harcourt 1992), sea lion predation has not been reported at other sites in Peru. There
are no other important terrestrial or aquatic predators of fur seals in Peru, except for humans (Majluf 1987b).

In many pinnipeds, as well as terrestrial mammals, juvenile mortality rates are density-dependent (reviewed by Fowler 1981). Based on findings by Harcourt (1992), I hypothesized that pup mortality rates for *A. australis* in Peru are density dependent, and would therefore decline following the dramatic population decline in 1997-98. I expected this because decreased population density would likely result in fewer female-female encounters, and thus fewer aggressive acts toward pups. At lower population numbers thermoregulatory sites would be less limited, so decreased thermoregulatory movements should lead to fewer encounters among females as well, and fewer pups being separated from their mother. I also hypothesized that pup mortality would be lower for populations breeding at flat, open beaches protected from heavy surf than at rugged beaches characterized by stacked rocks and heavy surf where I expected pups to be more likely to fall and/or be washed away. Fur seals tended to abandon flat, open beaches, and use rugged beaches for breeding following the dramatic population decline in 1998 (Chapter I).

In this chapter I compare pup mortality rates and factors influencing pup mortality for *A. australis* at (1) Punta San Juan, Peru before and after the dramatic population decline in 1997-98, and (2) two topographically different beaches (flat, open vs. rugged) at Punta Coles, Peru following the population decline.
METHODS

Study Areas

I compared pup mortality rates and factors influencing these rates before and after the dramatic population decline at Punta San Juan, Peru (15°22'S, 75°12'W). PSJ is a protected guano reserve with about 3 km of coastline, and has been one of the most important fur seal breeding areas in Peru over the past three decades (Majluf and Trillmich 1981, Majluf 1987b, M. Arias, IMARPE, unpub. data). I determined pup mortality at beach ‘South 2’ (S2) in 1999, and compared it with pup mortality estimates from an unpublished data set for beach ‘South 3’ (S3) in 1990-93. After the population decline in 1997-98, seals abandoned S3 as a breeding site, but continued breeding at S2. S2 is adjacent to S3 – a steep rocky outcrop separates the two beaches. The study area at S3 has about 100 m of shoreline and is surrounded by a 25-30 m cliff. The shoreline has complex topography, with both sandy and rocky sections interspersed with tide pools. At the rear is a small cave, and there are offshore rocks that protect the beach from heavy surf. The study area at S2 has about 50 m of shoreline and is backed by a 10 m cliff. The shoreline is rugged and rocky with no tide pools, and the rest of the beach is comprised primarily of stacked rocks with a sandy area to the rear. There are no offshore rocks and the beach is exposed to heavy surf.

To compare pup mortality between sites with different topographies, I studied a different fur seal population in 2000 at Punta Coles (Coles), Ilo, Peru (17°42'S, 71°22'W), where greater numbers of seals were breeding than at PSJ (population sizes in 1999 were 345 at PSJ and 3,982 at Coles – M. Arias, IMARPE, unpub. data). Coles (also a protected guano reserve) has about 6 km of coastline. I compared two sites at Coles – beach ‘North-facing-9’ (N9) and beach ‘South-facing-12’, (S12), which are about 0.5 km apart. N9 has about 75m of
shoreline and is backed by a 2-5m cliff. The beach is comprised primarily of stacked rocks – particularly at the shoreline, which is exposed to heavy surf during high tides and rough seas. Smaller sections of N9 have gradual-sloping, broad, flat rocks with tide pools. Overhangs and crevices at the rear of the beach provide some shade. S12 is a flat, open beach comprised of a single layer of rocks interspersed with tide pools, and has sand (no cliffs) at the rear. I delineated a 175 m-long section of beach that I could observe clearly for the study site. The beach is not exposed to heavy surf, and has almost no shade. No beaches in this study have sufficient shade for more than a few individuals to be in the shade for an entire day, so the most important thermoregulatory features were the shoreline and tide pools.

**Pup Mortality Rates at PSJ Before and After the Population Decline**

Data on pup mortality at PSJ before the population decline were collected as part of a separate study. Each year from 1990-1993, 41-75 mother-pup pairs were captured and tagged at beach S3 (detailed methods in Majluf 1987a, Majluf and Goebel 1992). To facilitate long-range recognition, females and pups were also given large dye (Clairol Born Blonde®) marks on their backs. To determine pup mortality rates, I divided the number of pups of marked females not seen ≥20 days after birth (most pup mortality occurs within this time frame – Majluf 1987a) in a given year by the total number of marked females. If a pup was first recorded missing shortly before 20 days from its birth, at least five more days of observations were completed before concluding that the pup had died.

After the population decline in 1997-98, seals abandoned S3, which had been the primary breeding site at PSJ since the early 1980s when the population was first studied. Beginning in 1999, beach S2 became one of the most important breeding sites, and some females tagged at S3 were seen breeding at S2. To obtain information about pup survival at
PSJ after the population decline, females at beach S2 were marked before the breeding season by squirting them with hair dye using a 100 cc syringe or hitting them with a dye-filled egg (Clairol Born Blonde®) from behind a blind or natural barrier. Females with newborn pups were also marked opportunistically during the breeding season. Seals had become very skittish after the population decline, and no captures were performed. Pup mortality rate was determined using the same method as for beach S3 at PSJ in 1990-93.

**Variables Influencing Pup Mortality for Different years at PSJ**

At beach S3 in 1990-1993, behavioral observations were conducted throughout the seals' breeding season (October-December) during all daylight hours (0600-1800). Marked females and their pups were followed from day 2-3 postpartum for at least 18 days. Two observers scanned the beach (Martin and Bateson 1993) every 30 min from a blind atop the cliff (about 25 m from the rear of the colony), and recorded for each marked female on the beach her behavior (suckling, active, resting, moving, swimming, aggressive to others, copulating) and the substrate where she was located (open water, tide pool, wet rock, wet sand, dry rock, dry sand, or back beach/cliff walls). At least 68 instantaneous samples were obtained for each female, and 61,178 samples were obtained for all 186 focal females.

At beach S2 at PSJ, behavioral observations were also made from a cliff-top blind, (about 12 m from the rear of the colony) and were conducted during all daylight hours during the seals' breeding season, and into January until females were observed for at least 20 days postpartum. Seals were about 10-30 m from the observation blind. Thirty-minute focal observations (Martin and Bateson 1993) of marked females were performed daily by two observers during two 3-4 h periods, with all times equally represented. I followed 22 females for ≥20 days postpartum, obtaining 2-14 h of observation per female for a total of 237 h of
Observation. Females with low numbers of observations were included in the analysis because they lost their pups within a few days of birth and I did not want to eliminate these important individuals. I recorded a set of social and habitat variables (expanded from those examined in Majluf's study) that I expected might influence probability of a pup surviving (Table 3-1). Variables related to density, distance to features on the beach, and substrate were recorded at the start of the focal period (i.e., I did not adjust the data if the female moved during the observation period). I measured density of females by determining the mean number of females within 2 body lengths (BL) of focal females. To compare density with estimates reported in the literature I counted the number of females within a quadrat in the center of the colony where density was maximal. Area of the quadrat was estimated using $1BL = 1.5 \text{ m}$. 
Table 3-1. Variables recorded during 30-min focal observations of female fur seals (focal female = FF) with pups at Punta San Juan, Peru in 1999-2000, and at Punta Coles, Peru in 2000-2001.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date</td>
<td>30 Oct.=1, 31 Oct.=2, etc.</td>
</tr>
<tr>
<td>Pup or pup-yearling</td>
<td>Whether FF was seen suckling only a pup, or both a pup and a yearling</td>
</tr>
<tr>
<td>Substrate (Sub) rock</td>
<td>Water, sand/gravel, solid rock, or stacked ('stacked rock' was considered to be rocks providing sufficient three dimensional structure to potentially provide shade for the FF within 1 BL of FF)</td>
</tr>
<tr>
<td>Percentage of 30-min focal periods that included:</td>
<td></td>
</tr>
<tr>
<td>Aggression (Agg)</td>
<td>FF exhibits open mouth threat or bites (Miller 1975) at other seal</td>
</tr>
<tr>
<td>Movements (Move)</td>
<td>FF moves &gt;1 Body length (BL)</td>
</tr>
<tr>
<td>Approaches (App) by females</td>
<td>Other female approaches FF within 1 BL</td>
</tr>
<tr>
<td>Approaches (App) by subadult males (SA male)</td>
<td>SA male approaches FF within 1 BL</td>
</tr>
<tr>
<td>Approaches (App) by territorial males (T male)</td>
<td>Territorial male approaches FF within 1 BL</td>
</tr>
<tr>
<td>Alert</td>
<td>FF in a position in which she appeared likely to visually detect an approach (e.g., eyes open, head up)</td>
</tr>
<tr>
<td>Suckling a pup (%SP)</td>
<td>FF suckling a pup</td>
</tr>
<tr>
<td>Suckling a yearling (%SY)</td>
<td>FF suckling a yearling</td>
</tr>
<tr>
<td>Exposed to rough seas (SEA) ‡</td>
<td>Waves and/or sea spray reaching FF</td>
</tr>
<tr>
<td>Density within 2 body lengths (BL)</td>
<td>Number of heads of other females within 2 BL of the head of the FF (A female is more likely to threaten a female close to her head than close to her tail, and is more likely to threaten another female whose head is close to her head than one whose tail is close to her head.)</td>
</tr>
<tr>
<td>Distance to water</td>
<td>Distance (BL) from a FF to the sea or a tide pool</td>
</tr>
</tbody>
</table>

‡ variable recorded only at Coles
Pup Mortality Rates at Two Breeding Beaches at Coles

To compare mortality rates between beaches N9 and S12, I attempted to mark seals using the same method as used for beach S2 at PSJ. I was able to follow 31 marked females at N9 for 20 days postpartum. I was unable to mark females at S12 because the flat, open nature of the beach did not allow us to approach seals without disturbing them. At N9 I performed observations from a blind atop a cliff about 3 m from the rear of the colony. To perform observations at S12 I constructed a 4 m wooden tower with a blind about 15 m from the rear of the colony.

To estimate pup mortality rate at N9 I used the same method as described for PSJ, by following marked females. To compare pup mortality rates between N9 and S12 I used a different method of estimation because individuals could not be identified at S12. I performed daily counts of live and dead pups at beaches N9 and S12 during censuses and focal observations. Dead pups could be seen easily because of scavenging vultures (Catarthes aura), and I avoided counting pups more than once by recording their location on a map of the beach. Heavy surf did not occur at S12, so pups were not likely to be washed away. Because live pups may have been obstructed from view by other seals or contours in the topography, I used Equation 1 to estimate total pups born ($B^T$):
Equation 1. Estimation of total pups born ($B^T$).

\[ B^T = \sum (B^{\text{min}} \ldots B^{\text{max}}) \]

\[ B^{\text{min}} = (B^{\text{min-1}} + b - d + p/D) \]

where:

- $B^{\text{min}}$ = the number of births estimated to have occurred on the first date that births occurred
- $B^{\text{max}}$ = the number of births estimated to have occurred on the last date that births occurred
- $b$ = the number of births and placentas observed on day $n$
- $d$ = the total number of dead pups observed on day $n$
- $p$ = total number of pups observed on day $n$ in excess of $B^{\text{min-1}} + b - d$
- $D$ = number of days between day $n$ and the last date when $p \geq 1$

Because this method is likely to underestimate the number of pups that died at a site, I determined a correction factor for my estimate for S12. I divided percent mortality at N9 as estimated using marked individuals by percent mortality at N9 as estimated by counting pups. I multiplied this correction factor times the estimate of pup mortality for S12 to obtain a corrected estimate to compare with the estimate for N9.
Variables Influencing Survival of Pups at Coles

I used the same methods as for S2 at PSJ to determine factors important in distinguishing females whose pups survived from those whose did not at N9. Because few females were successfully marked at S12, I instead observed random females for focal observations so that social and microhabitat features of females could be compared between N9 and S12. Hours of the day observations were performed and environmental conditions were the same for N9 and S12. When no marked females were visible at N9 I observed random females. To select females to observe I divided the beaches into sections and chose females in equal numbers from each section. To select a female within the section, a coin was tossed to eliminate one half of the section until a single female was isolated.

Statistical Analyses

To determine whether pup mortality rates differed between years and sites, I used chi-square goodness-of-fit tests. To identify variables important in discriminating females whose pups survived for ≥20 days (coded 1) from females whose pups died within 20 days of birth (coded 0), I used stepwise (α to enter and remain = 0.15) logistic regression (SYSTAT® 9, Statistics I, SPSS, Inc., Chicago, IL). Because many focal observations had values of 0 for the variables Aggression, Movements, and Approaches, I calculated percentages of observations during which these variables occurred for each female instead of using mean values. I eliminated any pair of continuous variables with an $r^2 \geq 0.5$ to control for multicollinearity (Bowyer et al. 1999); and I set tolerance values at 0.001 to prevent entry of variables into the model that were highly correlated with variables already in the model (SYSTAT® 9, Statistics I, SPSS, Inc., Chicago, IL). I tested for interactions between significant variables and included any significant interactions in the final models.
For variables that were significant in the logistic models, I performed t-tests using Bonferroni corrections or chi-square goodness-of-fit tests to determine whether there were differences between N9 and S12 at Coles in 2000. To increase consistency between S12 and N9, and to maximize certainty that unmarked females used in this comparison had pups, I used only focal observations during which a female was observed suckling her pup. For cases in which there were multiple observations for a marked female, I avoided pseudoreplication by using the mean values of variables for the females. Means ± SE for females at N9 and S12 were determined using focal observations of random females and means from multiple observations of marked females. Results were considered significant at P<0.05.

RESULTS

Pup Mortality Rates at PSJ Before and After the Population Decline

For beach S2 at PSJ in 1999, pup mortality was 45% (Table 3-2). For beach S3 at PSJ in 1990-1993, pup mortality within the first 20 days of life ranged from 24.1-37.5% and differed significantly among some years (Table 3-2). Pups were least likely to die in 1992 (24.1% mortality; X^2 = 16.41, df = 3, P<0.001), followed by 1990 (29.3%; X^2 = 11.44, df = 2, P=0.003); and pups were most likely to die in 1993 and 1991 (31.4% and 37.5% respectively). Numbers of pups that died did not differ between 1991 and 1993 (X^2 = 0.128; df = 1, P=0.721). Pup mortality for S2 in 1999 was the highest of the estimates at PSJ, but was not significantly greater than for S3 in 1990-1993 (X^2 = 3.67, df = 4, P=0.452). At S2 I observed four percent of pups with apparent bite injuries, three percent washed away, and two percent killed by sea lions.
Table 3-2. Numbers and percentages of marked pups that died and survived during the first 20
days after birth at various sites and years in Peru. Values were determined by monitoring
marked females and pups (F&P), marked females only (F), by counting births and dead pups
(Counts), or using counts with a correction factor (see methods).

<table>
<thead>
<tr>
<th>Year</th>
<th>Site</th>
<th>Method</th>
<th>Died</th>
<th>Survived</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>1990</td>
<td>PSJ (S3)</td>
<td>Marked F&amp;P</td>
<td>12 (29.2%)</td>
<td>29 (70.7%)</td>
<td>41</td>
</tr>
<tr>
<td>1991</td>
<td>PSJ (S3)</td>
<td>Marked F&amp;P</td>
<td>15 (37.5%)</td>
<td>25 (62.5%)</td>
<td>40</td>
</tr>
<tr>
<td>1992</td>
<td>PSJ (S3)</td>
<td>Marked F&amp;P</td>
<td>13 (24.1%)</td>
<td>41 (75.9%)</td>
<td>54</td>
</tr>
<tr>
<td>1993</td>
<td>PSJ (S3)</td>
<td>Marked F&amp;P</td>
<td>16 (31.4%)</td>
<td>35 (68.6%)</td>
<td>51</td>
</tr>
<tr>
<td>1999</td>
<td>PSJ (S2)</td>
<td>Marked F</td>
<td>17 (45.9%)</td>
<td>20 (54.1%)</td>
<td>37</td>
</tr>
<tr>
<td>2000</td>
<td>Coles (N9)</td>
<td>Marked F</td>
<td>10 (32.3%)</td>
<td>21 (67.7)</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>Counts</td>
<td></td>
<td>18 (15.4%)</td>
<td>99 (84.6)</td>
<td>117</td>
</tr>
<tr>
<td>2000</td>
<td>Coles (S12)</td>
<td>Counts</td>
<td>22 (9.61%)</td>
<td>207 (90.4%)</td>
<td>229</td>
</tr>
<tr>
<td></td>
<td>Corrected estimate</td>
<td></td>
<td>46 (20.1%)</td>
<td>183 (79.9)</td>
<td>229</td>
</tr>
</tbody>
</table>

**Variables Influencing Pup Mortality for Different Years at PSJ**

Maximum density of females in the center of the colony at S2 in 1999 was less than
one third that of S3 in 1987-88 (0.4 females/m² vs. 1.4 females/m², Harcourt 1992). For
beach S3 at PSJ in 1990-1993, females whose pups survived spent more time suckling their
pup (Table 3-3a). Stepwise logistic regression identified two variables that discriminated
females whose pups survived from those whose did not: percent time suckling (t-ratio =
5.435, P<0.001) and year (t-ratio = 2.757, P=0.004). Variation in percent time suckling and
year of birth explained a large proportion of the variation in pup mortality (McFadden’s rho-
squared = 0.397; P<0.001); values between 0.20 and 0.40 are considered “very satisfactory” (Hensher and Johnson 1981).

Table 3-3. Time budgets (a), and percent time spent on various substrates (b) (±SE) for female fur seals whose pups died within 20 days of birth and for those whose pups survived at beach S3, PSJ in 1990-1993. Means (in bold) and standard deviations were determined using instantaneous scan sampling on individually identifiable females. Asterisks indicate variables that contributed significantly to distinguishing females whose pups survived from those whose did not in the logistic regression model.

<table>
<thead>
<tr>
<th></th>
<th>Resting (±1.26)</th>
<th>Active (±0.87)</th>
<th>Suckling (±0.23)</th>
<th>Swimming (±0.45)</th>
<th>Aggressive (±0.16)</th>
<th>Moving (±0.11)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Died</td>
<td>58.5</td>
<td>32.1</td>
<td>1.7*</td>
<td>4.1</td>
<td>1.8</td>
<td>0.9</td>
</tr>
<tr>
<td>Survived</td>
<td>57.4</td>
<td>31.4</td>
<td>5.5*</td>
<td>2.6</td>
<td>1.7</td>
<td>1.0</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Water (±1.95)</th>
<th>Pools (±0.76)</th>
<th>Sand-W (±0.45)</th>
<th>Sand-D (±2.51)</th>
<th>Rock-W (±0.91)</th>
<th>Rock-D (±2.08)</th>
<th>Back/Cliffs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Died</td>
<td>2.5</td>
<td>7.7</td>
<td>3.4</td>
<td>37.4</td>
<td>12.1</td>
<td>23.4</td>
<td>13.4</td>
</tr>
<tr>
<td>Survived</td>
<td>1.6</td>
<td>6.5</td>
<td>4.3</td>
<td>37.4</td>
<td>13.6</td>
<td>26.0</td>
<td>10.3</td>
</tr>
</tbody>
</table>

Of 37 marked females at beach S2 in 1999 for which I could determine whether her pup survived ≥20 days (Table 3-2), I had sufficient data to analyze factors influencing mortality for 22 females. Insufficient numbers of females were observed suckling to compare percentages of time spent suckling between females whose pups survived and those whose did not, but I was able to include the variable ‘pup or pup-yearling’ (Table 3-1). Twenty three percent of marked females with pups were also suckling yearlings.
Stepwise logistic regression identified two variables (distance to water, t-ratio = 2.016, P=0.044, table 3-4a; and time spent on sand/gravel, t-ratio = 2.122, P=0.034) that distinguished females whose pups survived from those whose did not (McFadden’s rho-squared = 0.422, P=0.006). Females whose pups died within 20 days were most often nearer to water than females whose pups survived (8 of 11 females whose pups died were most often <5 body lengths from water, vs. 3 of 11 females whose pups survived), and were more likely to have never been sighted on sand/gravel (9 of 11 females whose pups died vs. 4 of 11 whose pups survived). Three of the four females that were suckling both a yearling and a pup lost their pup; however, because eleven pups of focal females died, whether a female was nursing a yearling did not contribute significantly to the model predicting whether a pup would survive.
Table 3-4. Means (in bold) and standard error for variables recorded during 30-min focal observations of identifiable female fur seals at (a) beach S2, PSJ in 1999 and (b) beach N9 at Coles in 2000. The variables are defined in Table 3-1. In this table, Agg, Move, and App are percentages of observations for a female during which the variable occurred; and Sea is the percentage during which she was exposed to high seas.

<table>
<thead>
<tr>
<th>Date</th>
<th>Agg</th>
<th>Move</th>
<th>App (female)</th>
<th>App (SA male)</th>
<th>App (T male)</th>
<th>Density (2 BL)</th>
<th>Alert</th>
<th>%SP</th>
<th>%SY</th>
<th>Water</th>
<th>Sea</th>
</tr>
</thead>
<tbody>
<tr>
<td>(a)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
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<td>52.3</td>
<td>27.6</td>
<td>41.0</td>
<td>15.6</td>
<td>6.3</td>
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<td>25.4</td>
<td>3.55*</td>
<td>2.8</td>
<td>6.4</td>
</tr>
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<td>4.4</td>
<td>5.0</td>
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<td>2.3</td>
<td>0.2</td>
<td>3.7</td>
<td>0.28</td>
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</tr>
<tr>
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<td>46.4</td>
<td>27.8</td>
<td>45.9</td>
<td>11.9</td>
<td>11.8</td>
<td>2.3</td>
<td>21.4</td>
<td>4.46*</td>
<td>3.8</td>
<td>4.4</td>
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<td>0.2</td>
<td>2.5</td>
<td>0.93</td>
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<tr>
<td>(b)</td>
<td></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>56.7</td>
<td>22.4</td>
<td>22.4</td>
<td>33.1</td>
<td>7.7</td>
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<td>23.0</td>
<td>10.0*</td>
<td>15.6*</td>
<td>1.2</td>
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<td>7.1</td>
<td>5.6</td>
<td>5.6</td>
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<td>3.2</td>
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<td>4.2</td>
<td>3.7</td>
<td>0.2</td>
<td>4.5</td>
</tr>
<tr>
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<td>60.9</td>
<td>27.3</td>
<td>27.3</td>
<td>28.0</td>
<td>5.9</td>
<td>2.6</td>
<td>27.5</td>
<td>12.4*</td>
<td>5.6*</td>
<td>1.4</td>
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<td>3.4</td>
<td>3.3</td>
<td>3.3</td>
<td>3.1</td>
<td>1.3</td>
<td>0.2</td>
<td>3.4</td>
<td>1.7</td>
<td>0.2</td>
<td>1.4</td>
</tr>
</tbody>
</table>

**Mortality rates at two breeding beaches with different topographies at Coles**

Pup mortality within 20 days of birth for marked females at N9—a rugged beach comprised mainly of stacked rocks—was 32.3% (Table 3-2). My estimate of pup mortality for N9 obtained by counting births and live and dead pups throughout the breeding season was 14.4% (Table 3-2). Because this method seriously underestimated mortality, I divided 32.3% by 14.4% to obtain a correction factor of 2.24. I multiplied this factor times the estimate of pup mortality for S12 (9.6%) to obtain a corrected estimate of 20.1% (Table 3-2). My correction factor is consistent with findings by Baker (1984) that pup mortality estimates based on recovery of dead pups is about one half actual pup mortality (8.2% vs. 15.2%).
mortality was significantly greater at N9 than at S12 ($X^2 = 4.91$, df=1, $P=0.027$). At N9, I observed four percent of pups with bite injuries or obviously killed by aggression (i.e., apparently healthy pup was bitten and/or thrown by a female and the pup died immediately or shortly afterward), and at S12, two percent were observed with such injuries. One pup at N9 fell into the sea after being chased by a female, but the sea was calm at the time and the pup was able to climb back onto the beach. About 2% of pups at N9 were seen dead in a particular tide pool that was consistently used by adult seals for cooling, and had steep walls that were difficult for pups to climb. No pups were seen washed away or trapped in tide pools at S12.

**Variables influencing survival of pups at Coles**

Maximum densities at S12 and N9 were approximately 0.3 and 0.4 females/m² respectively. For my data from Coles 2000, stepwise logistic regression identified two variables that discriminated females whose pups survived from those whose did not: percent time suckling a yearling (%SY) ($t$-ratio = -2.534, $P=0.036$) and percent time suckling a pup (%SP) ($t$-ratio = 2.118, $P=0.047$; McFadden’s rho-squared = 0.332, $P<0.001$). Females whose pups died within 20 days were more likely to spend more time suckling a yearling and less time suckling a pup (Table 3-4b). Inclusion of the variable ‘exposed to rough seas’ (SEA) improved the explanatory power of the model (without SEA McFadden’s rho-squared = 0.288, $P=0.002$). The variable SEA was significant in distinguishing whether a pup survived when it was the only variable in the logistic regression model ($t$-ratio = 2.102; $P=0.036$), but not when added to the model already containing %SY and %SP ($t$-ratio = 1.241, $P=0.224$). Females whose pups survived were less often exposed to rough seas (e.g., waves or sea spray) while ashore with their pup (Table 3-4b). The fact that SEA was significant when it was the
only variable in the model, but not when added to %SY and %SP indicates that SEA is correlated with %SY and %SP; i.e., a female exposed more often to rough seas while ashore would spend less time nursing her pup and more time nursing a yearling than females exposed less often to rough seas. Fifty two percent of marked females with pups at N9 were also suckling yearlings.

Females observed with a pup at S12 during focal observations spent significantly more time suckling the pup (37.6±2.1%) than females observed with a pup at N9 (18.9±2.5%) (t=5.73, df=86, n=169, P<0.001). Time spent suckling a yearling did not differ between females observed with a pup at S12 and N9 (8.3±1.9% vs. 15.3±3.4% respectively; t=1.72, df=57, n=169, P=0.09). At S12, females were hit by waves and sea spray during fewer observations than at N9 (X²=5.28, df=1, n=169, P=0.02). Females at S12 and N9 did not differ in number of locations ≤1 BL from water (X²=1.44, df=1, n=169, P=0.23).

**DISCUSSION**

The results did not support my hypothesis that pup mortality for *A. australis* in Peru is density dependent, and subsequently reduced following the dramatic population decline associated with the 1997-98 El Niño. Density of females at PSJ in 1999 was only one third that prior to the decline, but pup mortality remained high (46% in 1999 - this study; 49% in 1987 and 31% in 1988 – P. Majluf, unpub. data; 24-35% between 1990 and 1993 – this study). The rugged topography at S2 may have been an important factor influencing high pup mortality at S2 even though population density was low (discussed below). If seals had continued to breed at S3 following the population decline, mortality rates might have been
lower following the decline. However, pup mortality was also high (20-32%) at Coles in 2000, where density of females was also low.

Further contradicting the hypothesis that pup mortality was density dependent is my finding that density was unimportant in distinguishing females whose pups died from those whose did not at both PSJ and Coles. This is contrary to Harcourt's (1992) findings that females in denser areas of the beach were more likely to lose their pup.

I did find that pup mortality is lower for a population breeding at a flat, open beach protected from heavy surf (e.g., beach S12 at Coles) than at a rugged beach characterized by stacked rocks and heavy surf (e.g., beach N9 at Coles). Pup mortality within 20 days after birth was 20.1% at S12 and 32.3% at the more rugged beach, N9. At N9, females whose pups survived spent more time suckling their pup, less time suckling a yearling, and less time in microhabitat exposed to high seas. Actual time spent suckling – not whether a female was suckling both a pup and a yearling – was important in my model. Females at the open beach experienced less high seas than females at the rugged beach. Mean time spent suckling pups and yearlings did not differ between beaches, suggesting the difference in mortality rates might be due to more pups drowning at the rugged beach. These results combined with those from PSJ suggest that at low population numbers, seals breeding in low densities at beaches with rugged topography have high pup mortality rates comparable to those for seals breeding at high densities at flat, open beaches. Perhaps pup survival is greatest for an 'optimal-density' population breeding at a flat, open beach, particularly if heat stress, predation, and human disturbance are minimal.

Variation in survival or condition of offspring can be influenced by intrinsic factors that relate to differences among individuals (e.g., age, experience, and condition) (Lunn,
Boyd, and Croxall 1994), and by external factors that relate to spatial or temporal differences (e.g., food availability, climate – Lunn et al. 1994; topography – Anderson and Harwood 1985; Gerrodette and Gilmartin 1990). For *A. australis* in Peru, female mass does not influence whether her pup survives (Majluf 1992). In *A. gazella*, two of the most important factors influencing pup survival are food availability and age of the mother (Lunn and Boyd 1993; Lunn et al. 1994). In Peru, food availability does not appear to influence variation in early pup mortality during non-El Niño years (Limberger et al. 1986, Trillmich et al. 1986, Majluf and Reyes 1989). As my study was conducted only during non-El Niño years, food availability was not likely a factor in pup mortality.

This conclusion is further supported by the lack of an association between anchovy catch and early pup mortality. For example, pup mortality was high in 1993, and lowest in 1992, but anchovy catches were the same in both years (5 million metric tons – IMARPE). In 1999 when pup mortality was greater than in 1993, anchovy catch was also greater (7 million metric tons). Food availability may have been low enough throughout the study to result in high pup mortality, but I do not have data to address this question.

In other pinnipeds, high early pup mortality has been associated with the combination of heavy surf and high density (Reiter et al. 1981), high rates of movement through the colony to and from the shore (Baker 1984), and heat stress resulting from reduced wind and breeding habitat far from water (De Villiers, D. J. and Roux, J.-P. 1992). Despite earlier reports of the importance of density dependent factors in pup mortality rates for *A. australis* in Peru (Majluf 1987a, Majluf 1992, Harcourt 1992), my study showed that pup mortality remained constant regardless of population size, suggesting that non-density dependent factors are more important especially in small populations.
Two non-density dependent factors that appear to be implicated are topographical features of the breeding site and the percentage of females suckling both a pup and a juvenile. After the population decline in Peru, fur seals abandoned some historically important breeding areas and instead selected more rugged habitat that received less human disturbance (Chapter I). In this Chapter I report that such rugged habitat results in higher pup mortality. It appears that fur seals that breed in a hot environment where they are exposed to human disturbance make trade-offs among maximizing their environment for thermoregulation, safety of pups, and avoiding disturbance.

In Peru, a female may continue suckling her offspring for up to 36 months, whereas in most other fur seals pups are weaned within their first year (Riedman 1990). This long lactation period stems from the unpredictable food supply associated with El Niño events. If females who spend more time suckling a yearling are more likely to lose their pup, then perhaps high pup mortality rates in Peru, even at low population densities, are related to a high percentage of females nursing yearlings or juveniles (which is most likely attributable to low food availability). My finding that 40-47% of females suckling both a pup and a yearling had pups die is similar to results from a study of A. galapagoensis, a species that also exhibits extended lactation especially in relation to El Niño effects. In that study, 33% of pups whose mothers continued suckling a yearling died within 30 days of birth (Trillmich 1987).

If El Niño events continue to increase in frequency and severity, availability of habitat remains constant, and human disturbance continues at present levels, prospects for the recovery of fur seal populations in Peru may be poor. On the other hand, if the amount of suitable habitat for breeding that is protected is increased, and human disturbance to breeding
areas decreased, fur seals might be less likely to select suboptimal habitat associated with high pup mortality.
CONCLUSIONS

In this study I examined how habitat features and human disturbance influenced selection and use of breeding habitat by female South American fur seals (Arctocephalus australis) in Peru, and how survival of pups was influenced by habitat features, the social environment on the beach, and female behavior. Habitat features associated with thermoregulation and avoiding human disturbance were most important to female fur seals in selecting and continuing to use a breeding beach (macrohabitat). Because of intense solar radiation in Peru, fur seals breeding there must have access to water or shade to avoid overheating. Females have various options for cooling substrates that involve trade-offs among maximizing their environment for thermoregulation, safety of pups, and avoiding disturbance. After the 1997-98 El Niño, when the fur seal population declined dramatically (72%) in Peru, seals abandoned some of their former primary breeding sites, but continued breeding at either adjacent beaches that were more rugged or on nearby offshore islands. My results suggest that at low population numbers, fur seals in Peru selected breeding beaches that minimized accessibility to humans, but where thermoregulatory behavior by mothers proved potentially dangerous to pups (e.g., giving birth at steep, rocky shorelines with heavy surf where pups could easily fall or be washed away, or have more difficulty escaping from aggressive females).

Within breeding beaches, female fur seals in my study used microhabitat characterized by stacked rocks, and to a lesser extent solid rock. This is consistent with the seals’ selection of macrohabitat characterized by stacked rocks. Females did not use
sand/gravel substrate, likely because it reaches very high temperatures at midday and is more accessible to humans. Females selected birth sites adjacent to water where tide pools among flat rocks were available, but farther from water where topography was rugged and associated with heavy surf. At the rugged beach, birth sites and thermoregulatory sites were spatially separated, leading to females at the rugged beach having higher rates of movement and pup mortality than at the flat beach. The flat and rugged beaches did not differ in population density. Because population numbers were very low, this suggests that females might select breeding sites with a minimum density, possibly to avoid harassment by males (Trillmich and Trillmich 1984; Campagna et al. 1989; Boness 1991), increase vigilance to detect predators (Terhune 1985; da Silva and Terhune 1988), or to decrease the probability of being taken by a predator (Hamilton 1971).

Pup mortality has been high (15-49%) for fur seals in Peru since the population was first studied in the early 1980s (Majluf 1987a). These high rates stemmed from pups being injured or separated from their mothers when high densities of aggressive females made movements to limited thermoregulatory sites (Majluf 1987a; Harcourt 1992; Majluf et. al. 1996). In this study I found that pup mortality remained high (20-46%) following the population decline, despite population densities one third those prior to the decline. Pup mortality was greater at rugged, rocky beaches exposed to heavy surf than at flat, open beaches with abundant tide pools. Females whose pups survived for at least 20 days spent less time exposed to heavy surf, less time nursing the pup, and more time nursing a yearling than females whose pups did not survive. High percentages (23-52%) of females continued to suckle yearlings, possibly stemming from low food availability.
In this study I have demonstrated quantitatively the negative impacts human disturbance can have on a pinniped population. To avoid human disturbance, fur seals in Peru used suboptimal habitat that was associated with high pup mortality. Use of marginal quality habitat (Eberhardt & Siniff 1977), and high pup mortality (Congdon 1997; Durant 1998) are two important indicators of poor condition of a population. Population increases are not to be expected unless survival of juveniles is quite high or if adult survival is particularly high. Pup mortality is consistently high in Peruvian A. australis, and El Niño events – which result in high mortality for all age classes due to low food availability - occur regularly (e.g., Trillmich & Ono 1991). If El Niño events and human disturbance continue at current levels, prospects for population growth in Peruvian A. australis may be poor. Information about habitats selected and avoided by seals, and about habitats that are beneficial to pup survival are important for management of the species. Such information can be used to help mitigate factors causing seals to abandon areas, and to prioritize protection of sites with respect to current and possible future population sizes.
LITERATURE CITED


July 29, 2002

Patricia Woodbury
Academic Counselor
Graduate School
Thompson Hall

RE: Animal Use by Monica Stevens

Dear Trish:

This letter is to confirm that Monica Stevens did not need to get approval from the UNH Institutional Animal Care and Use Committee (IACUC) for her thesis work involving Southern fur seals. According to Ms. Stevens and her advisor, Professor Michelle Scott, Ms. Stevens’ data collection methods did not involve direct contact with any live animals. Ms. Stevens collected data purely from observations. The UNH Policy on the Care and Use of Animals requires that UNH agents get prior approval from the IACUC when there is to be direct contact with vertebrate animals or manipulation of their environment. Accordingly, Ms. Stevens did not require IACUC approval to perform this work.

Please do not hesitate to contact either of us if you have any questions.

Sincerely,

[Signature]

Roger Wells, D.V.M.
Director
Animal Resources Office

[Signature]

Julie Simpson
Regulatory Compliance Manager
Office of Sponsored Research

cc: Monica Stevens
    Michelle Scott, Advisor
    John Litvaitis, Chair, IACUC