*J. Zool., Lond.* (2003) **260**, 145–152 © 2003 The Zoological Society of London Printed in the United Kingdom DOI:10.1017/S0952836903003583

# Influences of habitat features and human disturbance on use of breeding sites by a declining population of southern fur seals (*Arctocephalus australis*)

Monica A. Stevens[1] and Daryl J. Boness[2]

[1]Department of Zoology, University of New Hampshire, 46 College Road, Durham, NH 03824, U.S.A.
[2]Department of Conservation Biology, National Zoological Park, Smithsonian Institution, Washington, DC 20008, U.S.A.

*(Accepted 2 October 2002)*

**Abstract**

Southern fur seals *Arctocephalus australis* in Peru have declined gradually over the past decade, and declined dramatically (72%) as a result of low food availability during the severe El Niño in 1997–98. In 1999, seals abandoned some historically important breeding sites. This is particularly alarming because new sites were not colonized. Our objective was to examine how habitat features and human disturbance influenced whether sites were currently used, abandoned or apparently not used in the past by fur seals for breeding. Data were collected on 14 variables at 70 potential breeding sites at three guano reserves in Peru. Discriminant analysis revealed significant multivariate differences among sites currently used for breeding, abandoned sites and unused sites ($F = 5.97$, $P < 0.00001$), and the model classified 74% of sites correctly. Currently used sites were less likely to have human disturbance and more likely to have offshore islands, stacked rocks, tide pools and abundant shade. Separate discriminant analyses for each reserve produced similar results. Habitat associated with thermoregulation (e.g. shade or pools) may be more important to fur seals in Peru, which breed at lower latitudes and are at greater risk of overheating on land than other populations. Habitat with minimized human access may be especially important to seals in small populations in which individuals may perceive themselves as more vulnerable because of decreased vigilance and dilution effects. Seals in our study selected breeding habitat with stacked rocks, which create shade and tide pools for thermoregulation and make human access difficult; but pups might suffer higher mortality in this habitat. We hypothesize that fur seals in Peru may exhibit an Allee effect, whereby suitability of habitat varies with population abundance.

**Key words**: fur seals, *Arctocephalus australis*, breeding habitat, El Niño, population decline, Allee effect

## INTRODUCTION

Major population declines are widely understood to be a key factor in the risk of extinction (Gerber & Hilborn, 2001). In taxa such as pinnipeds, which require specific habitat for breeding on land but are constrained by adaptations for feeding at sea (Stirling, 1983), understanding the factors important to selection of breeding habitat is particularly a key issue for assessing the prospects for recovery of small populations.

Southern fur seals *Arctocephalus australis* in Peru have been exploited by humans since *c.* 2000 BC (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 poaching continues to occur (Majluf, 1987*b*; M. Araujo, pers. comm.). Between 1996 and 1998, populations declined 72% as a result of low food availability during the severe El Niño in 1997–98 (Arias-Schreiber & Rivas, 1998). As a result, *A. australis* is now classified as in danger of extinction in Peru (Decreto Supremo No. 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 & 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 shell fishermen and researchers, competition with southern seal lions *Otaria flavescens* for space or food and predation by *O. flavescens* on fur seal pups (Arias-Schreiber & Rivas, 1998).

Concurrent with the recent extreme population decline, fur seals in Peru abandoned a number of historically important breeding sites (S. Insley, P. Majluf & D. Boness, pers. obs.). Abandonment of breeding sites is particularly alarming because new breeding sites were not colonized.

Besides extirpations of fur seal colonies resulting from 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 & Portflitt, 1991; Majluf, 1991); however, previously used sites were not abandoned.

Abandonment of breeding sites also is of concern because *A. australis*, like all otariids, tend to show a high degree of breeding-site fidelity (Majluf, 1987*a*; Majluf, Riveros & Parlane, 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. Majluf, 1987*a*; Riedman, 1990).

In 1999 at Punta San Juan (PSJ), Peru, fur seals previously marked at the abandoned primary breeding site 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 because of falls (M. A. Stevens, pers. obs.). High pup mortality at low population numbers would be of particular concern for *A. australis* in Peru, who reportedly have a higher pup mortality than other populations of fur seals (15–49% during the first month of life; Majluf, 1987*a*; Harcourt, 1992) and may suffer nearly 100% pup mortality during severe El Niño events (Majluf, 1991; S. Insley, P. Majluf, D. Boness & M. Stevens, pers. obs.; c.f. Trillmich & Dellinger, 1991 for Galapagos fur seals *A. galapagoensis* with 100% pup mortality during the 1983 El Niño). Most of this high mortality (excluding El Niño years) 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, 1987*a*; 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, 1987*a*; Harcourt, 1992), has been important at one site, PSJ, where 0.2–8.3% of pups were killed by sub-adult 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, 1987*b*).

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

## METHODS

### Study areas

Our 3 study areas were protected guano reserves that contain breeding sites 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 Coles; mean sea surface temperatures were 13.9 °C for PSJ and 15.3 °C for Coles (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, Atico has 5 km and Coles has 6 km.

Annual precipitation at all 3 sites is < 10 cm (Geelan & Lewis, 1992). Breeding habitats available to *A. australis* include: flat, open beaches comprising sand and/or pebbles and stones; beaches with a single layer (i.e. not stacks) of rocks, stones and boulders; beaches with stacked rocks; rocky platforms; offshore islands. Slopes at the back of beaches range from shallow to vertical, but none of them has vegetation. The entire coasts of all 3 reserves were considered to be potential breeding areas. To divide each coastline into different potential breeding sites, boundaries were designated using geographic features that clearly separated stretches of beach (e.g. peninsulas or inlets) or seemed 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 2 decades). Sites were only reported to have been abandoned following the 1997–98 El Niño. In 1996, *A. australis* numbered 2840 at PSJ, 3796 at Atico and 6897 at Coles (Arias-Schrieber & Rivas, 1998). In 1998, population numbers had declined to 232, 754 and 2847 for the 3 reserves, respectively (Instituto del Mar de Peru [IMARPE], unpubl. data). Abandonment of breeding sites most probably 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. Our study addresses a single abandonment event that occurred and persisted after the dramatic population decline following the 1997–98 El Niño.

### Characterization of breeding sites

Between January and July 2000, 14 variables (Table 1) related to habitat and human disturbance were recorded at 70 potential fur seal breeding sites: 17 sites at PSJ (5 abandoned, 6 currently used and 6 unused); 36 at Atico (5 abandoned, 9 currently used and 22 unused); 17 at Coles (1 abandoned, 8 currently used, 8 unused). ‘Reserve’ was also included as a variable (i.e. PSJ, Atico or Coles). Many of our variables were binary either because of the nature of the variable or our inability to access beaches to perform precise measurements. It was requisite for us to select variables that could be classified from a distance because some fur seals are present at breeding beaches year round and we did not want to disturb these seals. Our variables are a comprehensive composite of factors believed to be most critical to fur seals in selecting and maintaining breeding sites.

**Table 1.** Variables recorded at 70 potential fur seal *Arctocephalus australis* breeding sites in Peru

| Variable | Units measured |
|---|---|
| Aspect of the beach (two variables): | |
| North or south facing? (north = N, NW or NE; south = S, SW or SE) | North = 1, South = 0 |
| East or west facing? (east = E, NE or SE; west = W, NW or SW) | East = 1, West = 0 |
| Lowest slope at shore | $< 10°$ or $\geq 10°$ |
| Lowest slope at rear of beach | Degrees |
| Whether human disturbance was known to have occurred at the site (e.g. by shell fishermen or researchers) | Present = 1, Absent = 0 |
| Whether offshore islands existed perpendicular to the beach: 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 | Present = 1, Absent = 0 |
| Whether various substrates were present at the shore (four variables): | |
| Sand/gravel: substrate comprised predominantly of particles the size of sand to small stones ($< 3$ cm$^3$); stones 3 cm$^3$–0.07 m$^3$ were often present, and occasionally individual rocks or boulders, but not to the extent as to change the essential open character of the substrate | Present = 1, Absent = 0 |
| A single layer of rocks, stones, and boulders: substrate comprising rocks and stones $> 0.07$ m$^3$–0.4 m$^3$ in contact with the bottom substrate and not stacked on top of each other; isolated rocks or boulders 0.4 m$^3$–7 m$^3$ that were not stacked may have been present | Present = 1, Absent = 0 |
| Stacked rocks: large, angular rocks (0.4 m$^3$–7 m$^3$) stacked on top of one another forming sheltered areas and irregular contours, sometimes interspersed with rocks and stones ($> 0.07$ m$^3$–0.4 m$^3$), and rocks $> 7$ m$^3$ | Present = 1, Absent = 0 |
| 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 ($> 7$ m$^3$) may have been present to a limited extent) | Present = 1, Absent = 0 |
| Whether opportunities for abundant shade existed | Present = 1, Absent = 0 |
| Whether tide pools were present | Present = 1, Absent = 0 |
| Whether spray from waves occurred | Present = 1, Absent = 0 |
| Whether the area was bordered on both sides by peninsulas | Present = 1, Absent = 0 |

To define substrates, Bester's (1982) definitions were modified 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), the presence or absence of various substrate types was recorded at potential breeding sites instead of categorizing entire beaches. This enabled us 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, the presence of both substrates was recorded and the shore was not just categorized 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. Whether a beach faces north or south mainly influences exposure to wind and waves, which tend to come from the south. Whether a beach faces east or west mainly influences exposure to sun.

Current and former guards and biologists who had worked at the reserves were interviewed 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 we are confident that human disturbance is at least minimal at beaches that were considered not to have human disturbance.

## Analysis

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

Whether significant interactions occurred between variables included in the model was tested using factorial ANOVA (SYSTAT® 9 Statistics I, SPSS Inc., Chicago, IL), and $\chi^2$ goodness-of-fit tests (Zar, 1984) were used to determine how interactions among variables influenced whether beaches were currently used, abandoned or apparently not used in the past.

Although DA theoretically requires explanatory variables to meet the assumptions of joint normality and equality of covariance matrices, DA is 'remarkably

**Table 2.** Canonical discriminant functions (standardized by within variances) for variables comprising discriminant analysis models that distinguish currently used breeding sites from sites abandoned or unused by *A. australis*. Four models were produced – for all three reserves (Punta San Juan, Punta Atico, and Punta Coles, Peru) combined, and for each reserve separately

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

robust to violations of assumptions in terms of error rates, as long as interactions among explanatory variables do not affect the response' (Knoke, 1982). Others have used binary variables in discriminant analysis and have produced useful predictive models (Titterington *et al.*, 1981; Vlachonikolis & Marriott, 1982; Daudin, 1986). 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. sites) in canonical space, so ellipses may not reliably reflect overlap among groups (McGarigal, Cushman & Stafford, 2000). DA was chosen 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 we believe produces the most realistic and useful model.

## RESULTS

Discriminant analysis revealed significant multivariate differences among sites 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 2). The model classified 74% of sites correctly among the three categories.

Separate discriminant analyses of PSJ, Atico and Coles included some additional variables (Table 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.

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

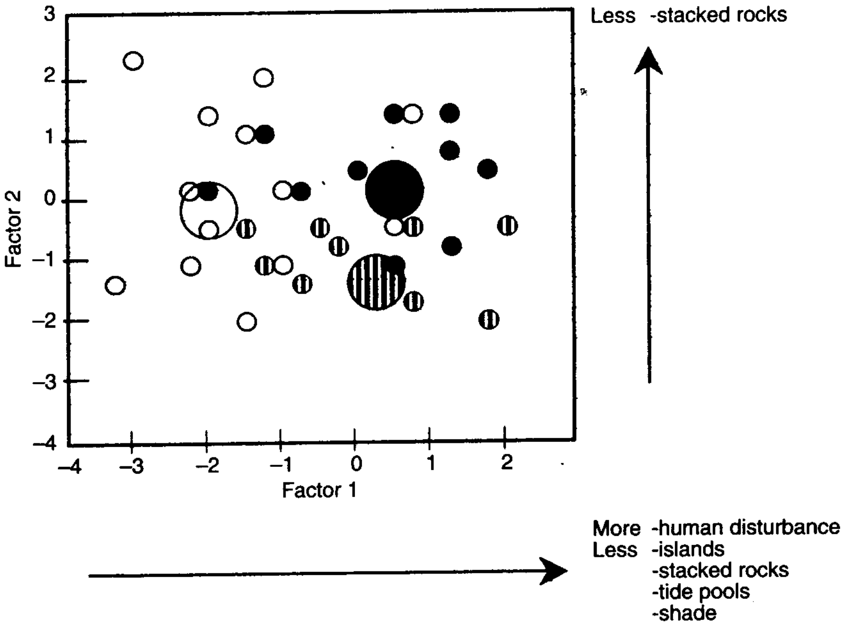

**Fig. 1.** Plots of canonical scores for all 70 potential fur seal *Arctocephalus australis* breeding sites sampled at Punta San Juan, Punta Atico and Punta Coles, Peru. Discriminant analysis revealed significant multivariate differences ($P < 0.001$) among the groups: sites currently used by fur seals for breeding (open circles); abandoned sites (striped circles); unused sites (closed circles); larger symbols indicate group means. There are fewer than 70 symbols because many sites had the same canonical score. Arrows point to variables driving the corresponding factor in that direction.

Significant interactions occurred between the presence of stacked rocks and the presence of offshore islands ($F = 4.12, P = 0.047$) and between the presence of stacked rocks and human disturbance ($F = 8.84$, $P = 0.004$). No other significant interactions occurred between any of the variables. Beaches lacking both stacked rocks and offshore islands were more likely to never have been used ($\chi^2 = 10.04$, $P = 0.007$, d.f. = 2) and less likely to be currently used ($\chi^2 = 8.30$, $P = 0.004$, d.f. = 1) than expected based on the null model. Beaches with stacked rocks and no human disturbance were more likely to be currently used than expected ($\chi^2 = 6.06$, $P = 0.049$, d.f. = 2); all beaches that had stacked rocks and were not disturbed were currently used. Beaches with human disturbance and no stacked rocks were more likely to never have been used than expected ($\chi^2 = 9.15, P = 0.01$, d.f. = 2). These significant interactions are consistent with results of the DA and do not influence interpretation of the general conclusions.

Although the variable reserve did not contribute significantly to distinguishing sites, discriminant analyses are presented for each reserve. These models also revealed significant differences among sites 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 sites correctly for Coles, 94% for PSJ and 66% for Atico. At Atico, human disturbance occurred at all potential breeding sites and was not useful for the model in distinguishing sites.

**Table 3.** Percentages of currently used, abandoned and unused fur seal *Arctocephalus australis* breeding sites that had categorical habitat and disturbance variables (Table 1) present at the site. All sampled sites ($n = 70$) from Punta San Juan, Punta Atico and Punta Coles, Peru are included. Bold, variables for which discriminant analysis revealed significant differences among currently used, abandoned and unused sites. Higher percentages of abandoned and unused sites had human disturbance. Higher percentages of currently used sites had offshore islands, abundant shade and tide pools. Lower percentages of unused sites had stacked rocks at the shore and sea spray

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

At PSJ, as in the overall model, human disturbance was associated with abandoned or unused sites, as were steep rear slopes. Offshore islands were associated with currently used sites. Stacked rocks and sea spray were more associated with abandoned than unused sites. At Atico, stacked rocks, tide pools and shade were associated with currently used and abandoned sites. Beaches bordered by peninsulas were associated with unused sites.

At Coles, offshore islands and stacked rocks were associated with currently used sites and human disturbance and north-facing beaches were associated with abandoned and unused sites.

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 sites (Table 3). As indicated by the discriminant analysis, mean shore and rear slopes do not apparently distinguish among sites. Mean rear slopes (degrees) ± SD for currently used, abandoned and unused sites 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.

## DISCUSSION

After the 1997–98 El Niño, when populations of *A. australis* in Peru declined dramatically, seals abandoned some of their former primary breeding sites, but continued breeding at adjacent beaches that were more rugged. Abandoned and unused sites were more likely to have human disturbance than currently used sites. Offshore islands were associated with currently used sites, which might also indicate avoidance of disturbance because the islands are difficult for humans to access.

Thermoregulatory features (shade, tide pools and stacked rocks, which provide shade and create tide pools) were also found to be more associated with currently used than abandoned or unused sites. *Arctocephalus* spp. that breed where they are susceptible to heat stress must select habitat features that enable them to thermoregulate. *Arctocephalus 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 & Ponce de Leon, 1987), *A. philippii* use shade from cliffs (Francis & 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 behaviourally because of their physical adaptations for fasting and foraging in cold waters (e.g. blubber and underfur) (Stirling, 1983). 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 with their mouth as they make daily movements between dry 'pup-safe' areas and the water where they go to cool.

Several habitat variables were important for distinguishing sites at one reserve, but not others. At PSJ abandoned and unused sites tended to have steeper rear slopes than currently used sites. 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 sites were less likely to be bordered by peninsulas. Such borders buffer rough seas and make beaches more accessible for shell fishermen approaching from the water (which is common at Atico). At Atico it is particularly difficult for a guard to spot intruders from above because topography is rugged at this reserve. At Coles, currently used sites were more likely to face north. North-facing beaches are the closest sites to a military base adjacent to the reserve, so avoidance of those sites was probably also a response to human disturbance.

It might have been informative for us to include a variable related to whether each beach was peripheral or central within each reserve. In other otariids (e.g. *C. ursinus*; Gentry, 1998), the total area used by a colony contracted toward the middle of the colony as the population declined. This trend, however, is not consistent with patterns of habitat abandonment in our study; breeding beaches were disjunct within reserves before the population decline, and after the decline, seals abandoned some central beaches while continuing to use more peripheral beaches.

Fur seals breeding in a hot environment where they are exposed to human disturbance must make trade-offs between maximizing their environment for thermoregulation, safety of pups and avoiding disturbance. Our results suggest that at low population levels, southern fur seals in Peru selected breeding sites where access by humans was difficult, but where thermoregulatory behaviour 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 human disturbance (Kenyon, 1972; Gerrodette & 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). Mediterranean monk seals *Monachus monachus* also now avoid exposed beaches and use only secluded caves as a result of a long history of persecution by humans (Panou, Jacobs & Panos, 1993). *Arctocephalus australis* has previously been reported to breed in macrohabitats where human disturbance was minimized (i.e. reserves and extremely remote areas (Trillmich & Majluf, 1981). Our study demonstrates the selection by *A. arctocephalus* of particular beaches within reserves with topography that is least accessible to humans.

The importance of stacked rocks in the breeding habitat of southern fur seals is unclear. Breeding sites of *A. forsteri* were found to be steeper and contain more ledges and crevices (i.e. conditions created by stacked rocks) than non-breeding sites (Ryan, Hickling & Wilson, 1997; Bradshaw *et al.*, 1999). Selection of stacked rocks by seals might reflect the dual possible advantages of this substrate; cool spaces for thermoregulation and lower accessibility to humans. A trade-off to the benefits of stacked rocks might be greater risks to newborn pups when manoeuvring on this substrate. This is supported by higher early pup mortality rates for *A. australis* breeding at a rugged, rocky beach than at a flat, open beach (32.3% *vs* 20.1%) at Coles in 2000 (Stevens, 2002). These rates are high compared with other *Arctocephalus* spp., for which early pup mortality does not generally exceed 20% (reviewed by Harcourt, 1992). Females whose pups died at PSJ and Coles following the population decline were more likely to be exposed to heavy surf (which occurs at rocky shores) and to use only stacked rocks than females whose pups survived (Stevens, 2002).

In other pinnipeds, topography of a breeding area has been shown to influence fitness or energy expenditure. Steep topography makes it difficult for northern elephant seal pups *Mirounga angustirostris* to escape high seas (Le Boeuf & Briggs, 1977). For grey seals *Halichoerus grypus*, pupping success was lower at a site 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 & 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 might be especially important to seals in small populations that might increase vigilant behaviour in an open habitat. In large groups, the vulnerability of individuals to predators is often reduced by 'the dilution effect' (e.g. Pulliam & Caraco, 1984). 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 & Terhune, 1988). Southern fur seals might have a 'breeding habitat search image' for microhabitat with three-dimensional structures that prevent direct access to them. In addition to limiting disturbance by predators or humans, such microhabitat would also limit harassment of females by male fur seals. In pinnipeds, females tend to prefer to be near other females to reduce harassment by males (Trillmich & Trillmich, 1984; Boness, 1991; Campagna *et al.*, 1992; Boness, Bowen & Iverson, 1995).

Allee suggested that habitat suitability varies with population density (Allee *et al.*, 1949; Stephens, Sutherland & Freckleton, 1999). Our results suggest that fur seals in Peru might assess habitat suitability differently at low densities. It is possible that because of 'selfish herd' or 'dilution' effects on predation/disturbance, seals find open, low-relief habitat unfavourable at low densities.

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 immature survival is quite high or adult survival is particularly high. Pup mortality is consistently high in Peruvian *A. australis*, 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 & 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.

## Acknowledgements

We are grateful to S. Insley, P. Majluf, M. Arias-Schreiber, the Instituto del Mar de Peru (IMARPE) and the Ministerio de Agricultura Proyecto Especial de Promoción del Aprovechamiento de Abonos Provenientes de Aves Marinas (PROABONOS) for generously sharing unpublished information and for logistical support that made the study possible. Permission to conduct the study was granted by PROABONOS through the assistance of IMARPE. Many thanks to O. Riofrío for assistance in the field and to S. Jara, P. Llerena, R. Paredes, D. Vega, C. Zavalaga and Sr. Benjamin for providing information about current and historical breeding sites. We thank J. Baker and S. D. Twiss for insightful comments that improved an earlier draft of this paper. M. Scott, J. Litvaitis, K. Ono and P. Bertilsson-Friedman also provided useful comments on earlier drafts. C. Neefus and J. Taylor provided advice on statistics. The study was supported by grants from the Smithsonian Institution Scholarly Studies Program, the University of New Hampshire (UNH) Center for Marine Biology, the UNH Graduate School and the UNH Department of Zoology.

## REFERENCES

Allee, W. C., Emerson, A. E., Park, O., Park, T. & Schmidt, K. P. (1949). *Principles of animal ecology.* Philadelphia: W. B. Saunders.

Anderson, S. & Harwood, J. (1985). Time budgets and topography: how energy reserves and terrain determine the breeding behaviour of grey seals. *Anim. Behav.* **33**: 1343–1348.

Arias-Schreiber, M. & Rivas, C. (1998). Distribución, tamaño y estructura de las poblaciones de lobos marinos *Arctocephalus australis y Otaria byronia* en el litoral Peruano, en Noviembre 1996 y Marzo 1997. *Inf. Prog. Inst. Mar Perú* N° 73: 17–32.

Bester, M. N. (1982). Distribution, habitat selection and colony types of the Amsterdam Island fur seal *Arctocephalus tropicalis* at Gough Island. *J. Zool. (Lond.)* **196**: 217–231.

Bonavia, D. (1982). *Los gavilanes (préceramico peruano), mar, desierto y oasis en la historia del hombre.* Lima: Editorial Ausonia. In *South American fur seal, Arctocephalus australis, in Peru.* Majluf, P. In *Status, biology, and ecology of fur seals*: 3–35. *NOAA Tech. Rep. NMFS 51.* Croxall, J. P. & Gentry, R. L. (Eds). Cambridge: National Marine Fisheries Service.

Boness, D. J. (1991). Determinants of mating systems in the Otariidae (Pinnipedia). In *The behavior of pinnipeds*: 1–44. Renouf, D. (Ed.). London: Chapman & Hall.

Boness, D. J., Bowen, W. D. & Iverson, S. J. (1995). Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? *Behav. Ecol. Sociobiol.* **36**: 1–10.

Bradshaw, C. J. A., Thompson, C. M., Davis, L. S. & Lalas, C. (1999). Pup density related to terrestrial habitat use by New Zealand fur seals. *Can. J. Zool.* **77**: 1579–1586.

Budd, G. M. (1972). Breeding of the fur seal at McDonald Islands and further population growth at Heard Island. *Mammalia* **36**: 423–427.

Campagna, C., Bisioli, C., Quintana, F., Perez, F. & Vila, A. (1992). Group breeding in sea lions: pups survive better in colonies. *Anim. Behav.* **43**: 541–548.

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

Congdon, J. D. (1997). Contributions of long-term life history studies to conservation biology. In *Principles of conservation biology*: 205–206. 2nd edn. Callicott, J. B., Carroll, C. R., Clark, T. W. *et al.* (Eds). Sunderland, MA: Sinauer.

da Silva, J. & Terhune, J. M. (1988). Harbour seal grouping as an anti-predator strategy. *Anim. Behav.* **36**: 1309–1318.

Daudin, J. J. (1986). Selection of variables in mixed-variable discriminant analysis. *Biometrics* **42**: 473–481.

Durant, S. (1998). A minimum intervention approach to conservation: the influence of social structure. In *Behavioral ecology and conservation biology*: 105–129. Caro, T. (Ed.). New York: Oxford University Press.

Eberhardt, L. L. & Siniff, D. B. (1977). Population dynamics and marine mammal management policies. *J. Fish. Res. Bd Can.* **34**: 183–190.

Francis, J. M. & Boness, D. J. (1991). The effect of thermoregulatory behavior on the mating system of the Juan Fernandez fur seal, *Arctocephalus philippi. Behaviour* **119**: 104–126.

Geelan, P. J. M. & Lewis, H. A. G. (Eds). (1992). *The Times atlas of the World*. 9th edn. London: Times Books Randomhouse.

Gentry, R. L. (1998). *Behavior and ecology of the northern fur seal*. Princeton, NJ: Princeton University Press.

Gerber, L. R. & Hilborn, R. (2001). Catastrophic events and recovery from low densities in populations of otariids: implications for risk of extinction. *Mammal Rev.* **31**: 131–150.

Gerrodette, T. & Gilmartin, W. G. (1990). Demographic consequences of changed pupping and hauling sites of the Hawaiian monk seal. *Conserv. Biol.* **4**: 423–430.

Green, R. H. (1974). Multivariate niche analysis with temporally varying environmental factors. *Ecology* **55**: 73–83.

Guerra, C., C. G. & Portflitt, K., G. (1991). El Niño effects on pinnipeds in northern Chile. In *Pinnipeds and El Niño: responses to environmental stress*: 47–54. Trillmich, F. & Ono, K. A. (Eds). New York: Springer-Verlag.

Harcourt, R. (1992). Factors affecting early mortality in the South American fur seal (*Arctocephalus australis*) in Peru: density-related effects and predation. *J. Zool. (Lond.)* **226**: 259–270.

Kenyon, K. W. (1972). Man *vs* the monk seal. *J. Mammal.* **53**: 687–696.

Knoke, J. D. (1982). Discriminant analysis with discrete and continuous variables. *Biometrics* **38**: 191–200.

Le Boeuf, B. J. & Briggs, K. T. (1977). The cost of living in a seal harem. *Mammalia* **42**: 167–195.

Limberger, D. F., Trillmich, F., Biebach, H. & Stevenson, R. D. (1986). Temperature regulation and microhabitat choice by free ranging Galapagos fur seal pups (*Arctocephalus galapagoensis*). *Oecologia (Berl.)* **69**: 53–59.

Majluf, P. (1987*a*). *Reproductive ecology of female South American fur seals at Punta San Juan, Peru.* PhD thesis. University of Cambridge.

Majluf, P. (1987*b*). South American fur seal, *Arctocephalus australis*, in Peru. In *Status, biology, and ecology of fur seals*: 33–35. *NOAA Tech. Rep. NMFS 51.* Croxall, J. P. & Gentry, R. L. (Eds). Cambridge: National Marine Fisheries Service.

Majluf, P. (1991). El Niño effects on pinnipeds in Peru. In *Pinnipeds and El Niño: responses to environmental stress*: 55–65. Trillmich, F. & Ono, K. A. (Eds). New York: Springer-Verlag.

Majluf, P., Riveros, J. C. & Parlane, S. (1996). Cool spots as 'hotspots': the evolution of lekking in the South American fur seal (*Arctocephalus australis*) in Peru: 26. In *Abstracts: International Symposium and Workshop on Otariid Reproductive Strategies and Conservation, National Zoological Park, Smithsonian Institution, Washington, DC.* Washington, DC: National Zoological Park.

McGarigal, K., Cushman, S. & Stafford, S. (2000). *Multivariate statistics for wildlife and ecology research.* New York: Springer-Verlag.

Panou, A., Jacobs, J. & Panos, D. (1993). The endangered Mediterranean monk seal *Monachus monachus* in the Ionian Sea, Greece. *Biol. Conserv* **64**: 129–140.

Peterson, R. S., Hubbs, C. L., Gentry, R. L. & DeLong, R. L. (1968). The Guadalupe fur seal: habitat, behaviour, population size, and field identification. *J. Mammal.* **49**: 665– 675.

Pulliam, H. R. & Caraco, T. (1984). Living in groups: is there an optimal group size? In *Behavioral ecology: an evolutionary approach*: 122–147. 2nd edn. Krebs, J. R. & Davies, N. B. (Eds). Oxford: Blackwell Scientific.

Riedman, M. (1990). *The pinnipeds: seals, sea lions, and walruses.* Berkley, CA: University of California Press.

Ryan, C. J., Hickling, G. J. & Wilson, K.-J. (1997). Breeding habitat preferences of the New Zealand fur seal (*Arctocephalus forsteri*) on Banks Peninsula. *Wildl. Res.* **24**: 225–235.

Stephens, P. A., Sutherland, W. J. & Freckleton, R. P. (1999). What is the Allee effect? *Oikos* **87**: 185–190.

Stevens, M. A. (2002). *Influences of social and habitat features on selection and use of breeding habitat and pup survival in South American fur seals.* PhD thesis, University of New Hampshire.

Stirling, I. (1983). The evolution of mating systems in pinnipeds. In *Recent advances in the study of mammalian behavior*: 489–527. *Special Publication, American Society of Mammalogy* No. 7. Eisenburg, J. F. & Kleiman, D. G. (Eds). Lawrence, KS: American Society of Mammologists.

Terhune, J. (1985). Scanning behavior of harbor seals on haul-out sites. *J. Mammal.* **66**: 392–395.

Titterington, D. M., Murray, G. D., Murray, L. S., Spiegelhalter, D. J., Skene, A. M., Habbema, J. D. F. & Gelpke, G. J. (1981). Comparison of discrimination techniques applied to a complex data set of head injured patients (with Discussion). *J. R. Stat. Soc.* **144**: 145–175.

Trillmich, F. & Dellinger, T. (1991). In *Pinnipeds and El Niño: responses to environmental stress*: 66–74. Trillmich, F. & Ono, K. A. (Eds). New York: Springer-Verlag.

Trillmich, F. & Majluf, P. (1981). First observations on colony structure, behavior, and vocal repertoire of the South American fur seal (*Arctocephalus australis* Zimmermann, 1783) in Peru. *Z. Saeugetierkd.* **46**: 310–322.

Trillmich, F. & Ono, K. A. (Eds). (1991). *Pinnipeds and El Niño: responses to environmental stress.* New York: Springer-Verlag.

Trillmich, F. & Trillmich, K. G. (1984). The mating systems of pinnipeds and marine iguanas: convergent evolution of polygyny. *Biol. J. Linn. Soc.* **21**: 209–216.

Twiss, S. D., Caudron, A., Pomeroy, P. P., Thomas, C. J. & Miles, J. P. (2000). Finescale topographical correlates of behavioural investment in offspring by female grey seals, *Halichoerus grypus*. *Anim. Behav.* **59**: 327–338.

Vaz-Ferreira, R. & Ponce de Leon, A. (1987). South American fur seal, *Arctocephalus australis*, in Uruguay. In *Status, biology, and ecology of fur seals*: 29–32. *NOAA Tech. Rep. NMFS 51.* Croxall, J. P. & Gentry, R. L. (Eds). Cambridge: National Marine Fisheries Service.

Vlachonikolis, I. G. & Marriott, F. H. C. (1982). Discrimination with mixed binary and continuous data. *Appl. Statist.* **31**: 23–31.

Zar, J. H. (1984). *Biostatistical analysis.* 2nd edn. Englewood Cliffs, NJ: Prentice Hall.