Marine Mammal Science

MARINE MAMMAL SCIENCE, **(*): ***–*** (*** 2011)

DOI: 10.1111/j.1748-7692.2011.00515.x

On-land habitat preferences of female New Zealand sea lions at Sandy Bay, Auckland Islands

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ABSTRACT

Terrestrial habitat is important for breeding in most pinnipeds. On land, most species remain near the shore, but New Zealand (NZ) sea lions, *Phocarctos hookeri*, often rest inland up to 1.5 km from the sea. Only three breeding areas of NZ sea lions exist today after the species was extirpated from its historical range (NZ mainland). The study was conducted at the Sandy Bay breeding colony, Auckland Islands, between December 2002 and March 2003. We used daily Global Positioning System locations of breeding females with pups and mapping in a Geographic

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Information System to determine terrestrial habitat use and preferences. Slopes less than 20° were preferred throughout the study. Females chose nursing sites with a seasonal change, preferentially based on the distance from the sea and habitat type. Comparisons with the other breeding colonies of NZ sea lions are presented and data are discussed in the context of the recolonization of the NZ mainland. Overall, the most suitable terrestrial habitat configuration for a breeding aggregation of NZ sea lions appears to be a sandy beach, with a wide area above high tide and moderate intertidal zone (for breeding), backed with vegetated sand dunes and forest on primarily flat terrain (for later dispersion).

Key words: recolonization, habitat, Auckland Islands, GIS, management, behavior, pinnipeds, *Phocarctos hookeri*, New Zealand sea lion.

Pinnipeds are marine mammals, but most species require terrestrial habitat for breeding (Bowen 1991). For pinnipeds with short lactation periods (most phocid species), the use of terrestrial habitat is short and a single habitat close to the sea is usually adequate (Boness 1991, Bowen 1991). However, many otariids nurse their pups on land between foraging trips for at least 8 mo and, consequently, pups and females spend more time on land and may use various habitat types (Jefferson *et al.* 2008). Contrary to phocids, where the females stay with the pups almost continuously during the lactation, otariid pups are left alone on land while the mothers are at sea. During this time, males of several species are known to injure or kill pups (Marlow 1975, Wilkinson *et al*. 2000, Kiyota and Okamura 2005). Young pups also have poor ability for thermoregulation and may die of overheating or cold (Thompson *et al.* 1987). Most pinnipeds show habitat preferences for sandy or rocky shores close to the water with water bodies (tidal pools, shallows, or creeks) to help with thermoregulation and provide safe swimming areas for pups (Bradshaw *et al*. 2002, Wolf *et al.* 2005). However, several individuals of various species have been reported in other habitat types such as pebble beach, bush, or forest (Eden 1955, Peterson and Bartholomew 1967, Gales *et al.* 1994, Wolf *et al.* 2005). Quantifying the use of different habitats by a species during different periods or seasons can reveal habitat preferences, and help the understanding of its behavior, and protecting it and its habitats (Festa-Blanchet and Apollonio 2003).

The New Zealand (NZ) sea lion, *P. hookeri*, is endemic to the NZ region and is classified as "vulnerable" by the International Union for Conservation of Nature (IUCN, http://www.redlist.org) and as "nationally critical" under the NZ Threat Classification System (Gales and Fletcher 1999, Baker *et al.* 2010). Before human exploitation, its historical range included most of the coastline of the NZ mainland (North and South Islands; Childerhouse and Gales 1998). Only three remnant breeding areas of the species exist, all in subantarctic islands (North Auckland Islands made of two breeding colonies: Dundas Island and Sandy Bay, Figure of Eight Island, and Campbell Island; Fig. 1; Robertson *et al.* 2006, Chilvers *et al*. 2007, DOC 2009). The total population estimate is fewer than 10,000 individuals and decreasing, likely due to a combination of low food resources, bacterial diseases, and fishing bycatch at these remnant colonies (Chilvers *et al.* 2006, Castinel *et al*. 2007, Chilvers 2008, Geschke and Chilvers 2009). Many studies have focused on marine habitat use to mitigate deaths in fishing gear, and determine competition with fishing activities (Childerhouse *et al.* 2001, Chilvers *et al.* 2005*b*, Meynier *et al.* 2009).

A prior study at the Sandy Bay breeding colony in the Auckland Islands revealed that the spatial behavior of female NZ sea lions consists of a breeding phase (December

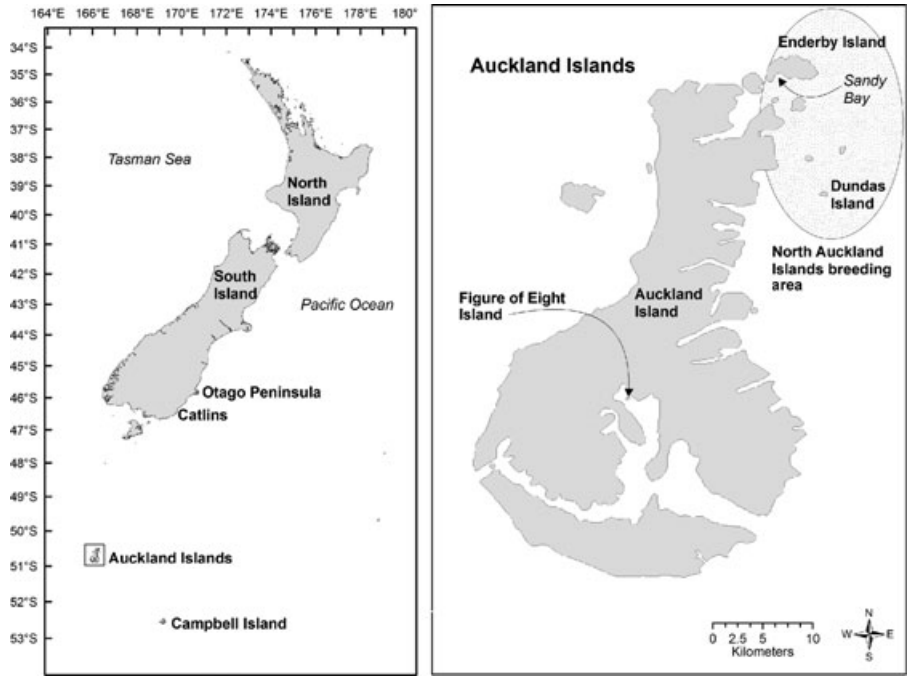

Figure 1. New Zealand sea lion breeding areas (Campbell Island, Figure of Eight Island, and North Auckland Islands), and sites being recolonized by this species (Catlins and Otago Peninsula).

to mid-January) during which females gather, give birth, and mate within a small part of the beach, followed by a dispersion phase when they move inland with their pups (Augé *et al*. 2009). Around the beginning of February, the first females start leaving Sandy Bay by taking their pups to other areas. Progressively, the number of females with pups declines and, by the end of the dispersion phase (approximately end of March), they have all swum away with their pups (Augé *et al*. 2009). The establishment of new breeding colonies of the NZ sea lion in its historical range is one of the main steps that would improve its conservation status (Baker *et al.* 2010). Consequently, further knowledge on terrestrial behavior, such as habitat preferences, may prove useful to manage the recolonization of the NZ mainland by this species.

Since the 1950s, male NZ sea lions have been sighted along the Otago coast (McConkey *et al.* 2002*a*; Fig. 1). A few females were also reported but none stayed to breed on the mainland until 1994 (Hawke 1993). A small group of female NZ sea lions, all descendants from a unique matriarch that immigrated from the Auckland Islands (Fig. 1), has now been recolonizing the historical breeding range of the species at the Otago Peninsula (McConkey *et al*. 2002*b*). However, the Otago coast has become partially urbanized and farmed and this creates a situation where interactions between humans and sea lions on land are expected to rise (Lalas 2008). The NZ fur seal, *Arctocephalus australis forsteri*, started recolonizing the NZ mainland in the 1970s and the issue of roadkills has arisen (Boren *et al.* 2008). While NZ fur seals are usually only found on rocky shores and do not often move inland, NZ

sea lions are known to use sandy beaches and to disperse inland up to 1.5 km from the sea, where the likelihood of interactions with humans is higher (McNally *et al.* 2001, Bradshaw *et al.* 2002, Augé *et al*. 2009). Because NZ sea lions are large and confident around humans, people often find them intimidating, especially when they are at unexpected places away from the sea. For instance, sea lions have been found on roads, golf courses, rugby fields, in private gardens and garages, and lavatory blocks of campgrounds.[2] Inland areas constitute an essential environment for NZ sea lions, especially for females with pups (Augé *et al.* 2009). Consequently, although the establishment of new breeding colonies is necessary for the species to recover from its threatened status (DOC 2009), this process is affected by the species' peculiar terrestrial habitat use. A better understanding of the terrestrial habitat preferences of NZ sea lions would be beneficial for wildlife officers on the mainland to manage interactions and public education.

In this study, we present the habitat use and preferences of breeding female NZ sea lions during breeding and early lactation periods at Sandy Bay, on Enderby Island in the Auckland Islands. Breeding females are the most important part of the population in a philopatric polygamous colonial species when considering recovery and extension of breeding range (Chilvers and Wilkinson 2008). Sandy Bay is one of only four sites where breeding aggregations of NZ sea lions consistently occur each year in December and January (Robertson *et al*. 2006, Maloney *et al*. 2009). The aims of this paper were to (1) model the expansion of the coastal area used by female NZ sea lions; (2) determine habitat preferences of female NZ sea lions across the breeding and early lactation periods; and (3) discuss the results in the context of the other breeding colonies of NZ sea lions and other pinnipeds, and of the implication and application of the results for the recolonization of the NZ mainland by this species.

Materials and Methods

Study Area

The study was conducted at Sandy Bay, Enderby Island (7 km^2; 50.50°S, 166.28°E), the only large sandy beach and sand dune of the Auckland Islands (Fig. 1). The Sandy Bay beach is 400 m long and is bounded by rocky shores and cliffs at each end. At mean sea level, the width of the beach was on average 34 m (24 m at high tide and up to 43 m at low tide). Behind the beach, an extensive vegetated sand dune is bordered by scrub and forest. Each year between December and the beginning of January, a breeding aggregation of NZ sea lions occurs on the sandy beach at Sandy Bay (Gales and Fletcher 1999). Approximately 400 NZ sea lion pups are born in the Sandy Bay breeding aggregation each year (Chilvers *et al.* 2007).

Fieldwork

Fieldwork took place over three seasons. From 6 December 2001 (Day 1) to 18 February 2002 (Day 74) and from 6 December 2002 (Day 1) to 21 March 2003 (Day 109), the study focused on lactating female NZ sea lions' movements. In December 2005 and January 2006, vegetation and terrain mapping were conducted. Each day

[2]Personal communication from Jim Fyfe, ranger, DOC Coastal Otago Area Office, Dunedin, New Zealand, January 2010.

Table 1. Descriptions of the habitat classes available to female New Zealand sea lions at Sandy Bay, Auckland Islands, and associated areas.

Class[a]	Description	Area[b]
Sand	Sandy beach and sandy areas with small pebbles in duneland.	22,650
Low sward	Short grassland dominated by *Rumex* spp., *Acaena sanguisorbae*, introduced European daisy, *etc*.	75,505
High sward	Grassland more than 30 cm high, including introduced pasture grass and megaherbs such as *Stilbocarpa polaris*.	156,180
Scrub	Short woody vegetation (dominated by *Myrsine divaricata* and *Hebe elliptica*), dense and limiting passage for large animals.	79,920
Forest	Southern rata forest with open ground cover (*Metrosideros umbellata*).	116,850
Water bodies	Lakes, ponds and streams.	1,992
Buildings	Huts, sheds, boardwalks.	283

[a]Rock and tussock habitats are found at Sandy Bay, but were outside the area described as available to female sea lions for analyses because they were never used and outside the Minimum Convex Polygon (MCP) of all locations.
[b]In m^2, within the MCP containing all locations of females recorded during the 2003 breeding season.

during the first two seasons, an observer with a handheld Global Positioning System (GPS) Garmin 12 (Garmin International Inc., Olathe, KS) recorded the locations where 76 individually recognizable (branded as part of a previous study; Wilkinson *et al*. 2011) females nursed their pups when they were onshore (see Augé *et al.* 2009 for more details on the location methods and sample sizes). During the third season, the study area was mapped using habitat classes as described in Taylor (1970) (see Table 1) and a satellite image of the island (panchromatic Quickbird satellite image, pixel size 65 cm). Forty Ground Control Points (GCP) and at least five sample GPS points per habitat class were collected evenly around the island using a handheld GPS GeoExplorer 3 (Trimble Navigation Ltd., Sunnyvale, CA). The terrain of the study area was mapped using GPS elevation points obtained from transects, spaced from 2 to 10 m depending on the topography with elevation points taken approximately every 3 m along each transect. In the scrub and forest areas, elevation points were, however, sparser due to dense vegetation and canopy.

Mapping Analyses

All GPS points obtained during the 2005/2006 season were differentially corrected using the Trimble-operated base station at Bluff (45°53′S, 168°17′E; 450 km from Sandy Bay). The habitat map of the study area was produced using *e*-Cognition 5.0 (object-oriented image classification, Definiens, Munich, Germany; Fig. 2). The elevation points were processed in Pathfinder Office (Trimble Navigation Ltd.). A total of 21,709 points were retrieved, with expected average horizontal and vertical maximum errors of 1.5 and 3 m, respectively. In a GIS (ArcGIS, ESRI, Redlands, CA), a Digital Terrain Model (DTM) of the study area and its extrapolated slope map were generated using an ordinary kriging technique.

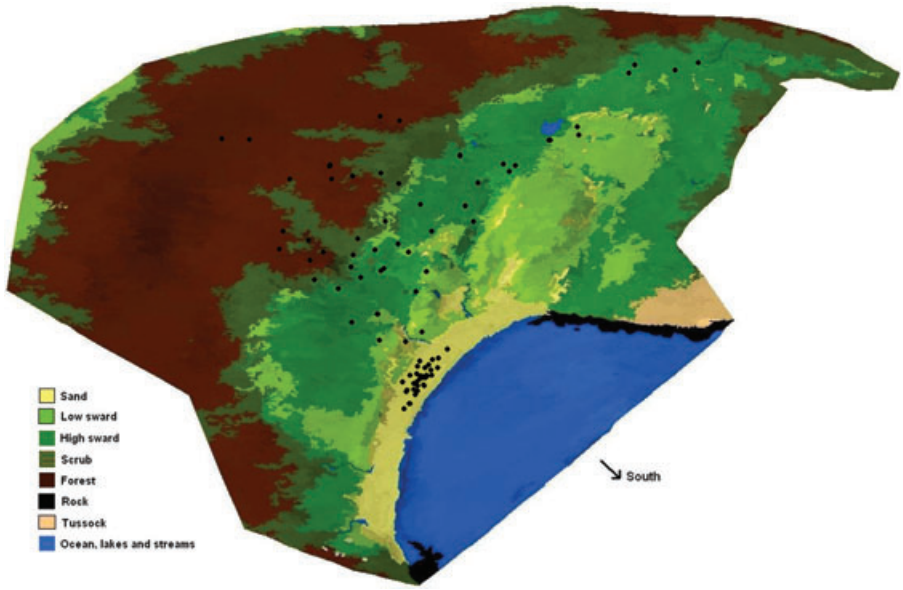

Figure 2. Map of the study area at Sandy Bay, Enderby Island, New Zealand, showing the Digital Terrain Model (in 3D, azimuth northeast at 315°, altitude 30°) overlaid with the habitat map. The black dots show examples of locations of three lactating female New Zealand sea lions from 6 December 2002 to 14 March 2003. For scale, the 3D modeling distorts distances, but the beach is 400 m long, the eastern most point of the study area is approximately 900 m from the beach and the northern most point approximately 550 m.

The DTM was used to produce the cost distance map using the function "Cost-weighted distance" of Spatial Analyst in ArcGIS. The mid-tide line was set as elevation 0 and as the zero-distance feature. The cost distances represent the minimum three-dimensional (3D) straight-line distances (*i.e.,* distances projected over slope surfaces) walked by females to reach their recorded on-land locations from the sea. The path was forced around any potential obstacles to sea lions (steep faces such as cliffs and deep gullies created by deep streams or lakes). Cost distances consequently integrate a symbolic energy cost induced by slopes and obstacles, but cannot be related to physiological data, as there are no available data on the energetic cost of walking for sea lions.

Sea Lion Movement Analyses

All female locations were integrated in ArcGIS for further analysis. Minimum Convex Polygon (MCP) analysis was applied to the females' locations to determine the increase of the cumulative area used by each female across the season at Sandy Bay (Mohr 1947). As all animals found at Sandy Bay came ashore on the beach, this method allowed including the area where females may have walked, found their pup, or rested on the way to or from the nursing site. MCPs were created incrementally for each new location using Hawth's analysis tools in ArcGIS (Beyer 2004). Any area of sea was excluded when the areas of the MCPs (MCPAs) were calculated.

Table 2. Descriptions of the classes for cost distance, slope, orientation, and distance to water bodies at Sandy Bay, Auckland Islands, and associated available areas to female New Zealand sea lions. The range of values of the different classes were delimited for their biological relevance to female New Zealand sea lions.

	Cost distance (in m)	Slope (in degrees)	Orientation	Distance to water bodies (in m)[b]
Range[a]	0–1,310	0–90	All	0–455
Classes (% of study area)	0–100	0–5	North	0–20
	4%	23%	22%	3%
	100–200	5–10	East	20–30
	3%	30%	20%	3%
	200–500	10–20	South	30–40
	11%	32%	30%	3%
	500–800	20–50	West	40–50
	19%	11%	28%	4%
	800–1,100	>50		>50
	31%	4%		87%
	>1,100			
	32%			

[a]Within the Minimum Convex Polygon containing all locations of females recorded during the 2003 breeding season (total area 453,380 m^2).
[b]Distance from inland water body, not from sea.

Regression analyses were performed in SPSS 14.0 for Windows (SPSS Inc., Chicago, IL) to determine the best-fit model for the expansion in the area used in 2003. A Pearson's correlation test was used between the predicted values of this model and the mean MCPAs calculated for the 2002 season to determine the behavioral consistency. Results are given as means ± standard deviations.

Temporal Habitat Preference Analyses

A site refers to the location where a female was recorded. Five habitat characteristics of a site were examined (descriptions and areas are presented in Table 2): habitat (from the habitat map), the symbolic cost distance to the site from the sea (from the cost distance map), slope and its orientation (or aspect, from the DTM), and distance from water bodies (from the habitat map). Each site was attributed a class for each of these characteristics. We chose these characteristics because of their potential benefits for a female at a particular site. The main disturbances of females and pups on land are weather and presence of males outside the breeding aggregation. The habitat type at a site can protect them from weather and make it more difficult for males to find them. The walking cost to reach a site may discourage male sea lions from reaching it. The orientation of a site may provide more or less sun and protection from wind. Steep slopes may be unsuitable for resting (Twiss *et al.* 2000). For thermoregulation and swimming initiation of pups especially, the proximity of water bodies may influence the use of an area (Bradshaw *et al.* 2002).

The analyses of habitat preferences were performed at the population level. The analyses followed the method described for a study design 1 in Manly *et al.* (2002). The available habitat was defined as the MCP containing all locations recorded during

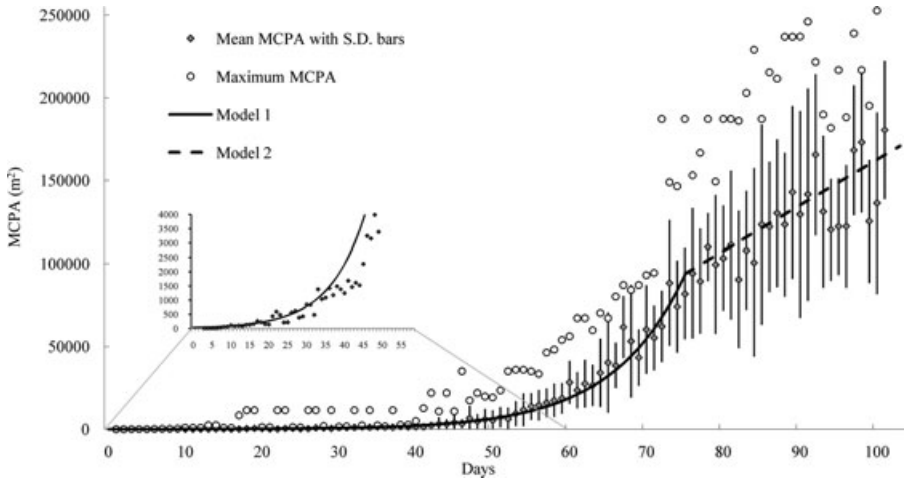

Figure 3. Best-fit models for the increase in land area (Minimum Convex Polygon Area, MCPA) used by breeding female New Zealand sea lions at Sandy Bay, Enderby Island, Auckland Islands, from 8 December (Day 3) to 21 March (Day 106).

the study but excluding the area covered by the sea from the mid-tide line (area: 0.45 km^2). Manly's standardized selection ratios, B, were calculated for each class of each characteristic (see Manly *et al*. 2002 for the calculation of this ratio). Preferences by females for the characteristics of a site were inferred statistically using log-likelihood chi-square tests for preference, encapsulated in Equation (1) (N = number of sites in class x during period t):

$$\chi^2 = 2\sum[N_{(x,t)} \log e(N_{(x,t)}/N_t \varepsilon_x)]. \quad (1)$$

The analyses of habitat preferences were conducted for periods of 5 d (to allow a large enough sample for analyses) when visual data exploration revealed a clear difference in use of the different classes across the season. In this case, results for each of the 21 periods are presented (total 106 d, the last period is for 6 d). Otherwise, chi-squares were conducted over the entire season.

Results

Expansion of the Coastal Area Used

The increase in the area used by female NZ sea lions at Sandy Bay across a breeding season from December to March was continuous until ultimate departure to other areas based on an exponential model followed by a linear model (Fig. 3). On 10 January (Day 37), the mean MCPA was 1,097 ± 561 m^2 (maximum MCPA of 2,309 m^2); by 18 February, this mean increased to 62,622 ± 19,712 m^2 (maximum MCPA of 93,161 m^2). Up to 21 February (Day 77), the extension of the area followed an exponential model of the form Area on Day $x = 23.55 \times e^{(0.106x)}$ (model 1; regression significance: df = 1, $P < 0.001$). From 22 February to 21 March

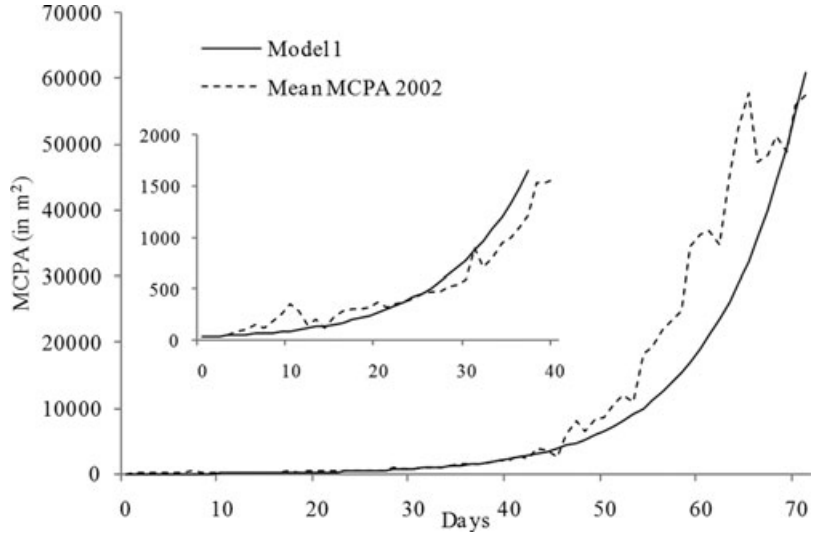

Figure 4. Comparison between the model fitted to the increase of Minimum Convex Polygon Areas (MCPAs) in 2003 and data obtained during another year (Mean MCPA 2002), from 8 December (Day 3) until 18 February (Day 74), for breeding female New Zealand sea lions at Sandy Bay, Auckland Islands.

(Day 106), the extension slowed down and followed a linear model of the form Area on Day $x = 2{,}751x - 120{,}655$ (model 2; regression significance: df $= 1$, $P < 0.001$). On the last day of the study, the mean MCPA was $185{,}756 \pm 41{,}896$ m^2 and the largest MCPA reached 246,131 m^2. The correlation test between mean MCPAs of the 2002 season and model 1 (Pearson's coefficient, $r = 0.95$; Fig. 4) showed that the dispersion model for the period Day 3–77 correctly predicted the area that a female used during another year.

Habitat Preferences

Goodness-of-fit chi-square tests showed no preference for particular classes of slope orientation (df $= 3$, $\chi^2 = 5.446$, $P = 0.142$) and no preference for the classes of distance to water bodies closer to water bodies (df $= 4$, $\chi^2 = 3.660$, $P = 0.454$). There was a constant preference for slopes less than 20° (df $= 4$, $\chi^2 = 45.637$, $P < 0.01$) while preferences for particular habitats and cost distances varied temporally. Some classes of these characteristics were significantly used only during certain periods (χ^2 for all periods, $P < 0.02$). Hence, further analyses focused on these two characteristics. Two habitat classes (water bodies, *i.e.*, lakes, ponds, and streams, and buildings) were not included in further analyses because they were never used by adult female NZ sea lions and represented less than 1.5% of the available area.

During December, lactating females selected sites exclusively on sand and within 100 m from the sea (Fig. 5). Once the breeding phase ended (median dispersion date 20 January; Augé *et al.* 2009), females preferentially used sites in high sward habitat, with a progressive preference for sites farther from the sea. From mid-March,

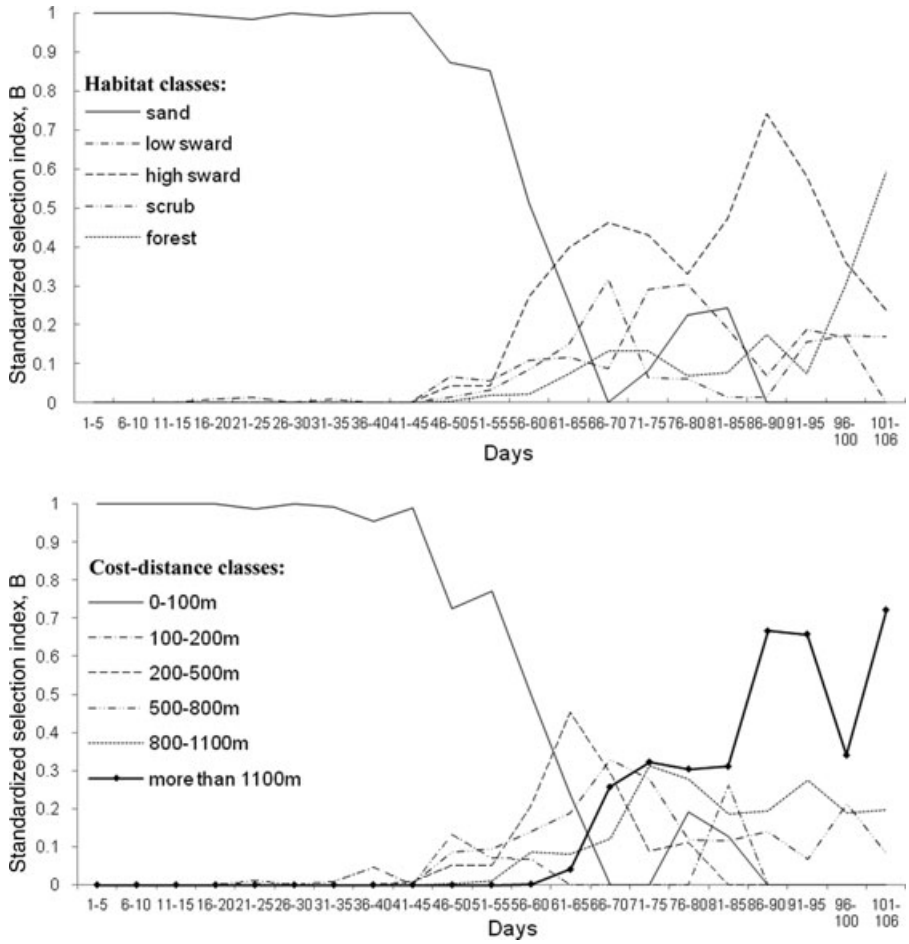

Figure 5. Standardized selection index, *B*, for habitat classes (top) and cost distance classes (bottom) showing habitat preferences of breeding female New Zealand sea lions at Sandy Bay, Auckland Islands, during periods of 5 d from 6 December 2002 (Day 1) until 21 March 2003 (Day 106).

they shifted to a preference for sites in the forest and at cost distances greater than 1,100 m from the sea. The number of sites used for these analyses decreased from 24 January (Day 50) when females started leaving Sandy Bay and taking their pups to other areas (see Augé *et al*. 2009 for details on numbers). However, selection indices were all significant (all SE < 0.12).

Discussion

Lactating female NZ sea lions at Sandy Bay, Enderby Island, exhibited a preference to reside on a sandy beach within 100 m from the sea during the breeding phase from December to the end of January. They later progressively changed preferences

from sand to sward and then forest. They always preferentially chose sites that were relatively flat. Based on spatial analyses of their locations only, female NZ sea lions choose randomly the specific locations that they used during the dispersion phase (Augé *et al.* 2009). This paper revealed that the nursing sites chosen by female NZ sea lions at Sandy Bay were preferentially used for their characteristics: slope, habitat, and distance from the sea. However, the other remnant NZ sea lion breeding colonies occur at sites with different habitat types, potentially due to the lack of preferred habitats in the subantarctic islands. Pup mortality and dispersion behavior may indicate how suitable the habitat of these breeding colonies is, compared with Sandy Bay on Enderby Island.

Does Sandy Bay Represent the Most Suitable Terrestrial Habitat for Breeding Aggregations in the Subantarctic Islands?

In the South of the Auckland Islands where no sandy beach is available, a small breeding aggregation (pup production is less than 100) occurs on a small forested island with rocky shores (Figure of Eight Island, 0.2 km^2; Chilvers *et al.* 2007). On Dundas Island (approximately 100 m across and total area of 0.1 km^2), the current largest breeding aggregation of NZ sea lions, with a pup production of approximately 1,500 pups each year, occurs on the sandy and pebble beach, but the dispersion phase (*i.e.*, inland dispersal) cannot take place due to the small size of the island (Gales and Fletcher 1999, Chilvers *et al*. 2007). Females leave this island with their young pups at the end of the breeding phase, but this move (minimum of 3.2 km straight line at sea from Dundas Island to the closest area where the pair can land on the main Auckland Island) involves high risks of hypothermia or exhaustion of pups that can lead to death (personal observation), and potential shark predation or loss of contact between the female-pup pair. Hence, the lack of space for on-land dispersal on Dundas Island makes this site less suitable than Sandy Bay for lactating females, from which females also swim with their pups to other sites but later in the season. The reason why the largest breeding aggregation currently occurs on Dundas Island is likely due to the facts that (1) it is probably the only breeding colony that escaped sealing due to its isolation, small island size, and surrounding reefs making it difficult to land on (no report was made of this island with several thousand sea lions until 1941; Childerhouse and Gales 1998) and (2) Sandy Bay may not have recovered to prehuman exploitation numbers after the population was exterminated by sealers.

Another site on Enderby Island, Pebble Point (also called South-East Point), used to produce up to 71 pups each year after an increase in the 1980s (Gales and Fletcher 1999). However, by 2010, this site was producing fewer than five pups following a progressive decline (B. L. Chilvers, unpublished data). As Gales and Fletcher (1999) hypothesized, this site appears to be suboptimal for breeding (exposed rocky shore and pebble beach) as the consistent high pup mortality indicates (mean mortality at 8 wk old: 19.9% $\pm$ 5.1% compared to 8.9% $\pm$ 2.2% at Sandy Bay for the previous 12 yr; Chilvers *et al*. 2007). Numerous breeding females usually gather at Pebble Point each year before moving to Sandy Bay or Dundas Island. Pups born at Pebble Point are likely to be from females that give birth early in the season prior to the general movement of sea lions to the main pupping sites (Gales and Fletcher 1999). In the Auckland Islands, the only other significant sandy beach apart from Sandy Bay and Dundas Island (but not backed by sand dunes and made of dark coarse sand) is

found at North Harbour. However, this beach has a broad intertidal zone of several hundred meters. Consequently, this site is likely to be unsuitable for a breeding aggregation because females would have to walk long distances to reach the safety of the breeding aggregation. It is during these movements that they are harassed by males and may be injured or killed (Chilvers *et al.* 2005*a*).

On the NZ mainland at the Otago Peninsula, the recolonizing breeding females mainly use a pine, *Pinus radiata*, plantation (a nonnative species to NZ, under which ground is mostly open) beyond a long sandy beach and small vegetated dunes (mainly covered in nonnative shrub species) to nurse and leave their pups while at sea (McConkey *et al*. 2002*b*). This corresponds to what we described in this study is the most suitable terrestrial breeding habitat for NZ sea lions. The availability of habitats influenced habitat use at the Auckland Islands where Sandy Bay is the only significant sandy beach with moderate intertidal zone and large inland area. As female NZ sea lions can adapt to introduced vegetation as shown on the Otago Peninsula, overall sandy beach and forest in relatively flat terrain consequently appear to be the preferred habitats.

Breeding Phase: Why Is a Sandy Beach Optimal?

The preference for a sandy beach habitat (*i.e.*, soft substrate) during the breeding phase of NZ sea lions at Sandy Bay limits critical injuries to pups when they are trampled by adult males. On Campbell Island at the Davis Point breeding colony, pups are born on a rock platform and have a higher death rate, than those born at Sandy Bay, mainly due to trauma (McNally *et al.* 2001, Childerhouse *et al.* 2005, Maloney *et al*. 2009). The short distance between the sea and the breeding aggregation also allows females to reduce the risk of being harassed, injured, or killed by nonterritorial males found around the breeding aggregation, by minimizing the distance they have to walk to reach the safety of the aggregation from the sea (Chilvers *et al.* 2005*a*). Similar preference for sites close to the sea was reported in most colonial pinnipeds during breeding; however, the preferred habitats where the breeding aggregations occur vary from rocky cliffs to mud flats (Bowen 1991). Edie (1977) reported that female Steller sea lions, *Eumetopias jubatus*, chose sites for pupping on a rocky habitat that had the easiest access from the sea, and were the flattest and most protected from waves. The rocky habitat used by this species does not appear to affect pup mortality as in NZ sea lions (*e.g.*, at Campbell Island; see Maloney *et al.* 2009), possibly because of different adult male behavior in the breeding aggregation, as male Steller sea lions defend large territories that are farther apart than in NZ sea lions (Robertson *et al.* 2006). Hence, territorial adult male Steller sea lions do not run into the middle of the group of females and pups, unlike adult male NZ sea lions that often trample pups (personal observation). The absence of large terrestrial carnivores that could prey on pups in NZ may allow NZ sea lions to use sandy beaches for breeding. Steller sea lions inhabit areas where such predators are abundant and their habitat use may be constrained to steep rocky isolated islands or base of rocky cliffs along the mainland to avoid predation risk. Female gray seals, *Halichoerus grypus*, choose the flattest sites of the rocky shore where the breeding colony occurs, with preference for the sites that are the closest to the sea (Twiss *et al.* 2000). The breeding system of phocids is largely different to that of otariids and rocky shore may not involve a higher risk of pup injuries than softer substrate because the mother protects the pups and adult males rarely trample pups (Bowen 1991). Female Galapagos sea lions, *Zalophus wollebaeki*,

mainly use flat sandy beaches during the breeding season, with a lower density using flat rock platforms and a preference for sites with the easiest access from the sea (Wolf *et al.* 2005). In Australian sea lions, *Neophoca cinerea*, male breeding behavior is similar to NZ sea lions and breeding occurs on sandy beaches (Gales *et al*. 1994). Overall, the habitat use of female NZ sea lions during the breeding phase is similar to that of many pinnipeds and is important for pup and female survival (Campagna and Lewis 1992, Twiss *et al*. 2000).

Dispersion Phase: Unusual Habitat Preferences and Potential Causes

During the dispersion phase later in the breeding season, female NZ sea lions progressively changed their habitat preferences to sward and forest habitat further from the sea. The dispersion phase starts when adult males depart Sandy Bay, leaving females unprotected from harassment by subadult males that sometimes kill pups (Wilkinson *et al.* 2000). Using sites far from the sea and in habitat where they can hide (*i.e.*, high sward, scrub, and forest) may limit this harassment. Preference for sites in the forest away from the coast may also reduce the effects of extreme weather, especially for pups (the forest environment is milder and less windy during cold days and shaded cooler habitat during hot days). Other variables, such as the dryness of the ground that depends on rainfall, the average air temperature or predominant winds, can vary from year to year and may also affect the choices of females for breeding sites.

Female Steller sea lions give birth and nurse their pups within 50 m of the sea, and the farthest sites from the water seemed to be the least favored (Edie 1977). No inland dispersion phase occurs in this species (Edie 1977). Both northern (*Mirounga angustirostris)* and southern (*M. leonina*) elephant seals move inland during molting and NZ fur seal pups may move away from the sea (Panagis 1985, Hatfield and Rathbun 1999, Boren *et al*. 2008). Female Australian sea lions are sometimes encountered in bush up to 100 m from the sea (Gales *et al.* 1992). Consequently, although some individual pinnipeds of various species may occasionally use bush or forest habitats and move several kilometers inland, it appears to be an individual behavior rather than a consistent preference reported at the population level as in the NZ sea lion.

Lactating female NZ sea lions exhibited a seasonal change of terrestrial habitat preferences between the breeding period (December and January) and the rest of the year, which has not been reported in any other pinnipeds. Kenyon and Rice (1961) described that during winter Steller sea lions could be found in large numbers inland from the rocky beach that they used during summer, probably as to avoid large waves and rough seas more frequent in that season. Although Wolf *et al*. (2005) described a seasonal change in habitat use in Galapagos sea lions between sandy beaches and rocky platforms, only small inland movements (mainly by adult males) were reported. The habitat use during the dispersion phase of the NZ sea lion does not mirror behaviors of other pinnipeds, even though it is likely affected by similar environmental and social causes as other pinnipeds' habitat use. Environmental differences, such as the absence of large natural terrestrial predators in NZ or the maritime climate (with unpredictable weather patterns, dramatic temperature changes, and occurrence of storms any time of the year, especially in subantarctic islands and in the South Island of NZ), may have led to the evolution of these particular habitat preferences, especially for forest habitat away from the sea, by a marine mammal.

Defining What Appears to Be the Most Suitable Breeding Habitat for NZ Sea Lions

The lack of preference by female NZ sea lions for sites closer to safe water bodies for thermoregulation contrasts with the usual reported behavior of otariids (Edie 1977, Bradshaw *et al.* 2002, Wolf *et al.* 2005). However, the Auckland Islands are in the most southern area of the historical breeding range of the NZ sea lion, with low average air temperatures (5°C–12°C) all year round, and this limits the risk of overheating. Pups are often found playing in small lakes and muddy ponds up on the sward at Sandy Bay during the dispersion phase when females chose sites nearby. In the main area of the historical range on the NZ mainland, air temperatures are higher and females may need sites with access to safe water bodies. On the Otago Peninsula, pups spend most time under a pine forest or in an inlet adjacent to the beach, often swimming in small tidal pools (personal observation).

The habitat distribution at Sandy Bay may have influenced the distances or habitats reached by females. However, forest habitat was available to females within 150 m of the sea and some females were found in high sward habitat at the greatest distances reported whereas this habitat was available within 100 m from the sea (see Fig. 2). Consequently, it is likely that a habitat configuration such as Sandy Bay offers with a significant sandy beach, with moderate intertidal zone, backed by forest habitat with open ground, and with some areas of duneland and safe inland water bodies nearby accessible to pups, represent the favored and most suitable terrestrial habitat for breeding female NZ sea lions, and hence for the occurrence of a breeding aggregation.

The main site where females currently raise their pups at Otago corresponds to the optimal terrestrial habitat configuration described here. Although females do not reach sites farther than 200 m inland at this site, it is likely due to the presence of fences limiting their movements and to the current small population size of female NZ sea lions that may not necessitate extensive dispersion (between three and six pups have been born at Otago each year since 2001; New Zealand Sea Lion Trust 2010). The few sites where archaeological remains of NZ sea lion pups were found on the NZ mainland also generally correspond to what we described here as the optimal terrestrial habitat configuration for breeding colonies (*i.e.*, large sandy beaches backed with coastal forest; see Childerhouse and Gales 1998 for exact locations).

The information contained in this paper could be used to determine where the establishment of new breeding colonies would be suitable by mapping all coastlines of the NZ mainland and identifying sites with adequate habitat and no human infrastructures such as roads or houses and to predict possible future detrimental interactions at those sites that have human influence. The modeling of the area used by female NZ sea lions where a breeding aggregation occurs, its ability to predict this area during another year, and our observations of similar spatial behavior at Sandy Bay during years following this study (from 2003 to 2011), showed that once such a breeding colony is established, the area that female NZ sea lions utilize is annually consistent for that site. However, the area that female NZ sea lions will use depends on habitat configuration of new sites. The dispersion model from Sandy Bay could be used as a proxy until particular habitat use at a new site where a colony actually establishes can be quantified. Results presented here are currently the best predictor of the most suitable habitat and what behaviors may be observed at new sites. This information can be used to develop management measures now, since waiting until breeding colonies are established on the mainland will be too late to use management practices to limit interactions with humans. A method using decoy females could

also help orientating recolonizing females that immigrate to the NZ mainland from the remnant populations to sites where interactions with humans will be limited, especially if they become resident on a part of the coastline where human presence and activities are significant (Augé and Chilvers 2010).

Like NZ sea lions, northern elephant seals and NZ fur seals are recolonizing their historical ranges. Colonies of both species reestablished at several sites where highways or railways were constructed within 15 m of the sea, causing numerous mortalities of animals, and dangers for motorists and train traffic (Hatfield and Rathbun 1999, Boren *et al*. 2008). Several males and one of the few female NZ sea lions at Otago have been killed on roads in the last decade (Lalas 2008). Contrary to elephant seals that have limited mobility on land and fur seals that usually move inland only during rough weather to avoid waves, NZ sea lions show preferences for inland habitats and use much larger areas. The cases of the northern elephant seals and NZ fur seals illustrate the importance of inland habitats for pinnipeds and why identifying potential suitable terrestrial habitats and orientating female NZ sea lions to breed at suitable sites would be beneficial for sea lions, wildlife managers, and local city councils' economies (Hatfield and Rathbun 1999, Boren *et al*. 2008). This study dealt only with the behavior of females with pups. However, male NZ sea lions also reside up to 500 m inland, especially during the breeding phase at Sandy Bay[3] and this will also need to be taken into account when considering the impacts of establishment of new breeding colonies on the NZ mainland. Overall, the results of our study, combined with possibility to orientate females to particular sites, should help predict and prevent, and at least better manage, situations where a breeding colony of NZ sea lions may establish at a site where issues such as those seen with elephant seals and fur seals will exist, and be magnified by their specific terrestrial habitat use.

In conclusion, our study quantified habitat preferences and showed that the best terrestrial habitat configuration for a breeding aggregation of NZ sea lions is a sandy beach with wide area above high tide and moderate intertidal zone, backed by vegetated sand dunes and opened ground forest on a relatively flat terrain. The preferences for inland and forest habitats exhibited by breeding female NZ sea lions outside the breeding phase will create considerable interaction between humans and sea lions on the NZ mainland, especially if a future breeding colony establishes in an area with high human presence. Detailed year-round surveys of locations where female NZ sea lions are found along the Otago coast should be ongoing to ensure that this information can complete that presented in this paper and provide management with the best knowledge of where potential breeding colonies may establish and what measures may be needed.

Acknowledgments

The authors thank the New Zealand Department of Conservation (DOC) Science and Research Unit and the University of Otago School of Surveying for funding and general support, and DOC Southland for permits and logistics support. This work was conducted under a DOC Animal Ethics committee approval (DOC AEC 86). Acknowledgments go to the Research and Enterprise Office of the Otago University for an Otago Postgraduate

[3]Unpublished data from Nathan McNally, Zoology Department, University of Otago, Dunedin, New Zealand, June 2010.

Publishing Award granted to A. A. Augé during the preparation of this paper. We thank everyone who helped during fieldwork, especially Matt Brown, Bruce Robertson, and Nathan McNally, and, in the lab, Jagannath Aryal and Justin Poole. We acknowledge Chris Muller, Simon Childerhouse, and three anonymous reviewers for helpful constructive comments on earlier versions of this paper.

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Received: 24 January 2010
Accepted: 17 May 2011