

HABITAT PREFERENCES OF CALIFORNIA SEA LIONS: IMPLICATIONS FOR CONSERVATION

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California sea lions (*Zalophus californianus*) occur along much of the Pacific coast of North America, but the number of breeding areas that are occupied is relatively small. Our understanding of the attributes that make these few sites preferable is currently limited. We quantified habitat characteristics—substrate type and coloration, aspect, slope, curvature of shoreline, and availability of shade, water pools, and resting areas—at 26 sites (7 islands) occupied by sea lions and 33 unused sites (8 islands) distributed throughout the Gulf of California, Mexico. Logistic regression models were used to explore how habitat characteristics explained sea lion occupancy patterns. Models discriminated very well between occupied and unused sites, and showed that occupied locations were more often located in sites with larger-size rocks (odds ratio [OR] = 1.209), lighter-color substrates (OR = 0.219), and convex shorelines (OR = 1.067). All of these preferred characteristics are likely to play a role in the prevention of heat stress in sea lions, suggesting that increases in temperature, such as those expected from global warming, may pose an additional risk for this already declining sea lion population. To partially offset this risk, our results may be used to identify, and protect, unused but suitable (i.e., thermally favorable) habitat. In addition, we recommend effective protection and monitoring of the currently occupied areas and their populations.

Key words: conditional logistic regression, habitat selection, pinniped, Sea of Cortes, thermoregulation

California sea lions (*Zalophus californianus*) occur along the Pacific coast of North America from British Columbia to the Baja California Peninsula and into the Gulf of California (Carretta et al. 2007), although their breeding range is restricted to areas south of the Channel Islands of California. Based on genetic differences, the species has been subdivided into 3 stocks (the United States stock, the Western Baja California stock, and the Gulf of California stock), which are managed independently in the United States and Mexico (Carretta et al. 2007; Maldonado et al. 1995). Although the United States stock has increased in recent years (Carretta et al. 2007), sea lions in the Gulf of California (hereafter, Gulf) have declined >20% in the last decade (Szteren et al. 2006). Sea lions have been exploited for subsistence and commercial purposes for centuries, and although large-scale exploitation is currently outlawed, human-induced mortality is still common in the Gulf (Bahre and Bourillón 2002). In fact, although the species is protected by the Mexican government (listed as under “Proteccion Especial,” NOM-059-ECOL-1994), management

is very limited and sea lion habitat may be threatened by pollution and unregulated tourism (Lluch-Cota et al. 2007). To ensure the population in the Gulf stock remains viable, it is important to understand sea lion habitat requirements.

The Gulf includes more than 200 islands and islets and hundreds of kilometers of coast. However, California sea lions have historically only used 13 islands as breeding colonies and 12 islands as nonbreeding or haul-out sites (Aurioles-Gamboa and Zavala-Gonzalez 1994; Szteren et al. 2006). In addition, 4 coastal areas have been identified as haul-out sites (Aurioles-Gamboa and Zavala-Gonzalez 1994). All of these haul-out and breeding areas are used year-round by sea lions. What characteristics make these particular islands or coastal areas attractive is currently not well understood. Understanding habitat preferences of California sea lions will allow identification of critical habitat and may suggest causes for local declines (i.e., those due to habitat degradation or alteration).

Anecdotal evidence suggests that sea lions prefer small and medium-sized islands (<3 km in length) with windy, rocky beaches (Aurioles-Gamboa and Zavala-Gonzalez 1994). However, no studies have quantified these habitat preferences to determine the key features of breeding and haul-out locations. In this study, we examine habitat preferences by identifying characteristics of occupied and unused sites, exploring the hypothesis that site preferences are affected by substrate

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TABLE 1.—Habitat variables recorded at each of 59 sites in the Gulf of California.

Variable	Description
Color	Rock coloration was visually estimated at each transect circle using a scale from 1 (light) to 5 (dark).
Curve	Curvature of a site measured as the angle formed by the waterline and an imaginary straight line traced between the water boundaries of the sites (measured in degrees with a compass). A negative value indicates a concave curvature (baylike) and a positive value indicates a convex curvature (peninsulalike).
East	Eastness is the sine of the aspect (measured in degrees with a compass). Values close to 1 indicate an east-facing orientation, whereas values closer to -1 represent west-facing aspects.
North	Northness is the cosine of the aspect (measured in degrees with a compass). Values close to 1 indicate a northward orientation, whereas values closer to -1 represent southward aspects.
Pool	Number of water pools >50 cm ² found partly or completely inside the circles defined along transects.
Rest	Percentage of the substrate visually classified as available resting surface for a sea lion. Resting surfaces were defined as flat, even areas that could accommodate a sea lion lying down.
Subst	Substrate type was visually estimated as the percentage of ground covered by each of 5 substrate classes (grain size): sand (0–2 mm), pebble (0.2–10 cm), cobble (10–50 cm), large rock (50–200 cm), and boulder (>2 m). A single value was then calculated as: Subst = 1 · sand + 2 · pebble + 3 · cobble + 4 · large rock + 5 · boulder.
Shade	Availability of shade was indirectly estimated as the percentage of the terrestrial site boundaries that were formed by high cliffs and large boulders, which could provide shade to the site.
Slope	Slope of the terrain measured in a straight line toward the waterline using an inclinometer.

composition and favorable thermal and pup-protection characteristics, which are features known to influence site quality in other pinnipeds (Ban and Trites 2007; Stevens and Boness 2003; Wolf et al. 2005). Although an important variable for other species, risk of predation was not explicitly evaluated in this study because both terrestrial (e.g., coyotes) and aquatic predators (e.g., killer whales) are relatively rare in the Gulf (Breese and Tershy 1993; Forney and Wade 2006). Similarly, proximity to foraging areas affects habitat selection in many species (e.g., Suryan and Harvey 1998) but was not considered in this study. Data on prey abundance and distribution in the Gulf are not currently available, and are logistically very difficult to gather because sea lions forage on numerous prey species and often at sites several kilometers away from their terrestrial habitat (Antonelis et al. 1990; Garcia-Rodriguez and Auriolos-Gamboa 2004). We recorded data on 9 habitat characteristics (Table 1) at 26 sites occupied by sea lions (located on 7 islands) and 33 unused sites (on 8 islands) distributed along the Gulf (Fig. 1). We used logistic regression models to explore how these characteristics explained sea lion occupancy. Our results shed light on local-scale habitat preferences of sea lions and have implications for identifying critical habitat and for the management for this population.

MATERIALS AND METHODS

Sampling and description of variables.—During June, July, and August of 2005–2007 we visited a total of 15 islands (Fig. 1). Seven of these islands are documented sea lion breeding colonies and haul-out areas (Auriolos-Gamboa and Zavala-Gonzalez 1994; Szyren et al. 2006) that were selected to represent the broad latitudinal gradient of sea lion colonies in the Gulf. The remaining 8 islands represented locations not used by sea lions, as determined from historical records and direct observation. At each island we identified sampling sites: sections of coastline with distinct boundaries (e.g., rock peninsulas, inlets, or steep cliffs). A range of 1–9 sites were sampled at each island (depending on the island's size) for

a total of 59 sites: 26 occupied and 33 unused. Sites within an island were selected randomly from those accessible to researchers by boat or land. We only sampled islands because sea lions rarely occupy mainland coastal areas in the Gulf (Auriolos-Gamboa and Zavala-Gonzalez 1994).

Sampled unused islands were generally located in the vicinity of the occupied islands to control for additional regional environmental variability that could not be directly measured in this study (e.g., proximity to foraging grounds). However, in some cases (e.g., the northernmost occupied island on Fig. 1) there were no neighboring islands (within 60 km) that could be sampled. Therefore, we created a subset of our data set that included 5 clusters representing a total of 39 sites (25 unused sites and 14 occupied sites; Fig. 1). Each cluster included only occupied and unused sites located in very close spatial proximity to each other (<3 km), such that sites within a cluster presumably shared the same regional environmental characteristics. For example, sea lions have an average foraging distance of 54.2 km (Antonelis et al. 1990); thus, sites separated by <3 km are likely to be perceived by sea lions as equidistant to foraging grounds that may be located >50 km away. Results from the cluster data set were compared with those from the complete data set (see “*Data analysis*” sections).

Upon arrival at a sampling site, we conducted a survey to determine sea lion presence and then recorded the habitat variables described in Table 1. All variables measured were predicted a priori to affect site quality for sea lions. For example, pup deaths due to wave action are not uncommon in other sea lion species (Ban and Trites 2007), thus, sea lions may generally avoid areas exposed to open ocean currents and favor more concave shorelines (Curve). The need for behavioral thermoregulation also has been shown to influence site choice in pinnipeds (Heath 1989; Stevens and Boness 2003; Twiss et al. 2000) and other mammals (Cain et al. 2006; Hill 2006). Summer air temperatures in the Gulf exceed those at which sea lions can regulate body temperature physiologically (Whittow et al. 1975). Therefore, we predicted that sea lions would choose thermally favorable environments, such as

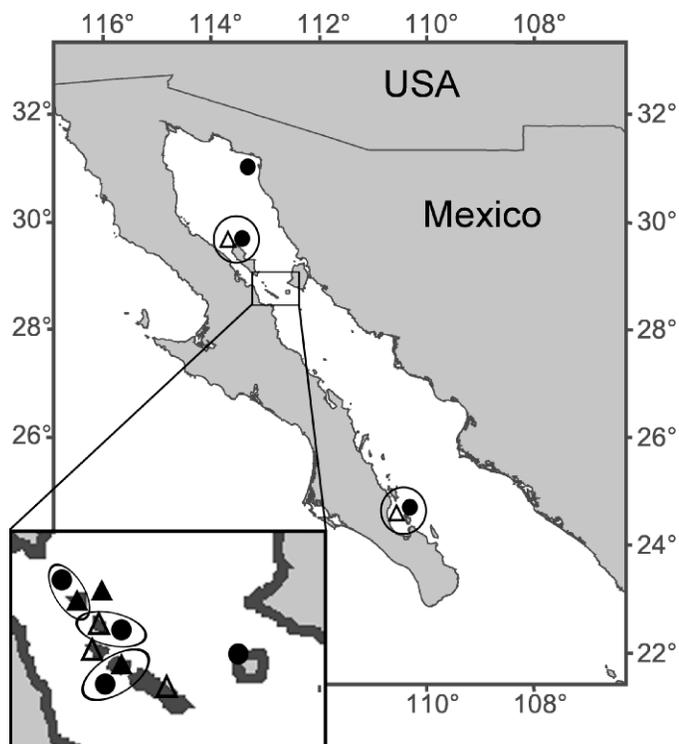


FIG. 1.—Map of the Gulf of California, Mexico. Closed circles represent sampled islands with sea lion colonies or haul-out sites and triangles (open and closed) identify sampled unused islands. Our model predicted that some unused sites could be suitable habitat for sea lions (see “Results”), these sites are located on islands identified by closed triangles; open triangles represent the remaining unused islands. The 5 clusters defined for the cluster data-set analysis (see “Materials and Methods”) also are illustrated.

those with abundant shade (Shade), numerous water pools (Pool), gentle slopes (Slope) that facilitate access to water, and lighter-colored substrates (Color—Redman et al. 2001; Twiss et al. 2000; Wolf et al. 2005). In addition, the orientation or aspect of a site has been suggested to affect sea lion distribution (Auriolos-Gamboa 1988). Aspect was measured at each site and transformed into northness (North) and eastness (East) to reflect the fact that values close to 0° and 360° represent similar orientation (see Table 1 for transformations). Finally, substrate type (Subst) and resting area (Rest) gave a quantitative general description of substrate size and site morphology. Site and substrate morphology influence habitat preferences in other pinnipeds (e.g., Montgomery et al. 2007).

The variables Curve, East, North, and Shade were recorded only once at each site. The remaining variables were recorded in transects run parallel to the shoreline at 10-m intervals. Variables were measured inside circles (diameter = 4 m) defined every 9 m along these transects (see Fig. 2 for a schematic of this sampling approach). Sites varied in their length and width, and thus the number of transects (and circles per transect) varied across sites. For our analysis we used the mean value per site for variables recorded in transects. In addition, we recorded surface temperature of 9 sets of rocks at 1 of the sites sampled (San Jorge Island, northernmost point in Fig. 1). Each rock set contained 5 similarly

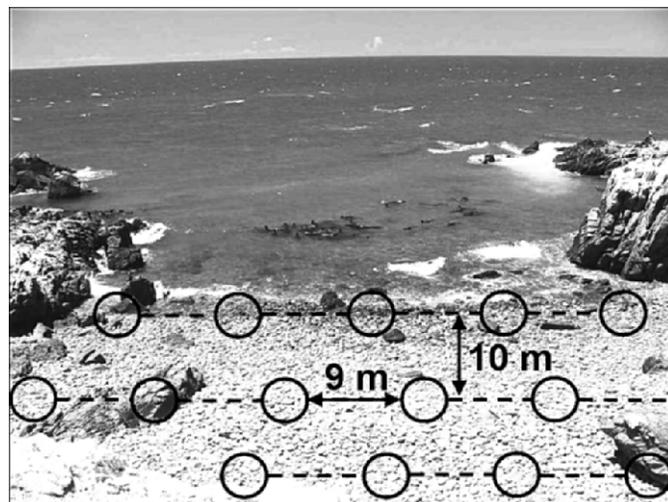


FIG. 2.—Schematic of the sampling approach used at each site. Dotted lines indicate transects and their sampling circles (diameter = 4 m). The number of transects and circles within transects vary at each site to reflect differences in sizes among sites. The photograph is of an occupied site with concave curvature (Curve), mostly lightly colored substrate (Color), and a prevalence of cobbles and boulders (Subst). The site is located on San Jorge Island (31°01'N, 113°15'S).

shaped, cobble-size rocks each representing 1 of the color rank values (see Table 1). Sets were arranged in a flat surface such that all rocks receive the same amount of solar radiation. After 1–2 h of direct sun exposure we recorded surface temperature in the center of each rock using a handheld laser thermometer (Cen-Tech; Harbor Freight Tools, Camarillo, Texas).

All sampling procedures were approved by the Arizona State University Animal Care and Use Committee (protocol 07-918R) and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Data were not collected when tides were at their highest or lowest level. To minimize disturbance of sea lions at occupied sites we limited our sampling to 20–30 min per site. Because sites were only briefly visited at different times during the reproductive season (between June and August) population densities at occupied sites could not be accurately estimated. For example, the peak of births occurs during mid- to late June (Garcia-Aguilar and Auriolos-Gamboa 2003); therefore, counts conducted during early June can underestimate the pup production at a site. Similarly, females generally embark on longer feeding trips as the end of the reproductive season approaches (Garcia-Aguilar and Auriolos-Gamboa 2003). Therefore, counts made in August may underestimate female density. Consequently, for the present study we used only presence–absence data.

Data analysis: complete data set.—Initially, the correlation among variables was explored using Kendall’s tau statistics, in order to eliminate highly correlated variables ($\tau > 0.4$). We used the LOGIT procedure in R 2.4.1 (R Development Core Team 2008) to develop logistic regression models that predicted sea lion occupancy based on habitat characteristics (Hosmer and Lemeshow 2000). The best-fitting model was selected using an information-theoretic approach (Burnham

TABLE 2.—Kendall's tau correlations among 9 variables recorded at 59 sites in the Gulf of California. Variables are described in Table 1.

Variable	Color	Curve	East	North	Pool	Rest	Subst	Shade	Slope
Color	1.00	0.03	-0.01	0.10	0.13	-0.15	0.30*	0.09	0.08
Curve		1.00	0.03	-0.11	0.00	0.05	0.08	0.03	0.05
East			1.00	0.10	0.03	-0.02	-0.03	-0.03	-0.04
North				1.00	-0.02	0.11	0.01	-0.05	0.14
Pool					1.00	-0.37*	0.52*	0.21	-0.04
Rest						1.00	-0.59*	-0.46*	-0.16
Subst							1.00	0.37*	0.23
Shade								1.00	0.18
Slope									1.00

* Significant correlation (at a nominal level of $P < 0.05$) after Bonferroni correction for multiple tests.

and Anderson 2002). This approach requires the development of a set of plausible candidate models based on a priori predictions. In this study, all recorded variables were hypothesized a priori to affect sea lion occupancy (see previous section), so all potential models resulting from linear combinations of uncorrelated variables were considered. No interactions among variables were included. As suggested by Burnham and Anderson (2002) we only explored models in which the number of parameters (k) did not exceed $n/10$, where n is sample size. This allowed exploring models with 6 or fewer parameters only ($n = 59$). To aid in model selection we used Akaike's information criterion corrected for small sample sizes (AIC_c), the difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), and AIC_c weight (w_i). The model with the lowest AIC_c and those with $\Delta AIC_c < 2$ were considered to be supported. In addition, the relative variable importance of predictor variable j (w_j) was determined as the sum of the w_i across all models where j occurs. Larger w_j values indicate a higher relative importance of variable j compared to other variables (Burnham and Anderson 2002). We also estimated the odds ratio (OR) and its 95% confidence interval (95% CI) for all variables considered (Hosmer and Lemeshow 2000). In particular, ORs were estimated as $OR_j = \exp(c\hat{\beta}_j)$, where $\hat{\beta}_j$ is the average coefficient and c is the change in units to be considered. We consider $c = 1$ for all variables except for substrate size (Subst) for which we considered $c = 10$ to reflect the wider range of values this variable could take (range = 0–500). $\hat{\beta}_j = \sum_{i=1}^R w_i \beta_{j,i}$, where $\beta_{j,i}$ is the coefficient of variable j in model i , and w_i is the model weight (Burnham and Anderson 2002). The 95% CI of OR was estimated as $95\% CI = \exp(c\hat{\beta}_j \pm cz_{1-\alpha/2} SE\hat{\beta}_j)$, where $SE\hat{\beta}_j$ is the unconditional standard error for $\hat{\beta}_j$. $SE\hat{\beta}_j = \sqrt{\sum_{i=1}^R w_i SE(\beta_{j,i}) + (\beta_{j,i} - \hat{\beta}_j)^2}$, where $SE(\beta_{j,i})$ is the standard error of variable j in model i (Burnham and Anderson 2002).

Finally, we explored the discriminative ability of the selected model(s) using the nonparametric estimate of the area under the curve (AUC) of receiver-operating characteristic plots (Hosmer and Lemeshow 2000). AUC indices range from 0.5 to 1, with ranges from 0.5 to 0.7 indicating poor discrimination, from 0.7 to 0.8 acceptable discrimination, from 0.8 to 0.9 excellent discrimination, and > 0.9 outstanding discrimination. In addition, we used the selected model(s) to calculate predicted sea lion occupancy, and compared predictions to observed values. This

allowed us to identify unused locations that appear to be suitable habitat for sea lions.

Data analysis: cluster data set.—The cluster subset described above was used to develop conditional logistic regression models. Conditional logistic regressions were used to predict sea lion occupancy based on habitat characteristics while controlling for additional environmental variability that could not be measured in this study and could confound our results (Hosmer and Lemeshow 2000). Conditional logistic regression is analogous to a paired t -test in which occupied locations are grouped with unused sites in close proximity, thus controlling for group effects and confounding variables. This method is frequently used in medical case-control studies but also has been applied to studies of habitat selection (e.g., Bakker and Hastings 2002). Conditional logistic regression models were implemented using the PROC PHREG command in SAS (version 9.1; SAS Institute Inc., Cary, North Carolina). We explored all possible linear combinations of the same variables used in the logistic models. However, because the cluster data set only included 39 sites only models with 4 or fewer parameters were explored (Burnham and Anderson 2002). The selected models and variable weights (w_j) obtained from both data sets were compared to determine if confounding variables affected the results.

RESULTS

Variable selection and rock surface temperature.—Four variables, generally related to site morphology, were strongly and significantly correlated (Table 2). In particular, substrates (Subst) with larger rocks were associated with reduced resting surfaces (Rest), more water pools (Pool), and greater availability of shade (Shade; Table 2). To avoid collinearity issues in our models the analyses were focused on Subst, which most generally reflects site morphology among the correlated variables. Darker substrates (Color) also were significantly associated with larger rock sizes (Subst) but the correlation was weak (tau = 0.30; Table 2), and thus both variables were considered. Therefore, logistic models included the variables Color, Curve, East, North, Subst, and Slope. The linear combination of these variables generated 64 possible models (including the null model) that were compared using an information-theoretic approach.

TABLE 3.—Selection results from logistic regression models investigating the effects of habitat characteristics on sea lion occupancy. For the top 10 models, we report the number of parameters (*k*), the small sample-size-adjusted Akaike’s information criteria (AIC_c), the difference in AIC_c between each model and the model with the lowest AIC_c (ΔAIC_c), and the AIC_c weight (w_i). Variables are described in Table 1.

Model						<i>k</i>	AIC_c	ΔAIC_c	w_i
Color	Curve	East	North	Subst	Slope				
×	×			×		4	56.865	0.000	0.329
×	×			×	×	5	58.366	1.501	0.155
×	×		×	×		5	58.368	1.503	0.155
×	×	×		×		5	59.017	2.152	0.112
×	×		×	×	×	6	59.847	2.983	0.074
×	×	×	×	×		6	60.566	3.702	0.052
×	×	×		×	×	6	60.717	3.853	0.048
×				×		3	62.074	5.210	0.024
×				×	×	4	63.784	6.919	0.010
×			×	×		4	63.945	7.080	0.010

Surface temperature significantly differed among rocks of different colors (analysis of variance, $F = 2.67$, $df = 44$, $P = 0.046$), with lighter rocks (color 1) remaining $>4.5^\circ\text{C}$ cooler than darker rocks (color 5). The mean temperature ($\pm SD$) for each color rank was: color 1 = 36.93 ± 2.37 , color 2 = 37.99 ± 2.85 , color 3 = 38.77 ± 3.47 , color 4 = 39.95 ± 3.69 , and color 5 = 41.57 ± 3.82 .

Complete data-set analysis.—Three models were supported by the data ($\Delta AIC_c < 2$; Table 3). In these top models, the variables Color, Curve, and Subst were always present, North and Slope were included in 1 of the top models, and East was not included in any of the 3 models. The relative importance of these variables also was reflected in the variable weights. Three variables (Subst, Color, and Curve) had strong weights, whereas the remaining variables (North, Slope, and East) had relatively low weights (Table 4). The ORs (Table 4) indicate that the probability of occupancy was 20.9% greater with a 10-unit increase in substrate size (Subst), was 21.9% lower with a 1-unit increase in coloration (Color), and 6.7% greater with a 1-unit increase in curvatures (Curve). The ORs also suggest that occupied sites had more southeastern aspects (North and East) and flatter slopes (Slope) than unused sites (Table 4). However, the 95% CIs for these variables overlap widely with 1, revealing high levels of uncertainty in these patterns (Table 4).

The discriminating ability of the top models was excellent. The top model had an AUC = 0.867 ($P < 0.0001$), 2nd model AUC = 0.864 ($P < 0.0001$), and 3rd model AUC = 0.882 ($P < 0.0001$). Predictions from all 3 top models correctly classified 73% of the used sites and 88% of the unused sites. Four unused sites located in 3 islands were identified as suitable sea lion habitat (Fig. 1).

Cluster data-set analysis.—For this data set we consider only models with 4 or fewer parameters, which resulted in 42 possible models (including a null model). This best-supported model included the same variables as the top model supported by the complete data set: Color, Curve, and Subst ($w_i = 0.541$). The 2nd model (2nd lowest AIC_c) included Color and Subst but was only weakly supported ($\Delta AIC_c = 3.933$, $w_i = 0.140$). The relative importance of the variables based on the variable weights was similar to that revealed by the complete data set.

The most important variables were Subst ($w_j = 0.921$), Color ($w_j = 0.780$), and Curve ($w_j = 0.669$). The remaining 3 variables had very low weights (Slope [$w_j = 0.171$], North [$w_j = 0.134$], and East [$w_j = 0.090$]).

DISCUSSION

The best-supported logistic regression models allowed excellent discrimination between occupied and unused sites, suggesting that habitat characteristics can predict sea lion site occupancy in the Gulf. The high variable weights and the ORs of Subst, Color, and Curve indicate that sea lions prefer habitats characterized by larger-size rocks, lighter substrates, and generally convex shorelines (Table 4). These preferences were detected using both the complete and the cluster data sets, suggesting that unexplored environmental variability did not affect our results. In fact, although the conditional logistic regression analysis apparently suggested stronger support for the top model, this difference was the result of the reduced number of models that were run in this analysis. Models with >4 parameters were not explored using the conditional logistic regression because of the smaller sample size of the cluster data set. However, in the complete data-set analysis several models with 5 and 6 parameters had relatively low AIC_c values (Table 2). When these models were not considered in the complete data-set analysis, the top model (with Subst,

TABLE 4.—Variable weight (w_j), average model coefficient ($\hat{\beta}$) with average standard error ($SE(\hat{\beta})$), odds ratio (OR), and the OR 95% confidence interval (95% CI) for all 6 explored variables. Variables are described in Table 1.

Variables	w_j	$\hat{\beta}$	$SE(\hat{\beta})$	OR	OR 95% CI
Subst	1.000	0.019	0.005	1.209 ^a	1.090–1.350
Color	0.989	−1.520	0.532	0.219 ^b	0.075–0.635
Curve	0.934	0.065	0.038	1.067 ^b	0.989–1.151
North	0.302	−0.507	0.510	0.602 ^b	0.217–1.677
Slope	0.299	−0.087	0.092	0.917 ^b	0.763–1.103
East	0.230	0.252	0.545	1.287 ^b	0.431–3.842

^a Change in probability of use with 10-unit increase.

^b Change in probability of use with 1-unit increase.

Color, and Curve) also was very strongly supported (results not shown). Therefore, we found no evidence that our results were affected by confounding factors, such as proximity to foraging grounds. Instead, our results provide strong evidence that sea lions prefer larger-sized rocks, lighter substrates, and convex shorelines.

The apparent preference for larger-sized rocks, lighter substrates, and convex shorelines likely reflects the benefits they provide to sea lions, such as the opportunity to avoid heat stress using behavioral thermoregulation (Stevens and Boness 2003; Twiss et al. 2000). Sea lions are sensitive to air temperature and direct solar radiation as a result of their thick layers of bubbler and fur (Peterson and Bartholomew 1967). Sea lions inhabiting the Gulf experience air temperatures $>30^{\circ}\text{C}$ during the breeding season. Because sea lions are unable to regulate body temperature physiologically at these temperatures, they must use behavioral mechanisms of thermoregulation to avoid thermal stress (Whittow et al. 1975). Light-colored substrates (Color) remained up to 4.5°C cooler than dark substrates when exposed to direct solar radiation, potentially transferring less heat to sea lions resting on these substrates. Larger-size rocks (Subst) also may play a role in thermoregulation by creating crevices that provide shade, particularly to pups (Auriolles-Gamboa and Zavala-Gonzalez 1994; Bradshaw et al. 1999). A preference for larger rocks also has been reported for other pinnipeds (Ban and Trites 2007; Montgomery et al. 2007; Stevens and Boness 2003). In addition, convex sites (Curve) provide easier access to water than concave sites, because convex sites (peninsulalike) are mostly surrounded by water. Sea lions must access the water to forage and thermoregulate, and therefore they may favor sites with easier access. Interestingly, we initially expected a preference for concave shorelines because in other species exposure to wave action is associated with pup mortality (Ban and Trites 2007). The Gulf is sheltered from long-range swells and oceanic waves by the Baja California peninsula, and thus has a relatively calm wave environment. This calm environment makes wave-associated mortality in pups uncommon in this area (M. González-Suárez, pers. obs.), whereas the need to access water to cool down may be critical during hot summer months in the Gulf. The importance of thermoregulation also was reflected in 2 other variables recorded: shade availability (Shade) and number of water pools (Pool). Abundance of water pools and shade have been shown to aid in thermoregulation in other pinniped species (Twiss et al. 2000; Wolf et al. 2005). Although these variables were not included in the explored logistic models because of their strong correlation with substrate type (Subst; Table 2), occupied sites had generally greater shade availability (mean \pm *SD* of occupied sites: 49.81 ± 38.61 , unused sites: 19.15 ± 19.89) and a greater number of water pools (mean \pm *SD* of occupied sites: 0.49 ± 0.75 , unused sites: 0.13 ± 0.33). Finally, we found no clear association between sea lion occupancy and site aspect (North, East) or slope (Slope) as indicated by the low variable weights and the OR 95% *CI*s that widely overlapped with 1 (Table 4).

Overall, our analyses indicate that sea lions favor habitat characteristics that facilitate thermoregulation in extremely hot

conditions. The influence of thermoregulation in habitat selection, behavior, and population dynamics of many species that inhabit hot environments is well documented. For example, the need to thermoregulate strongly affects habitat preferences in a diversity of species, including California sea lions (Heath 1989), Galapagos sea lions (*Zalophus wollebaeki*—Wolf et al. 2005), northern elephant seals (*Mirounga angustirostris*—White and Odell 1971), many desert ungulates (Cain et al. 2006), garter snakes (*Thamnophis elegans*—Huey et al. 1989), and chacma baboons (*Papio ursinus*—Hill 2006). In turn, preferences for thermally favorable habitats affect mating behavior, and thus population dynamics, in species such as the California sea lion (Heath 1989), and the southern sea lion (*Otaria flavescens*—Campagna and Leboeuf 1988). These examples illustrate that for many species inhabiting hot environments, thermoregulation plays a key role in shaping behavior and habitat choices. Although in this study we did not directly monitor thermoregulatory behavior or record thermal characteristics of sea lions and their habitats, the identified habitat preferences strongly suggest that California sea lions in the Gulf actively choose thermally favorable habitats.

Thermally favorable habitats are likely to be critical in preventing heat stress. Unfortunately, the risk of thermal stress is likely to increase for many species in the near future. For example, mean annual temperatures in the Gulf based on global estimates are predicted to increase $2\text{--}3^{\circ}\text{C}$ by the end of the 21st century as a result of global warming (Intergovernmental Panel on Climate Change 2007). These predicted increases in temperatures may considerably affect this already heat-stressed sea lion population, and could limit suitable habitat in the future, putting the population at risk. In addition, sea lions in the Gulf are increasingly exposed to other potential threats, such as human disturbance via increasing levels of fishing pressure and tourism (Labrada-Martagon et al. 2005). Although human disturbance is currently quite low in most sea lion colonies in the Gulf (M. González-Suárez, pers. obs.), human disturbance can induce abandonment of breeding sites, alter behavior, and increase pup mortality in many pinniped species (Richardson et al. 1995; Suryan and Harvey 1999). Our visits to each site were limited to 30 min and thus, did not allow us to adequately explore effects of levels of human disturbance on habitat preferences. Future research should consider how the increasing anthropogenic impacts (e.g., increased temperatures and human presence) in the area might affect sea lion occupancy patterns and population dynamics.

Current habitat preferences may not adequately capture historical habitat choices or those that may occur in a distant future. Habitat preferences may be altered over time as a result of ecological changes or anthropogenic pressure. For example, northern fur seals (*Callorhinus ursinus*) historically occupied coastal areas in central California during the Holocene, but past human exploitation likely drove them away, changing their preferred habitat (Burton et al. 2001). In turn, the decline of the northern fur seal in this area likely reduced competition with other pinnipeds that were initially rare in this region, but are now common (Burton et al. 2001). Therefore, current habitat preferences should not be interpreted as definitive choices,

because habitat use may change with environmental conditions. Nevertheless, our results about current habitat preferences provide information appropriate for the time frame relevant to most management decisions, and help us understand contemporary ecological processes.

In conclusion, our results suggest that sea lions currently prefer larger-sized rocks, lighter substrates, and convex shorelines. We recommend that areas with these characteristics are carefully protected to ensure they remain undisturbed and available to sea lions. Active monitoring of site occupancy patterns and identification and protection of unused but suitable sites also would be desirable. Our analysis identified 4 of these potentially suitable, but currently unused sites (Fig. 1). Sites occupied at present may be abandoned as changes in climate and human use patterns take place; at that time the availability of alternative suitable sites may be critical to ensure the persistence of this species in the Gulf.

RESUMEN

El lobo marino de California (*Zalophus californianus*) se distribuye a lo largo de la costa norteamericana del océano Pacífico, aunque el número de colonias reproductoras es relativamente pequeño. Actualmente, se desconoce cuáles son las características por las que estos sitios son preferidos por el lobo marino. En este estudio cuantificamos características del hábitat—tipo y coloración del substrato, orientación, pendiente, curvatura de la costa, y disponibilidad de sombra, pozas de agua y zonas para descanso—en 26 sitios ocupados (7 islas) y 33 sitios no ocupados (8 islas) distribuidos a lo largo del Golfo de California, México. Se usaron modelos de regresión logística para explorar si las características del hábitat estudiadas pueden explicar los patrones de uso en el lobo marino. Los modelos que obtuvimos discriminaron claramente entre sitios ocupados y sitios no ocupados, y revelaron que los sitios ocupados generalmente están formados por rocas de mayor tamaño (oportunidad relativa [OR] = 1.209), substratos de coloración más clara (OR = 0.219), y líneas de costa convexas (OR = 1.067). Estas características probablemente juegan un papel en la prevención de estrés térmico en el lobo marino, sugiriendo que aumentos de temperaturas, como los asociados al cambio climático global, podrían suponer un riesgo adicional para esta población de lobo marino en declive. Para paliar, al menos parcialmente, estos posibles riesgos nuestros resultados podrían usarse para identificar, y proteger, sitios adecuados (favorables térmicamente) pero no usados por el lobo marino en la actualidad. Además, recomendamos la protección efectiva y el monitoreo de las zonas actualmente ocupadas así como de sus poblaciones.

ACKNOWLEDGMENTS

The 2005–2006 “Lobos” field teams helped collect data, especially D. Green, M. Toyama, M. Wasson, and J. Young. Comments from the members of the Gerber laboratory, K. Parris, J. Alcock, P. Hedrick, and 2 anonymous reviewers considerably improved previous versions of this manuscript. T. Lalonde and V. Bakker provided statistical advice, and C. D’Agrosa helped create Fig. 1. The Kino Bay Center for Cultural and Ecological Studies, the Centro Intercultural de

Estudios de los Desiertos y Oceanos (CEDO), and Centro Interdisciplinario de Ciencias Marinas del IPN (CICIMAR-IPN) provided logistic support. Funding for this research was provided by the National Science Foundation (grant 0347960 to LRG), and the Lisa Dent Memorial Fund (to MG-S). Secretaria de Medio Ambiente y Recursos Naturales authorized data collection (Oficios num/SGPA/DGVS/05325, /03269, and /02709).

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Submitted 25 March 2008. Accepted 17 April 2008.

Associate Editor was William F. Perrin.