Terrestrial Habitat Segregation Between the Guadalupe Fur Seal (*Arctocephalus townsendi*) and the California Sea Lion (*Zalophus californianus*) at Islas San Benito, México

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Abstract

The Guadalupe fur seal (*Arctocephalus townsendi*) and the California sea lion (*Zalophus californianus*) have co-inhabited the Islas San Benito since 1997. This archipelago is the only place where there is a sympatric occurrence of colonies of both species; this particular situation makes it an excellent model to explore overlap or spatial segregation in their terrestrial habitat. We used data collected at Islas San Benito in the summer of 2008 to test the hypothesis that local habitat use differs between the two species. We found evidence that there is terrestrial habitat segregation between species (Bray-Curtis distance = 0.64, *p* = 0.02), and our results show that the two species differed in their habitat use: Guadalupe fur seals used irregular beaches surrounded by cliffs, while California sea lions used open and flat beaches. The Guadalupe fur seal has been classified as vulnerable by the International Union for Conservation of Nature (IUCN), and the results obtained are important to understand the physical factors that affect its terrestrial habitat selection. The Guadalupe fur seal population at Islas San Benito continues to expand, and the statistical method employed in our study, applied through several counts, can be a useful tool to track changes in its distribution and patterns of habitat use.

Key Words: habitat segregation, cohabitation, Guadalupe fur seal, *Arctocephalus townsendi*, California sea lion, *Zalophus californianus*

Introduction

Habitat has been defined as the resources and conditions present in an area that support occupancy by a given organism (Hall et al., 1997). Presumably, animals select habitats to fulfill energy requirements and acquire resources necessary for reproduction and survival (Chamberlain et al., 2002). Otariids (fur seals and sea lions) rest and reproduce on isolated beaches on the mainland or islands. Most show annual reproductive cycles (Riedman, 1990), and the distribution of individuals on land is determined by the available space that contains resources suitable for mating, birthing, lactation, thermoregulation, and, in some cases, escape from predators (Crawley & Wilson, 1976; Limberger et al., 1986). Because lactation is long, females alternate nursing periods on land with feeding trips at sea (Trillmich, 1990; Boness & Bowen, 1996).

The Guadalupe fur seal (*Arctocephalus townsendi*) was intensively hunted during the 19th century and declared extinct in 1897; but in 1954, a small group was discovered on Isla Guadalupe (Wegeforth, 1928; Hubbs, 1956). For many years, fur seals were limited to this island, but then in 1997, a colony of less than 300 individuals was discovered on Islas San Benito (Maravilla-Chávez & Lowry, 1999) (Figure 1A). At present, the fur seal population of Islas San Benito is experiencing an exponential increase (Aurioles-Gamboa et al., 2010); however, reproductive activity is still virtually negligible, and population growth seems driven by fur seals immigrating from Isla Guadalupe (Aurioles-Gamboa et al., 2010). Although the fur seal world population is steadily increasing, this species is still at risk because the total population size remains low (less than 15,000 individuals; Aurioles-Gamboa & Trillmich, 2008).

The California sea lion (*Zalophus californianus*) breeds on shores and islands from British Columbia, Canada, to Baja California, Mexico, and within the Gulf of California (King, 1983). Rookeries of this sea lion on the west coast of the Baja California Peninsula are found on eight islands or archipelagos: (1) Islas Coronados, (2) Islote El Zapato, (3) Isla San Jerónimo, (4) Isla Cedros, (5) Islas San Benito, (6) Isla Natividad, (7) Isla Asunción, and (8) Isla Margarita (Figure 1A) (Le Boeuf et al., 1983; Lowry & Maravilla-Chávez, 2005). The total population on these islands was estimated at ~80,000 to 85,000 individuals; the main rookeries
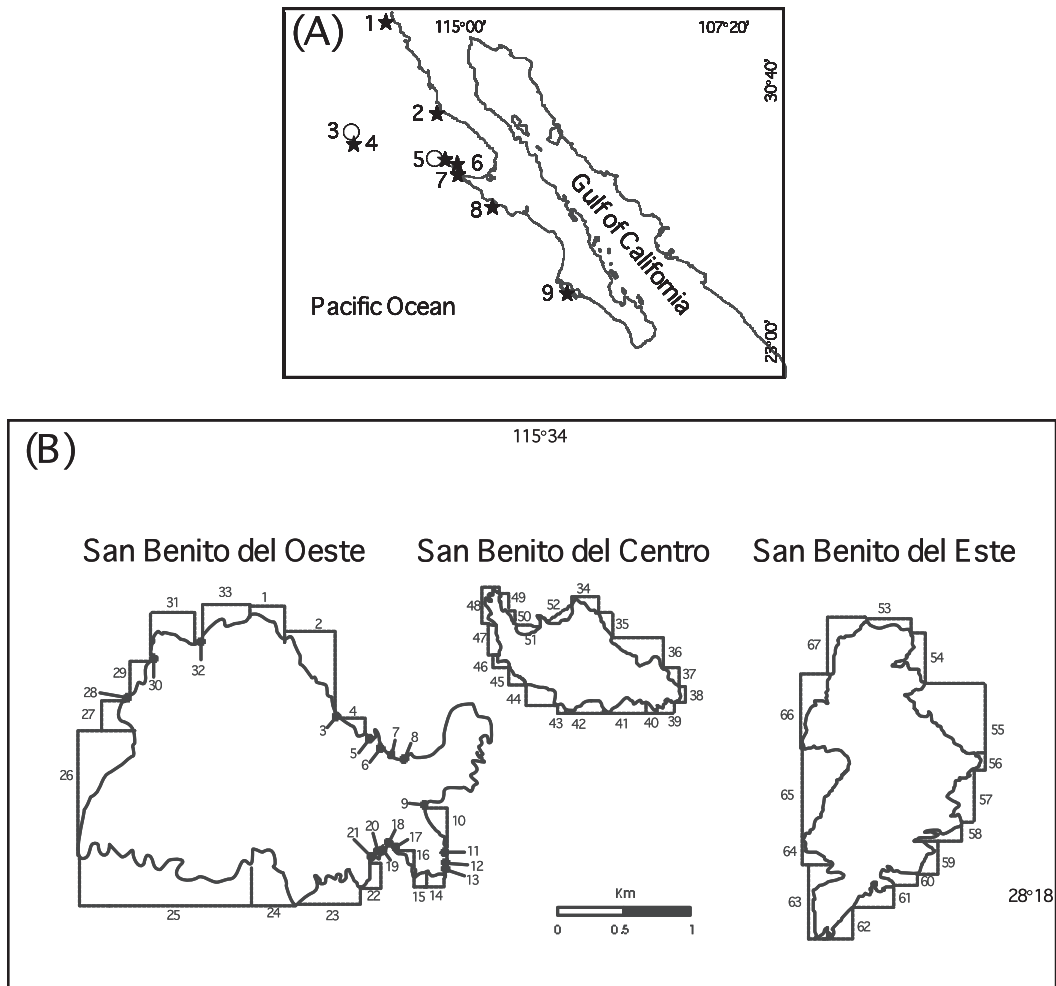
Figure 1. (A) Location of rookeries of Guadalupe fur seal (*Arctocephalus townsendi*) (white circles) and California sea lion (*Zalophus californianus*) (black stars) on the west coast of the Baja California Peninsula: 1 = Islas Coronados, 2 = Isla San Jerónimo, 3 = Isla Guadalupe, 4 = Islote El Zapato, 5 = Islas San Benito, 6 = Isla Cedros, 7 = Isla Natividad, 8 = Isla Asunción, and 9 = Isla Margarita; (B) the 67 sample sites on Islas San Benito.

are on Islas San Benito and Isla Cedros (Lowry & Maravilla-Chávez, 2005).

The Guadalupe fur seal and the California sea lion reproduce in the summer, from June to mid-August (Peterson et al., 1968; Odell, 1975), and Islas San Benito is the only place where there is a sympatric occurrence of colonies of both species. This particular situation makes it an excellent model to explore overlap or spatial segregation in their terrestrial habitat. We used data from surveys of the Islas San Benito collected in the summer of 2008, during the breeding season of both species, and tested the hypothesis that local habitat use differs between the two species.

Methods

The Islas San Benito (28° 18' N and 28° 21' N, and 115° 22' W and 115° 32' W) are located 28 km northwest of Isla Cedros, off the central west coast of the Baja California Peninsula, Mexico. The archipelago is composed of three islands: (1) San Benito del Oeste (SBW), (2) San Benito del Centro (SBC), and (3) San Benito del Este (SBE) (Figure 1B).

For data collection, the islands were partitioned into 67 unequally sized sites based on habitat characteristics (i.e., beach orientation) (Figure 1B). Tropical and temperate otariids need to stay close to the water for thermoregulation, and this leads to

a linear spread of colonies along the coast (Wolf et al., 2005). Use of space by the sea lions and fur seals at these islands can be characterized by the length of one-dimensional access lines parallel to the coast rather than by area (Wolf et al., 2005). Lengths of each site (km of shoreline) were measured using the software *ArcView* 3.2 (Esri Inc., Redlands, CA, USA).

Observations and data collection were conducted from 4 to 6 August 2008. At the three islands, the field crew walked along the shoreline recording habitat variables and counting fur seals and sea lions. Inaccessible parts of the islands were surveyed from a small boat (approximately 10 to 30 m from shore) using Bushnell 7 × 50 binoculars. Surveys on SBW were done from the beach, except on the southwest coast, which was surveyed by boat. Because neither fur seals nor sea lions occupied the northeast coast and to avoid disturbing the elephant seals that rest there during the summer, this area was not surveyed. SBC was surveyed from the beach, and SBE from a boat.

Ten habitat variables were selected based on variables identified in previous studies (Stevens & Boness, 2003; Wolf et al., 2005; González-Suárez & Gerber, 2008) and recorded as being present or absent (Table 1). Counts of individuals of both species were done simultaneously. Because animals can move from one site to another, each island site was sampled sequentially, and all islands were surveyed in a single day. During the counts, individuals of both species were categorized into five age-sex-classes: (1) adult males, (2) subadult males, (3) adult females, (4) juveniles (immature individuals of both sexes), and (5) pups. For the description of age-sex-classes of each species, see Peterson et al. (1968) and Le Boeuf et al. (1983). Animals that could not be identified during the census were classified as unidentified.

The Kendall's rank correlation was used to eliminate highly correlated variables (tau ≥ 0.40) (Daniel, 1978). We applied cluster analysis (city-block [Manhattan] distance) to group the sampling sites into discrete habitat types based on uncorrelated physical variables derived from Kendall's correlation analysis (Legendre & Legendre, 1998; McGarigal et al., 2000).

Correction factors were not applied to our counts, and habitat selection and use analyses were completed using the total number of individuals counted for two reasons. First, counts were made in August, at the end of the both species' breeding seasons, and at that time an unknown proportion of females were feeding at sea. Therefore, counts conducted during August may underestimate female density and abundance. Second, because a proportion of individuals could not be identified in the field and were classified as unidentified, the necessary age and sex specific correction could result in an over- or underestimate of the density of some classes.

We assumed that animals of both species had equal access to all available habitats in the study area. Animals were not identified individually (i.e., no ID was used) in the field, and the study was constricted by measuring the use and availability of habitat at the population level (Thomas & Taylor, 1990, 2006; Manly et al., 2002). We compared habitat use to its availability, which was defined as the extent of the habitat accessible to the animals during the study period (Manly et al., 1993). The electivity score, π_i (Manly, 1974), which is a measure of relative density in habitat i, was calculated as

$$\pi_i = \frac{\delta_i}{\eta_i \sum_{i=1}^{N} \frac{\delta_i}{\eta_i}}$$

where δ_i is the number of individuals of each species counted in habitat type i and η_i is the proportion of cover of habitat type i when

Table 1. Physical variables recorded at 67 sites in Islas San Benito, Mexico

Variable	Units measured
Slope at shore	$< 10° = 0, \geq 10° = 1$
Abundant shade (Shade availability was attributed to sites' boundaries that were formed by high cliffs and large boulders.)	Present = 1, Absent = 0
Wave spray	Present = 1, Absent = 0
Tidal pools	Present = 1, Absent = 0
Beach bordered on both sides by headlands	Present = 1, Absent = 0
Substrates present on shore (four variables):	
(1) *Sand:* Substrate comprised predominantly of small particles (0 to 2 mm).	Present = 1, Absent = 0
(2) *Pebble:* Substrate comprised predominantly of small stones (0.2 to 10 cm).	Present = 1, Absent = 0
(3) *Solid rock platform:* Continuous rock that could not obviously by divided into individual rocks.	Present = 1, Absent = 0
(4) *Large stacked rocks:* Large (50 to 200 cm) and angular rocks stacked on top of one another forming sheltered areas and irregular contours.	Present = 1, Absent = 0
Beach bordered by cliff	Present = 1, Absent = 0

$$, \text{when } \eta_i = \frac{L_i}{L_T}$$

where L_i is the length of shoreline corresponding to habitat type i, L_T is the total length of shoreline sampled (in km), and N is the number of types of habitat available.

Habitat overlap (or segregation) between species (X and Y) was determined using the Bray-Curtis distance ($D[X,Y]$) (Bray & Curtis, 1957; Pledger et al., 2007):

$$D(X,Y) = \frac{1}{2} \sum_{i=1}^{N} |\pi_{Xi} - \pi_{Yi}|$$

where $D(X,Y)$ has values between 0 (for completely matching values) and 1 (for the most extreme distance). The null hypothesis tested was that both species had the same pattern of use among the differing types of habitat. The significance of the $D(X,Y)$ value was evaluated by testing 2,000 randomizations (significance at $p < 0.05$).

For each species, habitat use was tested by constructing the Bonferroni adjusted $100(1-\alpha)\%$ confidence intervals (CI) (Namgail et al., 2004). A habitat was considered to be preferred by the species when it was occupied disproportionately to its availability (Manly et al., 1993). A habitat type was classified as *preferred* if $\pi_i >$ upper-CI, as *used* if lower-CI $\leq \pi_i \leq$ upper-CI, and as *avoided* if $\pi_i <$ lower-CI.

Results

Five habitat variables were strongly and significantly correlated with each other (Table 2). Abundant shade was correlated with the presence of large stacked rocks and beach bordered by cliff; and beach bordered on both sites by headlands was associated with substrate comprised of pebbles (Table 2). We focused on substrate types, which most generally reflect site morphology among the correlated variables (González-Suárez & Gerber, 2008); abundant shade and beach bordered on both sites by headlands were excluded from further analyses. The remaining variables included in the cluster analysis were beach slope, wave spray, tide pools, substrate types, and beach bordered by cliff. Cluster analysis grouped the 67 sampled sites into six habitat types (Table 3). SBW contains the six habitat types described, SBC contains three (B, D & F), and SBE contains two (B & C).

Our survey recorded 2,480 fur seals. The maximum number of individuals was observed on SBW (67.70%), followed by SBE (31.98%) and SBC (0.32%). Juveniles and adult females were the most abundant age-sex-classes (30.48 and 22.62%, respectively); adult males and subadult males represented 13.59 and 4.56%, respectively. Pups were the least abundant age-sex-class (1.21%). Unidentified individuals were 27.54% of the total number of fur seals counted. California sea lions totaled 5,956 counted individuals. The maximum number of individuals was observed on SBC (60.01%), followed by SBE (25.01%) and SBW (14.98%). Pups and adult females were the most abundant age-sex-classes (52.75 and 31.35%, respectively). Juveniles, adult males, and subadult males represented 5.27, 4.90, and 3.86%, respectively, and unidentified individuals accounted for only 1.86% of the sea lions.

We found sufficient statistical support to reject the null hypothesis of similar patterns of use: $D(X,Y) = 0.64$, $p = 0.02$, suggesting habitat segregation does occur between species. Fur seals occupied four habitats: they preferred habitat types A and E, while seeming to avoid habitat types D and F (Table 4). California sea lions also occupied four habitats, but they preferred habitat types D and F and avoided habitats A and B (Table 4). Both species occupied habitat type C, but the electivity scores were very low (Table 4).

Table 2. Kendall's correlation coefficient for variables recorded at Islas San Benito, Mexico; significant correlations are indicated with *. Ss = slope, Sh = abundant shade, Ws = wave spray, Tp = tidal pools, Bh = beach bordered on both sides by headlands, S = sand, P = pebble, R = solid rock platform, Ls = large stacked rocks, and Bc = beach bordered by cliff.

	Ss	Sh	Ws	Tp	Bh	S	P	R	Ls	Bc
Ss	1.00	0.18	0.10	0.12	-0.06	-0.19	-0.39	0.25	0.35	0.32
Sh		1.00	-0.17	0.03	0.21	0.14	-0.01	-0.11	0.41*	0.50*
Ws			1.00	0.29	0.11	0.02	-0.07	0.12	-0.05	-0.30
Tp				1.00	-0.16	-0.27	-0.07	0.23	-0.10	-0.18
Bh					1.00	0.04	0.42*	-0.39	-0.11	0.04
S						1.00	0.23	-0.39	-0.09	-0.18
P							1.00	-0.32	-0.26	-0.24
R								1.00	-0.16	-0.04
Ls									1.00	0.37
Bc										1.00

Table 3. Description of habitat types identified on Islas San Benito, Mexico; η_i = proportion cover of habitat type *i*.

Habitat type	η_i	Description
A	0.02	Solid platform rock with some large stacked rocks surrounded by cliffs and presence of tidal pool
B	0.60	Solid rock platform with relatively steep slopes and presence of tidal pool
C	0.24	Beaches covered by large stacked rocks with relatively steep slopes and surrounded by cliffs; presence of tidal pool and abundant wave spray
D	0.10	Flat beaches composed of pebbles and presence of abundant wave spray
E	0.02	Beaches composed of pebbles with relatively steep slopes and surrounded by cliffs
F	0.02	Sandy and flat beaches with abundant wave spray
Sum	1.00	

Table 4. Estimated habitat use for the Guadalupe fur seal and California sea lion on Islas San Benito, Mexico, during the summer of 2008. δ_i = number of individuals of each species counted in habitat type *i*; π_i = electivity score. Usage: 2 = used; 1 = occupied but not used; 0 = avoided.

Habitat type	Guadalupe fur seal			California sea lion		
	δ_i	π_i	Usage	δ_i	π_i	Usage
A	369	0.53	2	34	0.03	0
B	853	0.03	1	1759	0.04	0
C	960	0.08	1	1278	0.07	1
D	0	0.00	0	2098	0.28	2
E	298	0.36	2	312	0.23	1
F	0	0.00	0	475	0.35	2
Sum	2,480	1.00		5,956	1.00	

Discussion

In the last decade, the Guadalupe fur seal and California sea lion have converged on Islas San Benito. Our results show that they have neither identical distribution nor fully shared habitat use, suggesting both habitat and spatial segregation between these species at least at the time of this study. The fur seal preferred irregular shaped beaches surrounded by cliffs on SBW and SBE, while the sea lion preferred the open and flat beaches of SBC. One habitat type was occupied by both species to a similar degree (beaches covered by large stacked rocks with relatively steep slopes and bordered by cliffs), but neither species seemed to prefer this habitat.

Fur seals (*Arctocephalus* spp.) have varying terrain preferences. For example, *A. forsteri* prefers beaches covered by small rocks and gentle slopes (Bradshaw et al., 1999), while *A. philippi* prefers beaches surrounded by cliffs (Francis & Boness, 1991). Moreover, differences in habitat preferences in a species have been observed within its distribution range: at Gough Island (40° 19' S, 9° 55' W), *A. tropicalis* prefers open areas with sea spray (Bester, 1982); while at Macquaire Island (54° 30' S, 158° 57' E), it prefers irregular rock platforms or boulder beaches (Lancaster et al., 2010).

At Islas San Benito, Guadalupe fur seals preferred steep areas bordered by cliffs, which provide abundant shaded areas; still, fur seals also used either irregular rock platforms with large rock or pebble beaches. Anecdotal observations suggest that at Isla Guadalupe, before seal hunting, the species used open and pebble beaches; but in the last decades, it congregates on shores with abundant large rocks and lava blocks at the base of large cliffs (Peterson et al., 1968). Selection of beaches covered by large rocks has two advantages: (1) cool spaces for thermoregulation and (2) less accessibility by predators, including humans (Stevens & Boness, 2003). At Isla Guadalupe and Islas San Benito, fur seals occupied the eastern shores (Peterson et al., 1968; present study). In this region, there are persistent and relatively strong northerly surface winds during spring and summer, which produce waves and hazardous conditions for the pups (Taylor et al., 2008). We hypothesized that the fur seals occupied the east flank of islands where there is shelter from strong winds and persistent wave action.

In the Gulf of California, the California sea lion selects habitats with large-size rocks, lighter substrates, and convex shorelines, possibly because these sites help them avoid heat stress by using behavioral thermoregulation (González-Suárez & Gerber, 2008). Our results show that on Islas

San Benito, sea lions primarily used sand and pebble beaches rather than large rock areas and that they used open beaches more than convex shoreline. Nevertheless, areas with large rocks (habitat type C) were also used by sea lions in the Islas San Benito. The results are perhaps not that different from those of González-Suárez & Gerber (2008), who did not strictly differentiate between uses in their analysis. On the other hand, the habitats used on Islas San Benito also seemed to aid in meeting thermoregulatory needs—beaches exposed to prevailing winds and sea spray. Flat areas probably facilitate pup movement as was also reported for other otariids (Bradshaw et al., 1999).

Aside from terrestrial segregation, Aurioles-Gamboa & Camacho-Ríos (2007), in a study conducted at Islas San Benito, found that these two species have different diets, suggesting that each species hunts in areas with different prey. Dissimilar diets and feeding behavior have been observed when two or more species of otariids occupy the same habitat, reducing the trophic overlap (Paéz-Rosas & Aurioles-Gamboa, 2010). Terrestrial and trophic segregation might play a role in reducing interference and exploitation competition, facilitating coexistence of ecologically similar species (Pianka, 1978).

In this study, we analyzed terrestrial habitat segregation between the Guadalupe fur seal and the California sea lion at Islas San Benito based on methods applied to a single count conducted at the end of both species' breeding seasons. Our results showed that, at the time of the study, there was terrestrial habitat segregation between these species that suggested dissimilar patterns of habitat use. Still, other factors that could affect the distribution of the animals (e.g., interspecific competition) were not measured. Both of these otariid species are territorial during the breeding season, and it is possible that one of the two species occupies the beaches prior to the other, affecting the type of habitat ultimately used by the later arriving species. Nevertheless, we consider the results obtained to be important in understanding the physical factors that affect terrestrial habitat selection by the Guadalupe fur seal.

Acknowledgments

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