Spatial and temporal patterns of territory use of male California sea lions (*Zalophus californianus*) in the Gulf of California, Mexico

Kathy L. Robertson, C.W. Runcorn, Julie K. Young, and Leah R. Gerber

Abstract: Little is known about the spatial distribution patterns of territory use throughout the breeding season and the potential influence of these patterns on male behavior and fitness for California sea lions (*Zalophus californianus* (Lesson, 1828)). We used empirical data from behavioral observations to document the distribution of 1271 territories during the 2004–2006 breeding seasons at three breeding colonies in the Gulf of California, Mexico. Territories were depicted as circular objects and overlaid over one another in ArcINFO®, separated by island and year. Areas with consistent overlap in territory use were identified among years. Territory boundaries and locations were spatially distinct within breeding seasons and at each of the breeding colonies. Males occurring in these areas were partially influenced by island, year, territory size, number of females, aggressive interactions, and distance to nearest neighbor (best fitting model — AIC = 1273.09, $\omega_i = 0.99$). However, the best model only accounted for 30% of the variation, indicating that other variables are needed to explain the occurrence of these "hot spots". Territory site selection, therefore, may be influenced by extrinsic factors under which female choice may be operating resembling a lek-like mating system.

Résumé : Chez les lions de mer de Californie (*Zalophus californianus* (Lesson, 1828)), on connaît mal les patrons de répartition spatiale de l'utilisation du territoire durant la saison de reproduction et l'influence potentielle de ces patrons sur le comportement et la fitness des mâles. Des données empiriques provenant d'observations du comportement nous ont servi à établir la répartition de 1271 territoires durant les saisons de reproduction de 2004–2006 dans trois colonies reproductives du golfe de Californie, Mexique. Nous avons représenté les territoires comme des objets circulaires et superposés dans ArcINFO® et les avons séparés par île et par année. Nous avons identifié les zones où il se produit des chevauchements persistants dans l'utilisation des territoires au cours des années. Les limites et les emplacements des territoires sont spatialement distincts au cours des saisons de reproduction et dans chaque colonie reproductive. Les mâles qui se retrouvent dans ces zones sont en partie influencés par l'île, l'année, la taille du territoire, le nombre de femelles, les interactions agressives et la distance du voisin le plus proche (modèle le mieux ajusté — AIC = 1273,09, $\omega_i = 0,99$). Cependant, le meilleur modèle n'explique que 30 % de la variation; il est donc nécessaire de trouver d'autres variables pour expliquer le développement de ces « points chauds ». La sélection du site du territoire peut donc être influencée par des facteurs extrinsèques; dans ces conditions, il se peut que le choix des femelles fonctionne dans un système d'appariement ressemblant à un type lek.

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Introduction

Understanding territory spatial patterns may provide insight to understanding mating systems and more broadly for understanding population dynamics (e.g., fitness, recruitment, and survivorship; Gordon 1997; Adams 2001). Classic patterns of random, clumped, or uniform territories may indicate the overall availability of resources, the degree of resource distribution, and territory quality (Brown and Orians

K.L. Robertson, C.W. Runcorn, J.K. Young,[1,2] and L.R. Gerber. Ecology, Evolution and Environmental Science, School of Life Sciences, Arizona State University, College and University Drive, Tempe, AZ 85287-4501, USA.

[1]Corresponding author (e-mail: jyoung@wcs.org).
[2]Present address: Wildlife Conservation Society, Northern Rockies Field Office, Division of Biological Sciences, The University of Montana, Missoula, MT 59812-4824, USA.

1970; Davies 1991). At the individual level, however, territories may be fluid (Gordon 1997) and their spatial patterns may change in response to environmental variability, resource fluctuations, intraspecific competition, and the competitive ability of males (e.g., size, age, aggressiveness; Brown and Orians 1970; Gordon 1997; Adams 2001). But as territory size increases, so does the cost to defend it (Alcock 2001). In polygynous mating systems males typically provide no parental care, but instead increase reproductive success by mating with many females (Emlen and Oring 1977). Males defend territorial areas occupied by females during the reproductive season and the density of females largely determines their distribution. Female distribution may be dependent on both the availability of local resources and the fitness of territorial males in terms of their reproductive success (Emlen and Oring 1977). Thus besides securing a territory, male reproductive success can also be influenced by territory location and size (Brown and Orians 1970). As such, much variation can occur among individual settlement patterns and within the mechanisms driving the spatial patterns of territory use.

California sea lions (*Zalophus californianus* (Lesson,

1828)) are polygynous, sexually dimorphic pinnipeds that are believed to exhibit a lek-like mating system (Heath 1989). Sea lions range along the Pacific coast from Baja Mexico to British Columbia, Canada, and throughout the Gulf of California, Mexico. The breeding season occurs from mid-May to early August (Peterson and Bartholomew 1967), during which females form dense aggregations to give birth, rear pups, and copulate (Bartholomew 1970). Most females give birth to one pup by late May or early June, then begin making 1- to 3-day foraging trips to sea ~4 to 5 days later. Females enter into estrus 2–4 weeks after giving birth (Peterson and Bartholomew 1967; Odell 1975), which is a considerably longer period than seen in most pinnipeds (Francis 1987; Riedman 1990). Thus mating typically occurs between the 1st week in June and the end of July (Le Boeuf et al. 1983; García-Aguilar and Aurioles-Gamboa 2003) on land or in shallow tidal pools (Riedman 1990; Boness 1991).

Males usually arrive at the colonies in mid-May (Peterson and Bartholomew 1967), but their exact timing is unclear (e.g., arrival before females or simultaneously; Odell 1975; García-Aguilar and Aurioles-Gamboa 2003). Only a small fraction of dominant adult males establish and maintain breeding territories, while nonbreeding adult males and subadults aggregate in adjacent "bachelor pads" or nonbreeding areas. Territories are acquired through physical fights and are more intense during the end of June through July, corresponding to the peak of the breeding season (Peterson and Bartholomew 1967; Odell 1975). Once boundaries are established, they are maintained by vocalizations, patrolling, and ritualized open-mouth displays.

Territories are established parallel to the contour of the shoreline in areas occupied by females (Peterson and Bartholomew 1967) and include both terrestrial and aquatic boundaries. The territories established early in the season are generally large and held by smaller males, but they are often taken over by larger males and become smaller in size nearer the peak of the breeding season (Heath 1989). Females are not confined by territorial boundaries and move frequently during the day seeking relief from the heat. Thus a female may mate in a different territory then the one she gave birth in (Francis 1987; Heath 1989). Males do not attempt to block female movement; herding behavior is rarely seen in California sea lions (Francis 1987). Territory tenure, the amount of time a male spends defending a territory, has been documented to vary between 9 and 45 days for California sea lions (Peterson and Bartholomew 1967; Odell 1975; Heath 1989).

Our goal was to describe the spatial use of territorial male sea lions in the Gulf of California. In particular, we seek to determine the spatial distribution patterns of territories during the breeding season and whether particular areas were occupied more consistently than others. We also aim to identify factors that may influence observed spatial patterns in territory use. Our prediction is that territories should be concentrated and thus boundaries highly contested in areas that are heavily used by females.

Materials and methods

Study areas

Field research was conducted at three breeding colonies

Fig. 1. Map of (1) San Jorge (31°01′N, 113°15′W), (2) Granito (29°34′N, 113°32′W), and (3) Los Islotes (24° 35′N, 110°23′W) in the Gulf of California, Mexico, where California sea lions (*Zalophus californianus*) were observed.
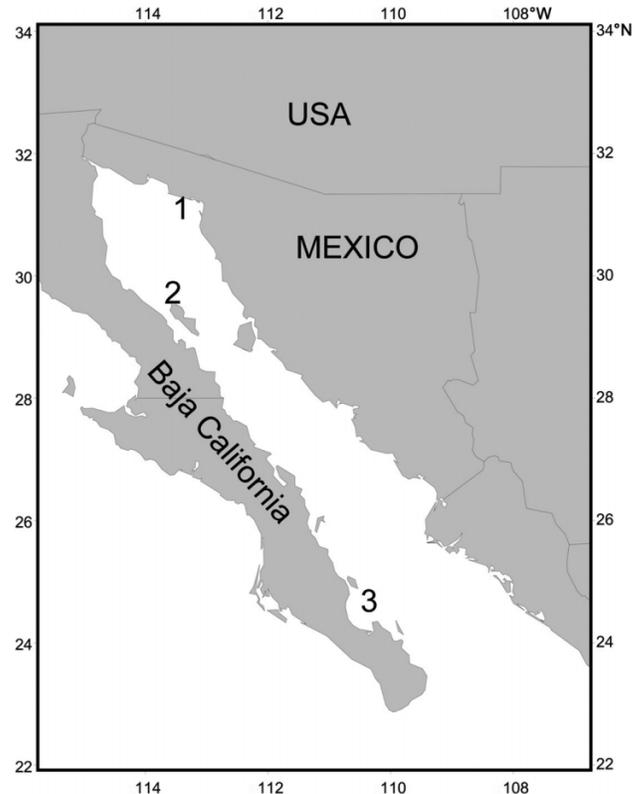
(San Jorge: 31°01′N, 113°15′W; Granito: 29°34′N, 113°32′W; Los Islotes: 24°35′N, 110°23′W) in the Gulf of California, Mexico, during the 2004, 2005, and 2006 breeding seasons (Fig. 1). The breeding colonies differ topographically. San Jorge, located in the northern part of the Gulf of California, is 1.10 km long and 0.55 km wide with the highest point 62 m above sea level. The beaches are mostly rocky with large boulders. Granito is centrally located and is 1.04 km long and 0.24 km wide with the highest point 50 m above sea level. It consisted of both rocky and sandy beaches backed by vertical cliffs and large boulders. Los Islotes is located in Baja California, Sur, and is ~0.25 km long. Formed originally from volcanoes, the beaches consisted predominately of rock platforms surrounded by rocky inlet channels. Mean temperatures at each island during the study ranged between 32 and 39 °C. Recent surveys of the rookeries report that the populations at San Jorge and Los Islotes are increasing, while Granito is decreasing in abundance (Szteren et al. 2006).

Male census

Daily observations were conducted during a 6-day period between 0700 and 1900 in June and July of 2004–2005, and June, July, and August of 2006 (Table 1). Two teams consisting of two to three people were assigned to each of the two breeding sites and were responsible for daily observations at that site during the entire observation period. Each team was positioned no closer than 20–30 m to the nearest animal to minimize disturbance. When possible, we identi-

Table 1. Dates when behavioral observations on California sea lions (*Zalophus californianus*) were made during the study.

Season	Island	Trip 1	Trip 2	Trip 3
2004	San Jorge	19–25 June	10–17 July	
	Granito	28 June – 3 July	21–26 July	
	Los Islotes	1–7 July	21–27 July	
2005	San Jorge	15–20 June	15–20 July	
	Granito	15–20 June	15–20 July	
	Los Islotes	15–20 June	15–20 July	
2006	San Jorge	11–19 June	8–16 July	5–13 Aug.
	Granito	14–22 June	8–16 July	5–13 Aug.
	Los Islotes	17–25 June	7–15 July	5–13 Aug.

fied territorial males based on natural marks (primarily scar patterns from bites or lacerations) and assigned unique identification codes. In the few cases where no distinguishing marks were evident, males were assigned a generic identification (i.e., male 1) for each day of the observation period. Because not all individuals were uniquely identified, we focused our study on broad patterns in territory use within and between breeding seasons. Thus, we were not able to determine if males returned between years or the degree of site fidelity.

We conducted a census of territorial males approximately three times per day. For 2004, territory size and boundaries plus nearest neighbor distances were visually estimated by observing territorial behavior (i.e., patrolling and aggression) throughout the day. In 2005 and 2006, a 5 m × 5 m grid was painted at each breeding site and was used to estimate territory size to the nearest 1/4 of a grid. During each census, we recorded the location of each male, the number of females and pups within each territory, and the distance to the nearest neighbor in 5 m intervals based on the male's location with respect to the grid. We also recorded male aggressive interactions during 1 h intervals, two to three times each day, at each of the two breeding sites. Male aggression was defined as any male–male interaction such as open-mouth threats, vocalizations directed at other males, or physical contact.

Spatial pattern of territorial males

To determine the spatial pattern of territorial males, we recorded their locations using either a handheld global positioning system (GPS) or a compass and range finder. We then plotted these data using ArcView® version 3.3 (Environmental Systems Research Institute, Inc. 2002) Distance/Azimuth tools version 1.6 (Jenness 2005). We used GPS locations for the geographical center of the territory. To create a conceptual model of territorial spatial patterns, we drew circles around the GPS points using circular buffers with the area equal to the estimated territory size of each male. Territory size (A) was converted to radius (r) values for the circular buffers using $r = \sqrt{A/\pi}$.

Buffers were then separated into different layers within ArcINFO® version 9.1 (Environmental Systems Research Institute, Inc. 2004). Each layer represented the distribution of territorial males within the breeding site during June and July 2004–2006, and August 2006. In total, there were ≤3

layers per day that we next converted into a 5 m × 5 m grid (raster) format using ArcINFO® according to the painted grid used at each breeding site. Each grid cell was assigned a value of 1 (containing a territory) or 0 (no territory). All layers were then combined so that values derived from overlapping cells were summed together per day to create a single layer representing the observed frequency of male occupancy during each month. To account for the differences in number of daily male census periods between years, these values were weighted by dividing the cell value by total number of observations during that month.

We then combined the frequency layers for each year into two different layers: (1) mean values and (2) standard deviations of the month within that year. The cell values of the mean and standard deviation layers were classified into three qualitative levels (low, medium, and high) so that the cells with the high qualitative value had the highest means and lowest standard deviations. These cells represented locations with high mean occupancy frequency and low standard deviation based on areas of overlap within a year (i.e., single breeding season). These locations, or "hot spots", indicated areas of high use among all territorial males at each breeding site. Within each site, a buffer was generated around high-value cells based on that site's mean territory size. Finally, all male census data were separated into two groups for statistical analysis: one group for data within high-value cells and one for data outside high-value cells.

Data analysis

To test what factors may potentially influence the distribution of hot spots (areas having a high mean frequency of occupation), we determined if there was a relationships with hot spots (1 = yes, 0 = no) and six variables with a binary logistic regression model using SPSS® version 14 (SPSS Inc. 2005). The variables being compared were island, year, mean territory size, mean number of females per territory, male aggressive interactions, and mean distance to nearest neighbor. Because we found a quasi-complete separation in SPSS® when we used breeding site, this variable was removed from further analyses. We used Akaike's information criterion (AIC) to determine which model was the best predictor of hot spots, where the model with lowest AIC value, relative to all competing models, represents the best fit (Burnham and Anderson 2002). To aid comparisons between models and to rank them, we calculated the ΔAIC (Δ_i) from the difference between the AIC value of the best model to

Fig. 2. Mean territory size, mean number of females, aggressive interactions per day, and distance to nearest neighbor (distNN) for all known territorial male California sea lions (*Zalophus californianus*) at San Jorge (SJ), Granito (GR), and Los Islotes (LI) during the 2004–2006 breeding seasons. Error bars indicate standard error.
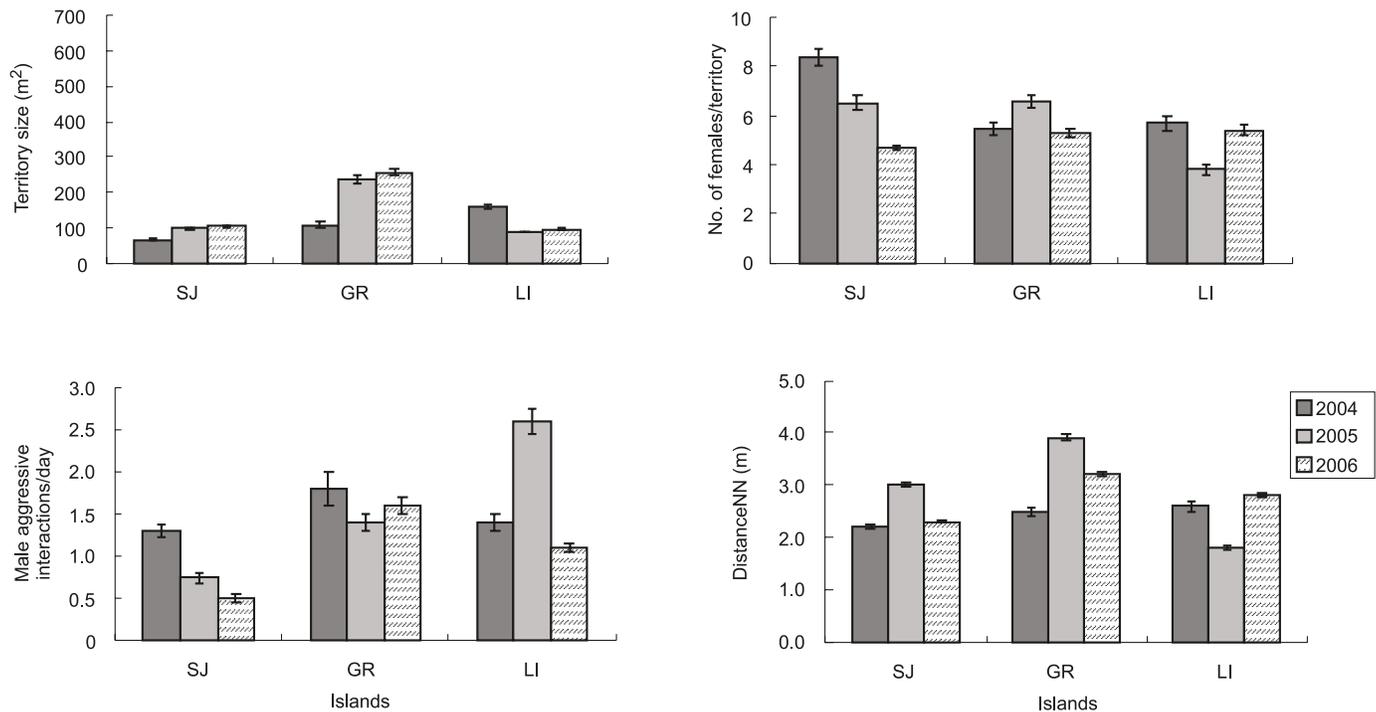
the AIC values of all other models (Burnham and Anderson 2002). We also used AIC weight (ω_i) to asses the strength of the best model in providing support to our prediction (Burnham and Anderson 2002). We used a Kruskal–Wallis test to examine changes in distance to nearest neighbor among each colony by year. All results are reported as means ± SE.

Results

Male census

Approximately 292 territorial males were censused ≤3 times per day between 2004 and 2006, resulting in 1271 territories. Mean territory size varied by year at each breeding colony (Fig. 2). On San Jorge, the mean territory size was 93.3 ± 4.2 m² (range 5–750 m²), 224.5 ± 17.1 m² on Granito (range 5.0–1125.0 m²), and 110.0 ± 3.8 m² on Los Islotes (range 6.0–600.0 m²). In general, territory size increased between 2004 and 2005 at San Jorge and Granito, but decreased at Los Islotes. Between 2005 and 2006, territory size stabilized at San Jorge, decreased at Granito, and increased at Los Islotes. In 2004 and 2005 at Granito, when males abandoned their territory, neighboring males appeared to expand their territorial boundaries.

The daily mean number of females per territory appeared to have little relation to territory size. As territory size increased at Los Islotes in 2005 and 2006, the mean number of females per territory declined. The mean number of females per territory was 6.1 ± 0.3 (range 0–31) on San Jorge, 5.7 ± 0.2 (range 0–21) on Granito, and 4.8 ± 0.2 (range 0–38) on Los Islotes. The distribution of the mean number of females among all colonies and all years combined showed that 12.7% of the territories (*n* = 1271) contained no fe-

males, while 3.0% of male territories included ≥20 females for at least 1 day.

The mean number of aggressive interactions was low among all colonies and among all years. Daily mean aggressive interactions per male were 0.8 ± 0.1 (range 0–11) on San Jorge, 1.6 ± 0.1 (range 0–12) on Granito, and 1.7 ± 0.1 (range 0–28) on Los Islotes. Distance to nearest neighbor ranged 6–10 m on San Jorge, 11–15 m on Granito, and 6–10 m on Los Islotes. There were no significant differences between distances to nearest neighbor among years at San Jorge ($H_{[4]}$ = 4.88 *P* = 0.30), but nearest neighbor distances differed at Granito ($H_{[4]}$ = 35.63, *P* < 0.001) and Los Islotes ($H_{[4]}$ = 12.92, *P* = 0.01).

Spatial patterns of males

We found that certain areas were consistently used as territories across breeding seasons (Table 1, Fig. 3). These areas, or hot spots, typically contained some type of substrate (e.g., submerged boulders, parts of a rock platform, or cove) around which males established territories and defended boundaries. Of the 24 models that we tested to explain territory use, only 1 model was identified as having an influence on the occurrence of these hot spots. Based on the AIC criteria, the best model included island, year, mean territory size, the mean number of females per territory, male aggressive interaction, and distance to nearest neighbor (AIC = 1273.09, ΔAIC = 0.0, ω_i = 0.99; Table 2). The second best fitting model included island, year, and distance to nearest neighbor, but provided weak support (ω_i = 0.01) in explaining hot spots. The ΔAIC values for the remaining four models ranged 9.55–31.14 relative to the top model.

Fig. 3. Areas within territorial breeding sites at San Jorge site 1 (*a*), San Jorge site 2 (*b*), Granito site 1 (*c*), and Los Islotes site 1 (*d*) that have high mean and low frequency grid cell values based on territorial occupancy of California sea lions (*Zalophus californianus*) during the 2006 breeding season. Each cell represents a 5 m × 5 m area. For area estimates refer to Table 1.
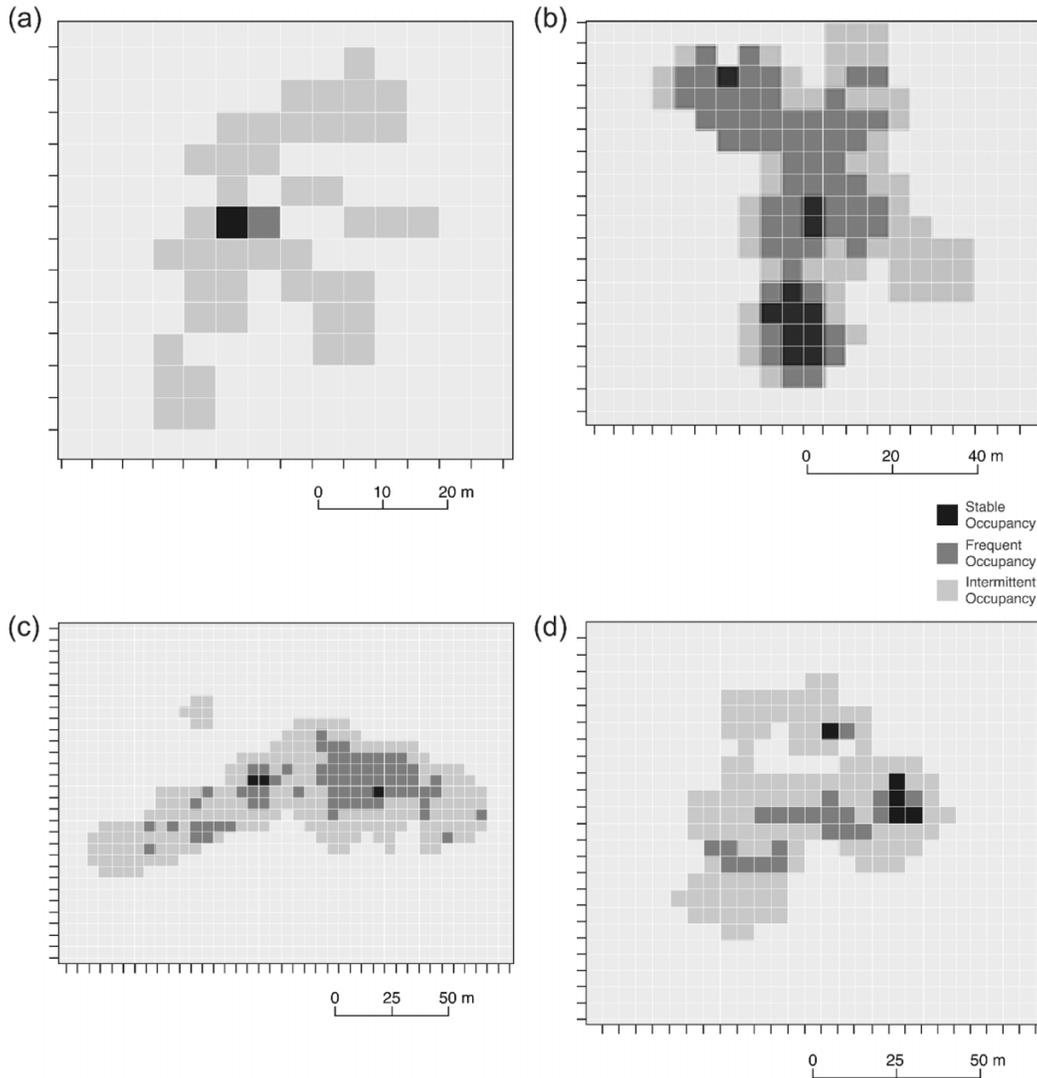
Discussion

Our study revealed that certain areas where male California sea lions establish territories are stable and are occupied consistently over the breeding season (Fig. 3). However, we did not find strong relationships between hot spots (i.e., areas of high mean frequency of occupation) and hypothesized factors that may contribute to the occurrence of these areas. Our best model could only account for 30% of the variation, suggesting that we are missing alternative variables that may best explain the location of hot spots. Alternatively, the occurrence of hot spots may not be related to intrinsic variables but may represent areas where boundaries are not clearly defined between neighboring males. Territorial boundaries showed minor fluctuations within a breeding season, creating patterns of territorial overlap. For example, at San Jorge in 2005, two neighboring territorial males shared a boundary delineated by a large boulder close to the shoreline. The shared boundary fluctuated on either side of the boulder in June and July. However, our examination over the entire season, (May–August) suggests that this boundary intersection was stable. Boundary stability at topographical landmarks was also evident on Granito and Los Islotes. Having a landmark, such as a boulder, along a boundary can be beneficial. It would provide a cue between neighbors that clearly delineates where each territory ends, thereby decreasing energy expenditure over boundary defense (Eason et al. 1999). At Los Islotes, males also established territories in between rocky inlets that provided both resting habitat and relief from the heat. Females routinely rest on wet boulders to seek relief from high temperatures (Gentry 1973; Francis 1987; Miller 1991). Males would thereby benefit by having boulders within their territory not only to attract more females but also to increase the amount of time spent interacting among females (Heath 1989), potentially increasing their mating opportunities (Odell 1975; Francis 1987; Heath 1989).

Hot-spot areas within each island varied especially in 2006 (Table 2). In 2006, the observation trips corresponded with a full moon and high tides, likely resulting in larger territories where terrestrial boundaries fluctuated with the

Table 2. Size of hot spots and total study areas (m²) among each breeding colony of California sea lions (*Zalophus californianus*) during the 2004–2006 breeding seasons. Hot spots represent areas of high mean and low frequency for mapped territorial distributions (see Methods).

Island	Year	Area ID	Hot spot area (m²)	Site area (m²)
San Jorge	2004	1	125	1918
		2	125	3500
	2005	1	225	1918
		2	200	3500
	2006	1	25	1918
		2	275	3500
Granito	2004	1	75	7032
	2005	1	125	7032
	2006	1	75	7032
Los islotes	2004	1	325	2441
	2005	1	375	2441
	2006	1	125	2441

tide. Because of this, spatial overlap was less prevalent then it was in previous years. Other sources of variation may have included boundary disputes and fluctuations around topographical features, as well as fluctuations in the number of territorial males. Thus the location of hot spots indicates a center of activity among neighboring males, but also the importance of topographical features in settlement decisions.

From the male census and the regression analysis, female distribution was independent of male distribution. In contrast to our expectations, we did not find a correlation between territory size and the number of females per territory (Fig. 2). We also did not find a strong relationship between the occurrence of hot spots and the mean number of females per territory (Table 3). A possible reason for this is that the observed number of females per territory may have been an underestimate of true abundance because we did not correct for the numbers of females potentially foraging at sea (Peterson and Bartholomew 1967; Aurioles-Gamboa and Zavala-González 1994). However, it is likely that the same proportion of females would have been at sea from each territory. A more likely reason relates to the frequency by which females move freely between territories within the breeding site. In tropical climates when temperatures exceed 30 °C, otariids will move seaward or find shade for relief (Gentry 1973). During our study, mean temperatures ranged between 32–39 °C. Males spent the majority of their time in the water, while females routinely spent the afternoon floating in female rafts or moving with their pups towards shoreline habitat. Therefore, the given number of females in a territory varied depending on the weather and time of day (Francis 1987). Although uncommon, we have observed females at Los Islotes nursing their pups in one area and walking to another distinct area to rest.

Territory size varied between year and island, which could be explained by several possible reasons. Locations of territories shifted with tidal fluctuations, although to what degree was beyond the scope of this study. In addition, fluctuations in territory size were partly due to an influx of new territorial males during the peak of the breeding season

and from males abandoning their territory in which neighboring males would expand their boundaries. Other sources of variation are likely from using different methods to estimate territory size between years, as well as determining the center of a territory based on the male's position at the time. Males appeared to prefer a certain range of territory sizes between 90 and 260 m². In such cases, rather than expanding territory size when space is available, males tend to establish relatively small territories (e.g., mean size at San Jorge was 93.3 m² compared with 225.0 m² at Granito and 110.0 m² at Los Islotes). This may indicate that an upper limit exists in which sea lions are energetically willing to defend and maintain boundaries while fasting.

Aggression between males was relatively low in all years and at all breeding sites (Fig. 2). Low levels of aggression would be advantageous to territorial males trying to monopolize females as a way to economically conserve energy, since males fast during territory tenure. In northern fur seals (*Callorhinus ursinus* (L., 1758)), Gentry (1997) found that behavior was not necessarily correlated to higher copulatory success. Males were more likely to restrain from fighting and remain silent as females chose mating sites. Instead, males relied on prior residence and added additional area to their territory when possible because territory size led to higher copulatory success in future years. Similarly, territorial male Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) that share stable boundaries decrease the amount of time spent on boundary displays in conjunction with increased female population and copulation rates (Gisiner 1985). Male California sea lions bark incessantly during the breeding season. Besides social communication, barking most likely suppresses the need to fight by advertising a large male's dominance and status among his neighbors (Schusterman and Dawson 1968). This would help conserve energy and avoid risking injuries. Additionally, it can also act as a cue to ward off subadults from attempting to enter a male's territory (Schusterman and Dawson 1968). We also found that although males occupied areas relatively close to one another and often shared boundaries with 3–4 neighbors depending on the colony, 52% of the males during the census periods had no aggressive interactions during all 3 years combined. This suggests a certain tolerance level or familiarity among neighbors (e.g., "dear-enemy"; Peterson and Bartholomew 1967; Heath 1989).

Nearest neighbor distances did not appear to exert strong influence on territorial spatial patterns, which was evident by the regression analysis (Table 3). This is somewhat expected given that California sea lions have a prolonged breeding season and are asynchronous in their timing of estrus. Males would not derive any benefits by aggressively competing for mates who become sexually receptive at different intervals and over an extended period. In other otariids, when females are highly synchronous in their timing of estrus and the breeding season is fairly short, male competition is intense such that territorial systems are more rigid with nonoverlapping boundaries (Campagna and Le Boeuf 1988; Gisiner 1985; Gentry 1997). In contrast, we found aggression was low and boundary overlap (i.e., hot spots) was common. However, we did find that nearest neighbor distances differed significantly between years on Granito and Los Islotes. On Granito, males were widely dispersed (11–15 m)

Table 3. Regression models, R^2, Akaike's information criterion (AIC), ΔAIC, Akaike weight (ω_i), and sample size for logistical regression analysis of the occurrence of hot spots, areas of high mean and low standard deviation, to island, year, mean territory size, mean number of females per territory, male aggressive interactions, and distance to nearest neighbor (NN means nearest neighbor) of California sea lions (*Zalophus californianus*).

Model	R^2	AIC	ΔAIC	ω_i	N
1. $\beta_0 - \beta_1(\text{island}) + \beta_2(\text{year}) + \beta_3(\text{territory}) - \beta_4(\text{female}) + \beta_5(\text{aggression}) - \beta_6(\text{distNN})$	0.30	1273.09	0.00	0.99	1271
2. $\beta_0 - \beta_1(\text{island}) + \beta_2(\text{year}) - \beta_3(\text{distNN})$	0.28	1282.64	9.55	0.01	1271
3. $\beta_0 - \beta_1(\text{island}) + \beta_2(\text{year}) + \beta_3(\text{territory}) + \beta_4(\text{female})$	0.27	1299.59	26.50	0.00	1271
4. $\beta_0 - \beta_1(\text{island}) + \beta_2(\text{year}) + \beta_3(\text{territory}) + \beta_4(\text{female}) + \beta_5(\text{aggression})$	0.27	1301.21	28.13	0.00	1271
5. $\beta_0 - \beta_1(\text{island}) + \beta_2(\text{year}) + \beta_3(\text{territory})$	0.26	1304.23	31.14	0.00	1271

most likely from the site's long coastline, which favors large territories that were uniformly spaced. Males also commonly haul out on land and rest among female aggregations while maintaining terrestrial boundaries against intruding subadults. Thus neighboring males in the water may expand their boundaries during this time. On Los Islotes, males were closer together (6–10 m) and variation most likely was due to males trying to maintain their positions among the rocky inlets and platforms.

The mechanisms influencing spatial patterns could not be fully explained by our hypothesis that males are clumped in areas heavily used by females. Rather, space use appeared to be more influenced by habitat characteristics that favor thermoregulation then expected. In the Galápagos sea lions (*Zalophus wollebaeki* Sivertsen, 1953), Wolf et al. (2005) found that during the reproductive season adult males will forego mating opportunities and choose to occupy poor-quality habitat that offer shade and relief from the heat. Within southern sea lion populations at Puerta Piramide, Argentina, territories containing tidal pools and boulders are highly contested among males. In fact, those who are able to secure territories having the largest tide pools copulated more than males in lesser territories (Riedman 1990). However, our ability to identify areas heavily used by males warrants further research at varying spatial scales to fully understand the occurrence of these hot spots. In other words, our study may be able to further examine previous findings between aggression at intersecting boundaries and preferred areas favored by females for copulation (Gisiner 1985; Heath 1989) where territories are clustered around these areas.

As such the mating system of California sea lions has been described as a modified lek (Heath 1989), where territories may act as display arenas to attract females. This is believed to have evolved in response to tropical temperatures, thermoregulation requirements, and the prolonged period between parturition and estrus (Boness 1991; Wolf and Trillmich 2007). Our study may provide some support for this view given that the spatial use of territories among male California sea lions is relatively stable within and between breeding seasons despite the numbers of females within a given territory. Heath (1989) suggests that there is an element of tradition in the selection of mating sites by females. Females may choose to mate in certain areas, which incites male competition and allows females an opportunity to mate with the most competitive male. Thus, as females cool off in shallow tidal pools, they are able to interact with territorial males and select a mate. Although we did not record reproductive success, 12.7% of the territories contained no females, while only 3% of males had more

than 20 females in their territory; these findings provide some evidence that females are selecting among certain males. Moreover, the territories within the breeding sites are relatively homogenous so that it is difficult to discern if individual males are monopolizing valuable resources for females. Thus males may be selecting territories based on favorable environmental attributes that benefit them, as well as using vocalizations, body size, and the sagittal crest to display and attract females (Schusterman and Dawson 1968; Heath 1989).

Our study indicates that the spatial use of territories among male California sea lions is relatively stable within breeding seasons. Territorial areas appear to be influenced by the shape of the breeding colony, topography, and the male's inability to clearly define boundaries. Future studies on the space use of territorial males should investigate the influence of environmental variables (e.g., tidal patterns, available shade, and surface temperature) and address the mechanisms of female distribution. In addition, variables such as the age of the male, past experience, site fidelity, and copulatory success (Gisiner 1985; Heath 1989; Gentry 1997) have also been shown to influence territoriality and may shed more light on the mating system of California sea lions.

Acknowledgements

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