The Influence of Social Composition on Reproductive Behavior of Territorial Male California Sea Lions

Julie K. Young[1, 2] and Leah R. Gerber[1]

[1]*School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA; E-mail: jyoung@wcs.org*
[2]*Northern Rockies Field Office, Wildlife Conservation Society, 32 Campus Drive #4824,*
The University of Montana, Missoula, MT 59812-4824, USA

Abstract

The behavior of territorial males in a polygynous mating species may be influenced by a variety of factors related to site-specific conditions. In this paper, the behavioral dynamics of territorial male California sea lions (*Zalophus californianus*) are characterized throughout the breeding season and across rookery sites at Los Islotes Island in the Gulf of California, Mexico. Observations focused on three spatially distinct rookeries at Los Islotes that varied in the number and density of territorial males, the number of females, and the number of subadult males. Rates of male and female aggression were similar among sites and across the season. However, differences in female/territory defense and self-maintenance behaviors were exhibited by territorial males among sites and throughout the breeding season. Multiple regression analysis revealed a relationship between self-maintenance behavior and the number of females and males present. The time territorial males spent moving and in territorial maintenance was associated with the density of females within a territory. Males also exhibited higher levels of movement when more males were present. Finally, male California sea lions showed lower movement rates but higher amounts of time spent in territorial defense as the breeding season progressed. By comparing behaviors of territorial male California sea lions under different social compositions, this study illustrates the costs, benefits, and mechanisms of male territoriality.

Key Words: sea lion, *Zalophus californianus,* activity budget, bachelor group male, behavior, territorial male

Introduction

California sea lions (*Zalophus californianus*) are an ideal species for examining breeding behavior because they are polygynous (Riedman, 1990), sexually dimorphic, and occur at high densities during the breeding season (Berta & Sumich, 1999). Male sea lions establish semi-terrestrial territories that are relatively easy to observe for natural behavior studies. By establishing territories along coastlines important to females with pups, territorial males control access to females and likely obtain more mating opportunities than non-territorial males (Boness, 1991). During the breeding season, California sea lions in the Gulf of California, Mexico, are known to undergo heat-related thermal stress at rookeries, which may be alleviated by close proximity to the ocean or other properties specific to breeding sites (Riedman, 1990). The breeding season occurs over a few months, typically from late May to mid-July (Odell, 1975; García-Aguilar & Aurioles-Gamboa, 2003). Non-territorial males are often found in bachelor groups, which typically use sites that are near but spatially separated from adult territorial males, adult females, and young sea lions (Issa-Cabrera, 2006).

In this study, we examined whether territorial male California sea lions exhibit behavioral variation between breeding sites and over the breeding season. We predicted that territorial male California sea lions engage in more territorial defense and less self-maintenance behaviors at sites with higher sea lion densities. We also predicted that agonistic interactions should occur more frequently as the breeding season progressed. We tested these ideas by (1) determining social composition and density at three California sea lion breeding sites at Los Islotes in the Gulf of California, Mexico, (2) evaluating behaviors of territorial male California sea lions across sites during the same season, (3) examining behavioral differences at each site within a breeding season, and (4) assessing site-specific population features that may have contributed to any observed differences. Determining the extent to which territorial male behavior is influenced by population characteristics in a polygynous system will ultimately help explain the costs, benefits, and mechanisms of territoriality.

Materials and Methods

Study Site

During the summer of 2003, field research was conducted at Los Islotes Island (24° 58' N, 110° 23' W) in the Gulf of California (GoC) as part of a large-scale project on population demographics of California sea lions (Gerber, 2006). The Los Islotes population is increasing in abundance (Szteren et al., 2006). Males are found at three spatially discrete sites (A, B, & C) defined by physical boundaries, such as large rock outcrops, that create a natural barrier between sea lions and prevent researchers from observing sea lions beyond the barrier (Figure 1). Sites A and B were used by all age classes and adult territorial males. Physically, Site A (802 m^2) was the largest of the

Figure 1. Large boulders, especially those forming the edge of a cove as depicted here, were used to define the edges of each study site on Los Islotes in the Gulf of California, Mexico.

three breeding sites, and Site B (122 m^2) was the smallest (Issa-Cabrera, 2006). Site A included a large and open platform-like area, whereas the platform-like area at Site B was narrow and surrounded by rocky edges. Site C (254 m^2) was the most exposed to the wind and sea. It was historically used by non-territorial adult and subadult males in a bachelor group but recently became occupied by several territorial males, adult females (i.e., ≥ 5 y of age), and young sea lions (i.e., juveniles: 1 to 4 y of age; pups: 0 to 1 y of age) (Issa-Cabrera, 2006). These three sites were selected to allow within-island comparisons based on the unique attributes of each (Table 1).

Data Collection

Data were collected during four field expeditions, which took place 5-10 June, 6-11 July, 17-21 July, and 29 July–3 August 2003 (hereafter identified as trips one to four, or T1 to T4, respectively). Trip dates were selected to include information throughout an entire breeding season (Odell, 1975; García-Aguilar & Aurioles-Gamboa, 2003). During each trip, equal time was spent collecting data at each of the three breeding sites. Sea lion behavior was observed at each site during 4 d on T1, 2 d on T2 and T3, and 3 d on T4. Using a rangefinder and compass, the distance to nearest territorial male (m), territory size (m^2), and the number of females within each territory were recorded for each territorial male. Territorial boundaries were determined through mapping the location of male movements and interactions between territorial males. All data were collected during daylight hours.

Scan- and focal-animal sampling techniques were used to obtain behavioral data on territorial

Table 1. Average density and standard error of territorial adult male (M), adult female (F), and subadult male (SA) California sea lions (*Z. californianus*) located at three distinct sites during four field trips in the summer of 2003 to Los Islotes Island, Gulf of California, Mexico

Trip	Site	Male			Subadult			Female		
		Average	SE	Density	Average	SE	Density	Average	SE	Density
1	A	3.1	0.4	0.00	2.6	0.7	0.003	16.9	2.5	0.02
2	A	6.5	0.3	0.01	0.9	0.4	0.001	45.5	1.1	0.06
3	A	6.7	0.1	0.01	0.3	0.1	0.000	49.1	3.7	0.06
4	A	6.6	0.6	0.01	0.6	0.1	0.001	52.0	3.9	0.06
1	B	3.8	0.5	0.03	7.3	1.7	0.060	26.6	2.8	0.22
2	B	5.5	0.5	0.05	0.9	0.2	0.007	24.8	2.2	0.20
3	B	7.0	0.3	0.06	0.3	0.2	0.002	20.1	1.6	0.17
4	B	5.7	0.3	0.05	0.5	0.2	0.004	23.3	1.8	0.19
1	C	6.5	0.4	0.03	13.2	1.7	0.052	9.3	1.7	0.04
2	C	7.9	3.1	0.03	7.0	3.3	0.028	22.7	3.1	0.09
3	C	6.9	0.0	0.03	7.3	1.4	0.029	28.5	3.1	0.11
4	C	7.5	0.3	0.03	4.4	2.1	0.017	32.7	4.1	0.13

males during each of the four trips (Altmann, 1974). Random focal-animal sampling without replacement was used to provide the proportion of time individuals spent in different activities; whereas scan-sampling provided a comprehensive approach to evaluate different activities of males among and across sites (Altmann, 1974). Potential effects of the presence of observers on site on sea lion behavior were reduced by conducting all scans and focal-animal observations from high points overlooking each site. Scan-sampling was conducted at multiple times each day, with at least a 30-min interval between samples (mean = 4.29 scans/d, range = 1 to 13, $n = 222$) and treated as a repeated measure. During scan-sampling, we recorded the number of males, females, and subadult males engaged in 11 distinct behaviors (Table 2). For behavioral analyses, we focused only on male behavior and categorized behaviors into four groups (Table 2). Scan samples also provided information on the number of sea lions of different sex and age classes present at the sites.

Focal observations of animal behavior were conducted for 30 min on different, randomly chosen territorial males during each observation day. Sketches were made of individual territorial males to identify males and avoid re-sampling animals. Each focal sample was therefore treated as independent for analysis. During focal-animal observations, the duration of the territorial male's behavior in each of the 11 behaviors was recorded, with one exception: scratching self. Grooming, and playing were combined into an "other" category prior to collapsing the data into the four behavioral groups for analysis. Behavioral categories were collapsed based on biological relevance (Table 2). For example, peace keep and herd are behaviors that indicate direct interactions between males and females. Although patrol may at first be thought of as a form of conspecific interaction, it was combined with female maintenance behaviors

into a female/territory defense for two reasons: (1) herd and patrol behaviors are often difficult to distinguish from one another and (2) males do not directly interact with conspecific males while patrolling. Instead, when males directly interact with another male during patrol behaviors, the behavior is typically then classified as aggression or fight. Collapsing behaviors into four categories was also necessary because some behaviors had too low a frequency of occurrence to be evaluated independently.

Territories of most males extended into the water. Because the water is typically shallow and clear around the breeding sites, the male's behavior was observable in the water and on land for both focal and scan samples. The observation was terminated if a male moved out of sight or swam into deep waters.

Numbers of aggressive interactions by adult male and adult female sea lions were also collected independently of focal and scan data. For logistical reasons, we only collected this information on males during T1, but included females on T2 to T4. For adult males, we recorded all occurrences of aggressive events with another adult male or with subadult males. All occurrences of aggression by adult females were limited to those involving other adult females. Data were converted to rate (number of events/minute) of aggressive events for analysis.

Data Analysis
Analysis of variance (ANOVA) was used to assess potential differences in the distance to the nearest territorial male, territory size, and number of females within male territories among the three sites, among the four trips, and to examine potential interactions from sites and trips. The date of the measurements was used to avoid pseudo-replication. Tukey's *post hoc* comparison was applied when ANOVA revealed a significant difference.

Table 2. Behavior types, definitions, and categories for analysis of focal- and scan-sample data

Category	Behavior	Definition
Conspecific interaction	Fight	Physical contact with other male
	Mock aggression	Vocalizing and lunging at nonterritorial males
	Aggression	Nonphysical fighting with territorial males
Female/territory defense	Patrol	Delimiting territories
	Peace keep	Conciliatory behavior to reduce female aggression
	Herd	Active prevention of female departure
Self-maintenance	Rest	Lie down
	Scratch self	Scratch self with flippers or against substrate
	Sit upright	Front flippers hold up upper body; lower body on ground
Move	Swim	Locomotion in water
	Terrestrial movement	Walk or run on land or in surf

Most California sea lions lack scars or markings, and although we were able to identify and track individual males during observations within trips, we could not accurately identify individual males between trips. Territory turnover occurs throughout the breeding season (Riedman, 1990), so we were unlikely to observe the same territorial males during different trips. Thus, territorial males detected during each trip were treated as new individuals.

All data collected from focal- and scan-animal sampling were converted to proportions and arcsine transformed prior to analysis to meet assumptions of normality (Sokal & Rohlf, 1981). Data from scan-sample observations were compared among sites using ANCOVA with trip and date as covariates (Childress & Lung, 2003; Boness et al., 2006). For focal samples, we used an ANCOVA with trip as a covariate (Boness et al., 2006). Bonferonni adjustments for multiple comparisons were applied. A *p*-value for focal and scan samples at ≤ 0.01 (four independent tests) was established as significant.

Site, trip, number of females, and number of males were used as independent variables in a multiple regression to model the cumulative effects on variation in the proportion of territorial males engaged in (1) self-maintenance and (2) territorial defense behaviors during scans. Correlation coefficients were used to test for problems with multivariate collinearity. A stepwise general linearized model (GLM) was used to select the best model. Rates of aggressive interactions for females and males were compared between sites with Kruskal-Wallis tests. All values are presented as mean ± SE unless otherwise stated. Statistical analyses were conducted in *R2*, Version 2.1 (R Development Team, Vienna, Austria, 2005).

Results

Site-Specific Variables
Differences in population characteristics between sites and trips were identified. The number of territorial males and pups increased after T1 at each site, while the number of subadult males decreased (Table 1). The number of adult females and subadults varied among sites (Table 1), with the greatest number of subadults consistently at Site C and the greatest number of adult females typically at Site A. Tukey's *post hoc* comparisons revealed site differences in the number of adult females between Sites A and B ($p = 0.029$). Also, a difference in number of adult females per territory across sites ($F_{2,163} = 2.01$, $p = 0.033$) and by interaction of sites and trips ($F_{4,163} = 4.92$, $p = 0.0009$) was detected. The number of adult females per territory increased at Sites A and C across trips

while it declined at Site B (Table 1). Density was consistently lowest for territorial adult males and adult females at Site A and highest for subadult males at Site C (Table 1).

Territory attributes differed among sites. For territorial males, there was a significant difference in distance to nearest neighbor among trips ($F_{2,16} = 16.45$, $p < 0.001$, $n = 164$) and sites ($F_{2,16} = 5.29$, $p = 0.0059$, $n = 164$). Territorial males tended to be farther apart at Sites A and B ($p = 0.066$; Table 1), with significant differences between Sites A and C ($p = 0.006$) but not between Sites B and C ($p = 0.09$; Table 1). Notably, there was no interaction between sites and trips. Finally, a significant difference in territory size was revealed across trips ($F_{2,58} = 88.26$, $p < 0.001$, $n = 59$), among sites ($F_{2,58} = 123.50$, $p < 0.001$, $n = 59$), and between sites and trips ($F_{3,58} = 70.77$, $p < 0.001$, $n = 59$).

Behavior
Agonistic behavior by males was observed over 13.6, 17.3, 8.8, and 23.1 h during T1, T2, T3, and T4, respectively, and agonistic behavior by females was observed for 9.6, 1.0, and 4.3 h during T2, T3, and T4, respectively. Although territorial attributes differed, the number of aggressive events per minute for territorial males was comparable among the three sites and four trips. Similarly, there were no significant differences for the number of aggressive events per minute by females located within male territories among sites.

Territorial males spent the greatest proportion of time resting, patrolling, and sitting upright. For individual behaviors recorded during focal samples, there was a significant difference in the proportion of time males spent in terrestrial movement among trips ($F_{3,11} = 11.71$, $p = 0.0027$). This difference reflected the significantly greater proportion of time males were engaged in movement during T1 compared to T2 ($p = 0.0042$), T3 ($p = 0.0042$), and T4 ($p = 0.0154$). Yet, based on the four behavioral groups, there were no significant behavioral differences among sites or trips.

Of the four behavioral groups used for scan samples, self-maintenance ($F_{2,219} = 16.09$, $p < 0.001$) and female/territory defense ($F_{2,219} = 28.39$, $p < 0.001$) behaviors were significantly different across sites, with more territorial males engaged in both behaviors at Site C. There were also differences across trips for the proportion of males engaged in self-maintenance ($F_{2,219} = 11.41$, $p < 0.001$) and territorial defense behaviors ($F_{2,219} = 19.24$, $p < 0.001$; Figure 2). Specifically, a greater proportion of territorial males were engaged in maintenance behaviors and fewer were engaged in female/territory defense behaviors during T1.
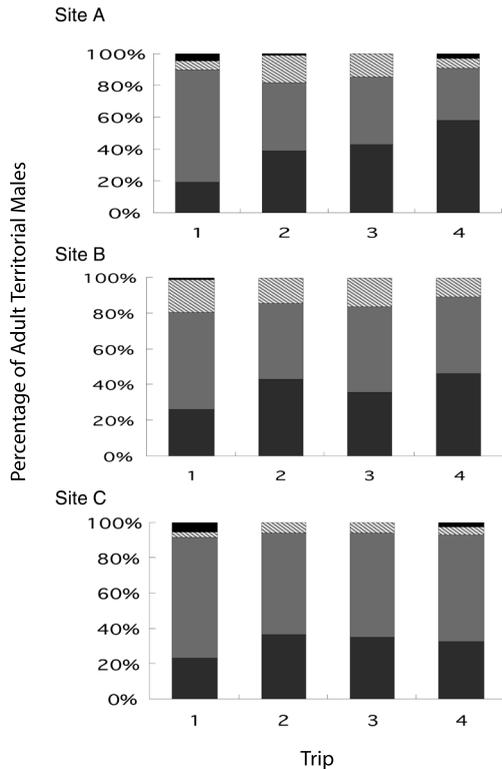
Figure 2. Percent of adult territorial male California sea lions engaged in four behavioral groups (interaction, movement, self-maintenance, and female/territorial defense) during scan samples across the breeding season at three sites on Los Islotes; trip dates were (1) 5-10 June, (2) 6-11 July, (3) 7-21 July, and (4) 29 July–3 August 2003.

The best multiple regression model for female/territory defense included site, trip, and the interaction between site and trip ($R^2 = 0.201$, $p < 0.001$). This differed from the best model for self-maintenance behavior, which included trip, number of females and males, interaction between site and trip, and the interaction between number of females and males ($R^2 = 0.191$, $p < 0.001$). Based on these models, female/territory defense behaviors were positively related to trip and the number of females present but negatively related to the interaction between trip and site and the number of males present; whereas self-maintenance behaviors were negatively correlated to trip and the number of conspecifics present.

Discussion

According to results from this study, territorial male California sea lions alter some behavioral strategies during the breeding season based on social group composition. Behavioral variation can explain variance in male reproductive success (Fabiani et al., 2004). Thus, determining if breeding behaviors of territorial males vary under different conditions may reveal some of the benefits, costs, and mechanisms of territoriality. Although in this study territorial male density varied across sites and throughout the breeding season, these differences did not translate into differing rates of agonistic interactions. In contrast, in grey seals (*Halichoerus grypus*), higher numbers of males were directly correlated with higher rates of aggressive events (Anderson & Hardwood, 1985; Twiss et al., 1998). When male grey seals were involved in agonistic interactions, incidental pup mortality and greater female harassment occurred (Higgins & Tedman, 1990; Boness et al., 1995; Chilvers et al., 2005). Furthermore, there is a trade-off between winning agonistic interactions and the energy demands of interactions (Modig, 1996). Male sea lions at Los Islotes may be actively avoiding interactions when the number of males increases. The observed increase in male territory size over the breeding season may alleviate the potential for agonistic interactions. The multiple regression results indicated males may engage in less self-maintenance and female/territory defense behaviors when more males are present. Altering behaviors may be another strategy to avoid engaging in more aggressive interactions. Mechanisms male sea lions use to avoid interactions at higher densities are unclear, and further research on the role of male aggression under different population compositions would shed light on these uncertainties.

Female sea lions are philopatric to breeding sites (Maldonado et al., 1995). Thus, as a breeding season proceeds, more females return from sea to occupy each site during parturition (García-Aguilar & Aurioles-Gamboa, 2003). Female gregariousness reduces the reproductive costs of interacting with males (Boness et al., 1995; Cassini & Fernández-Juricic, 2003; Kiyota & Okamura, 2005), which may further explain why the number of California sea lion females present within territories generally increased over the breeding season, even though the number of territorial males remained relatively stable (Table 1). Although in this study the number of females increased over the breeding season, there was no difference in the rate of female agonistic interactions. Similar to the results of this study, Francis (1987) found that the number of female California sea lions was not related to the frequency of aggressive interactions. However, a relationship between the number of females and rates of agonistic events was observed in South American sea lions (*Otaria flavescens*) (Cassini & Fernández-Juricic, 2003) and New Zealand fur seals (*Arctocephalus forsteri*) (Carey,

1992). Agonistic interactions between female New Zealand fur seals occurred most frequently in areas with shade and pools of water that were ideal for thermoregulation (Carey, 1992), while female South American fur seals (*A. australis*) with pups were more aggressive than females without pups (Harcourt, 1992). Furthermore, the increase in number of females per territory only occurred at two of three sites, suggesting ideal free distribution may occur in California sea lions (Fretwell & Lucas, 1970). It is unclear if females at Los Islotes preferred Site B. Female occupancy of Sites A and C only increased when there was limited space at Site B or if females engaged in site-specific philopatry. Since female preferences ultimately could result in different female quality patterns across breeding sites at the same island (Twiss et al., 2000), further studies are needed.

The results provided herein should be interpreted with caution in light of a few caveats: If sites include territorial males with completely aquatic territories, they were not included in this study; male behaviors occurring in water may have been underestimated; and climatic microhabitat conditions may vary between years. Based on observations within this study, there is no evidence suggesting fully aquatic territories occur at Los Islotes. If they do occur, they would probably be physically similar between sites. It is unlikely that exclusion of fully aquatic territorial males would influence the findings (Francis & Boness, 1991; Twiss et al., 2006). Finally, behavior is likely to vary based on changes in climatic and resource availability, or whether the individual is onshore, in surf, or in deeper waters. These changes would likely be expressed throughout the entire island, however, and therefore are unlikely affecting comparisons across sites.

The results of this study showed that territorial male sea lions altered their behavior between sites and over the breeding season. More males may have engaged in movement behaviors during the first trip because it was early in the breeding season when males may be less familiar with one another. Intrusions are less likely to occur once territorial males are familiar with neighboring males (Fisher, 1954; Hyman & Hughes, 2006). Indeed, these results indicated distance to the nearest territorial neighbor decreased over the breeding season without influencing the rate of agonistic interaction, and males at Site C, where the most nonterritorial, unfamiliar subadults occurred, engaged in the most female/territory defense behaviors. Self-maintenance behaviors declined with increasing numbers of females and males. Similarly, territorial male Steller sea lions (*Eumetopias jubatus*) with a greater number of females present, spend less time resting than other males (Mamaev,

1997). However, larger harem size in elephant seals (*Mirounga leonine*) did not correlate with male behaviors other than an increase in agonistic interactions (Modig, 1996). Results of this study suggest that site-specific conditions, such as immediate population structure (i.e., number of females present), had the most influence on territorial male behaviors, while seasonal variables (i.e., population density) are less influential. Additional investigations that examine male sea lion behavior across broader geographical and time scales should be pursued to clarify remaining uncertainties.

Literature Cited

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*, 227-267.

Anderson, S. S., & Hardwood, J. (1985). Time budgets and topography: How energy reserves and terrain determine the breeding behavior of grey seals. *Animal Behaviour*, *33*, 1343-1348.

Berta, A., & Sumich, J. L. (1999). *Marine mammals: Evolutionary biology.* San Diego: Academic Press. 576 pp.

Boness, D. J. (1991). Determinants of mating systems in the Otariidae (Pinnipedia). In D. Renouf (Ed.), *The behavior of pinnipeds* (pp. 1-44). New York: Springer-Verlag. 424 pp.

Boness, D. J., Bowen, W. D., & Iverson, S. J. (1995). Does male harassment of females contribute to reproductive synchrony in the grey seal by affecting maternal performance? *Behavioral Ecology and Sociobiology*, *36*, 1-10.

Boness, D. J., Bowen, W. D., Buhleier, B. H., & Marshall, G. J. (2006). Mating tactics and mating system of an aquatic-mating pinniped: The harbor seal, *Phoca vitulina*. *Behavioral Ecology and Sociobiology*, *61*, 119-130.

Carey, P. W. (1992). Agonistic behavior in female New Zealand fur seals, *Arctocephalus forsteri*. *Ethology*, *92*, 70-80.

Cassini, M. H., & Fernández-Juricic, E. (2003). Costs and benefits of joining South American sea lion breeding groups: Testing the assumptions of a model of female breeding dispersion. *Canadian Journal of Zoology*, *81*, 1154-1160.

Childress, M. J., & Lung, M. A. (2003). Predation risk, gender, and the group size effect: Does elk vigilance depend upon the behaviour of conspecifics? *Animal Behaviour*, *66*, 389-398.

Chilvers, B. L., Robertson, B. C., Wilkinson, I. S., Duignan, P. J., & Gemmell, N. J. (2005). Male harassment of female New Zealand sea lions, *Phocarctos hookeri*: Mortality, injury, and harassment avoidance. *Canadian Journal of Zoology*, *83*, 642-648.

Fabiani, A., Galimberti, F., Sanvito, S., & Hoelzel, A. R. (2004). Extreme polygyny among southern elephant seals on Sea Lion Island, Falkland Islands. *Behavioral Ecology*, *15*, 961-969.

Fisher, J. (1954). Evolution and bird sociality. In J. Huxley, A. C. Hardy, & E. B. Ford (Eds.), *Evolution as a process* (pp. 71-83). London: Allen & Unwin. 281 pp.

Francis, J. M. (1987). Interfemale aggression and spacing in the northern fur seal *Callorhinus ursinus* and the California sea lion *Zalophus californianus*. Santa Cruz: University of California. 155 pp.

Francis, J. M., & Boness, D. J. (1991). The effect of thermoregulatory behaviour on the mating system of the Juan Fernandez fur seal, *Arctocephalus philippii*. *Behaviour*, *119*, 103-126.

Fretwell, S. D., & Lucas, H. L., Jr. (1970). On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, *19*, 16-36.

García-Aguilar, M. C., & Aurioles-Gamboa, D. (2003). Breeding season of the California sea lion (*Zalophus californianus*) in the Gulf of California, Mexico. *Aquatic Mammals*, *29*(1), 67-76.

Gerber, L. R. (2006). Including behavioral data in demographic models improves estimates of population viability. *Frontiers in Ecology and the Environment*, *8*, 419-427.

Harcourt, R. (1992). Maternal aggression in the South American fur seal in Peru. *Canadian Journal of Zoology*, *70*, 320-325.

Higgins, L. V., & Tedman, R. A. (1990). Effect of attacks by male Australian sea lions, *Neophoca cinerea*, on mortality of pups. *Journal of Mammalogy*, *71*, 617-619.

Hyman, J., & Hughes, M. (2006). Territory owners discriminate between aggressive and nonaggressive neighbours. *Animal Behaviour*, *72*, 209-215.

Issa-Cabrera, M. (2006). *Comparacion de la conducta maternal y la condicion corporal de crias de lobo marino de California en dos zonas reproductivas de la colonia de lobo marino Los Islotes.* La Paz, Mexico: Universidad Autónoma de Baja California Sur.

Kiyota, M., & Okamura, H. (2005). Harassment, abduction, and mortality of pups by nonterritorial male northern fur seals. *Journal of Mammalogy*, *86*, 1227-1236.

Maldonado, J. E., Davila, F. O., Stewart, B. S., Geffen, E., & Wayne, R. K. (1995). Intraspecific genetic differentiation in California sea lions (*Zalophus californianus*) from southern California and the Gulf of California. *Marine Mammal Science*, *11*, 46-58.

Mamaev, E. G. (1997) Time budget and activities of *Eumetopias jubatus* (Pinnipedia, Otariidae) bulls in reproduction. *Zoologichesky Zhurnal*, *76*, 94-500.

Modig, A. O. (1996). Effects of body size and harem size on male reproductive behaviour in the southern elephant seal. *Animal Behaviour*, *51*, 1295-1306.

Odell, D. K. (1975). Breeding biology of the California sea lion, *Zalophus californianus. Rapports et Proces-Verbaux de Reunions Conseil International pour L'exploration de la Mer*, *169*, 374-378.

R Development Team. (2005). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. ISBN 3-900051-07-0. Retrieved 26 February 2008 from www.R-project.org.

Riedman, M. (1990). *The pinnipeds: Seals, sea lions, and walruses.* Berkeley: University of California Press. 425 pp.

Sokal, R. R., & Rohlf, F. J. (1981). *Biometry: The principles and practice of statistics in biological research.* San Francisco: W. H. Freeman Company. 859 pp.

Szteren, D., Aurioles, D., & Gerber, L. R. (2006). Population status and trends of the California sea lion (*Zalophus californianus californianus*) in the Gulf of California, Mexico. In A. Trites, S. Atkinson, & D. DeMaster (Eds.), *Sea lions of the world: Conservation and research in the 21st century* (22nd Wakefield Fisheries Symposium) (pp. 1-17). Fairbanks: Alaska Sea Grant College Program, University of Alaska Fairbanks. 653 pp.

Twiss, S. D., Anderson, S. S., & Monaghan, P. (1998). Limited intra-specific variation in male grey seal (*Halichoerus grypus*) dominance relationship in relation to variation in male mating success and female availability. *Journal of Zoology*, *146*, 259-267.

Twiss, S. D., Poland, V. F., Graves, J. A., & Pomeroy, P. P. (2006). Finding fathers: Spatio-temporal analysis of paternity assignment in grey seals (*Halichoerus grypus*). *Molecular Ecology*, *15*, 1939-1953.

Twiss, S. D., Caudron, A., Pomeroy, P. P., Thomas, C. J., & Mills, J. P. (2000). Finescale topographical correlates of behavioural investment in offspring by female grey seals, *Halichoerus grypus*. *Animal Behaviour*, *59*, 327-338.