

# Determinants of agonistic interactions in California sea lions

Julie K. Young<sup>1</sup>, Manuela González-Suárez & Leah R. Gerber

(School of Life Sciences, Arizona State University, Tempe, AZ 85287-4501, USA)

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## Summary

California sea lions aggregate in high density colonies during the breeding season. Competition for space and mates results in agonistic interactions that may have long-term population consequences. We explored how demographic, behavioral, and environmental variables influence the rate of agonistic interactions in male and female California sea lions at three breeding colonies with varying population trends and distributed across a wide latitudinal gradient within the Gulf of California, Mexico. Our results indicate that male agonistic interactions are related to environmental and spatial parameters, whereas female interactions are related to male interactions, operational sex ratio (OSR) and environmental parameters. Most demographic and environmental parameters were inversely related to rates of agonistic interactions, with the exception of positive relationships between agonistic interactions and territory size for males and OSR for females. In addition, the highest overall rates of aggression were associated with a declining population. Our findings suggest agonistic interactions may be useful in assessing population dynamics, but additional research is needed to identify mechanistic relationships.

*Keywords:* aggression, marine mammal, population ecology, population trend.

## Introduction

Game theory predicts that individuals should balance the cost of agonistic interactions with the value of potential resources that will be gained (Maynard Smith & Parker, 1976; Hammerstein, 1981; Parker & Rubenstein, 1981;

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<sup>1</sup>) Corresponding author's current address: Wildlife Conservation Society, Northern Rockies Field Office, University of Montana, Division of Biological Sciences, Missoula, MT 59812-4824, USA, e-mail: [jyoung@wcs.org](mailto:jyoung@wcs.org)

Hammerstein & Parker, 1982). In order to obtain and defend a resource, individuals must balance both direct (e.g., injury to participant) and indirect (e.g., reduced maternal performance) costs. For example, female grey seals (*Halichoerus grypus*) aggressively defend space for themselves and their pups, but aggression sometimes results in injuries to the female and reduced maternal performance (Boness et al., 1995). Injuries and reduced maternal performance can lead to lower weaning mass of offspring (Boness et al., 1995). Thus, aggression rates could ultimately influence population dynamics.

Agonistic interactions may influence population dynamics in several ways. Amplified male aggression rates can lower female survival and fecundity, causing populations to collapse (e.g., common lizard *Lacerta vivipara*; Le Galliard et al., 2005) or prevent recovery after population declines (e.g., Hawaiian monk seal *Monachus schauinsland*; Hiruki et al., 1993). Aggression can also increase emigration (e.g., female yellow-bellied marmots *Marmota flaviventris*; Armitage, 1991), prevent immigration (e.g., golden lion tamarins *Leontopithecus rosalia*; Baker & Deitz, 1996), or reduce recruitment by reducing neonate survival (e.g., northern elephant seals *Mirounga angustirostris*; Christenson & Le Boeuf, 1978). Further, studies have long recognized that aggression can limit or regulate mammalian reproduction through spatial and dominance behaviors (i.e., Errington, 1962; Krebs, 1970; Wasser & Barash, 1983). Thus, exploring aggressive behavior may help explain unexpected population trends, and could provide valuable insight for management of imperiled populations.

California sea lions (*Zalophus californianus*) occur along the Pacific coast of North America and into the Gulf of California, Mexico. The population in the Gulf of California (GoC) has declined >20% in the last decade (Szteren et al., 2006). However, rates of decline are not uniform among colonies, with some consistently increasing and others continuously declining or exhibiting fluctuations (González-Suárez et al., 2006; Szteren et al., 2006). Because population declines may result from increased agonistic interactions (e.g., Le Galliard et al., 2005), we compared agonistic behavior at three colonies with varying population trends. These colonies also capture environmental and geographical variability. The islands that harbor these colonies are distributed along a latitudinal gradient in the GoC and differ in size, proximity to other islands and urban areas, and morphology. These differences among the colonies allowed us to explore a range of variables that may elucidate the determinants of agonistic interactions in this species.

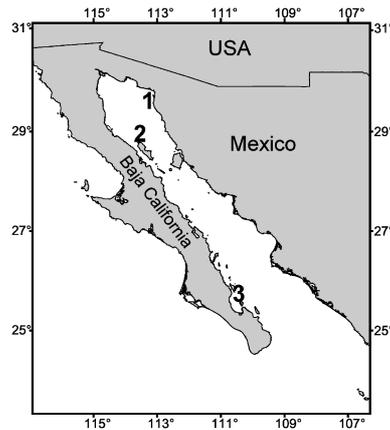
Air temperature is one of the variables that may differ across islands and could be important to sea lion behavior. Both female and male sea lions are sensitive to high air temperature and direct solar radiation as a result of their thick layers of blubber and fur (Riedman, 1990). During the breeding season, high temperatures in the GoC ( $>30^{\circ}\text{C}$ ) require the use of behavioral mechanisms of thermoregulation to avoid thermal stress (Matsuura & Whittow, 1975; Whittow et al., 1975). Cooling behaviors include occupying shaded and windy areas (Wolf et al., 2005) and reducing activity (Whittow et al., 1975). Strong waves and windy sea conditions may also affect behavior by reducing overall activity (Bjorge et al., 2002).

In this study, we evaluated the relationship between the demographic, behavioral, and environmental variables that may influence the rate of agonistic interactions in male and female California sea lions. Males should be less likely to engage in agonistic interactions if territories are larger and neighboring territorial males are further apart as fewer competitors will be found in close proximity. Thus, we hypothesized that higher rates of aggression in males will be positively related to site density, but that male aggression will be inversely related to female aggression rates, distance to nearest territorial neighbor, territory size, and the ratio of breeding females per breeding males, called operational sex ratio (OSR). Because adult female sea lions fight to defend space to give birth and care for pups, we predicted higher rates of female agonistic interactions at sites with higher OSR. We further predicted both males and females would fight over thermally favorable areas and that both sexes would reduce their overall activity (and, thus, their agonistic interactions) at higher temperatures. We also expected aggression rates to be negatively related to sea state. Finally, we expected higher rates of female and male aggression for declining populations (Le Galliard et al., 2005), and higher rates of female aggression for areas characterized by low reproduction rates (Cassini, 1999).

## **Material and methods**

### *Study site and species*

California sea lions are polygynous and sexually dimorphic pinnipeds that breed on land and likely exhibit site fidelity. Because adequate breeding areas are often limited, sea lions occur at high densities and engage in frequent



**Figure 1.** Location of three California sea lion breeding colonies (1, San Jorge, 31°01'N, 113°15'W; 2, Granito, 29°34'N, 113°32'W; 3, Los Islotes, 24°35'N, 110°23'W) in Gulf of California, Mexico.

agonistic interactions during the breeding season (May–July, García-Aguilar & Aurióles-Gamboa, 2003). Males fight to defend territories where females aggregate in order to secure mating opportunities (Riedman, 1990). Male territories are spatially distinct within breeding seasons, but females move among territories (Robertson et al., 2008). Most territorial males abandon their territories and some abandon the colonies outside of the breeding season. Females with young typically remain at the colony throughout the year.

During 2004–2006 we collected behavioral and population data at three, spatially discrete breeding colonies during each reproductive season (June–August) in the GoC, Mexico (Figure 1). These colonies include a rapidly increasing population at Los Islotes, a moderately increasing population at San Jorge, and a moderately declining population at Granito (Szteren et al., 2006). Data were collected from two replicate sites on each island. Sites were separated from one another by physical barriers that limited sea lion movement. For example, sites on San Jorge and Los Islotes were located on opposite coastlines, while sites on Granito were spatially distinct coves. Sea lions may move between sites, but most show site fidelity within a breeding season (e.g., Robertson et al., 2008).

#### *Field observations*

Each field season, we conducted two to three 10-day field expeditions to each island such that data were collected over the entire breeding season. At each

site, we recorded all male–male and female–female agonistic interactions for 1 h, two or three times each day.

Agonistic interactions included aggressive encounters (e.g., chasing and calling) and fights (physical contact) between two adults of the same sex. Aggression between adults of opposite sex is rare in sea lions and, therefore, not considered in our study. Occasionally a pair of individuals interacted multiple times over a short period of time. These repeated interactions were treated as a single event if they occurred within 3 min of one another. Interactions initiated more than 3 min after the last bout were recorded as a new event.

Some individuals were likely observed more than one time per day or trip. Because we could not always identify individuals, some could be over-represented in our treatment of all interactions as independent. During 2006, we identified all territorial males at San Jorge using photo identification (M. González-Suárez, unpublished data). In this study, we recorded aggressive interactions from 92% ( $N = 23$ ) of the identified males. Although data from females and other islands or years may be different; we have no reason to expect deviation from this pattern.

We also obtained data on parameters that may be related to agonistic interactions. First, we conducted daily counts of the total number of individuals at each site within each age/sex category based on demographic definitions established by Le Boeuf et al. (1983). Counts were used to determine site density and reproductive rates. For density, area estimates for each site were obtained by creating polygons in ArcGIS from the GPS coordinates of each site's perimeter (land and water). For reproductive rates, we used the ratio of the daily maximum number of pups standardized over the maximum number of females at each site. Maximum counts per trip were used because previous research suggests that the number of pups is frequently underestimated in population counts (Le Boeuf et al., 1983), and similar underestimates likely occurred for females because individuals feeding at sea would not be counted. Second, we monitored territorial male behavior three times each day. We recorded information specific to each territory, including territory size, number of females and pups present, and distance to nearest territorial neighbor. Prior to observations, the intersections of  $5 \times 5$  m cells were painted at each site to obtain more accurate estimates of territory size and distance to nearest neighbor. Direct observations of border disputes and patrolling behaviors helped us delineate territory boundaries. The number of females present per territory was used to

estimate OSR (Gerber, 2006). Finally, we obtained daily measurements of air temperature and sea state on the Beaufort scale. Air temperature was recorded in the shade using hand-held thermometers up to six times a day at each site. The same location was used at each site to record temperatures. Sea state on the Beaufort scale was measured by direct observations.

### *Statistical analyses*

Aggression events were converted to a rate (number of events/hour) and each hourly rate was treated as an independent sample in our analysis. Statistical analyses were conducted in SAS (SAS 9.13). We used analysis of variance to determine if there were differences across islands in all measured variables. Sites within islands were used as a covariate. To determine if there were differences between islands in male–male and female–female hourly agonistic interaction rates, we used a repeated measure of variance (PROC MIXED procedures in SAS (SAS 9.1.3)) with trip and year as repeated measures. To evaluate the influence of other parameters on hourly aggression rates for males and females, we used generalized linear models (PROC GENMOD with Poisson distribution in SAS). We selected Poisson distribution because the data are discrete observations and agonistic interactions are infrequently observed. We used trip and year as repeated measurements, such that there were up to seven repeated periods per site. Repeated measures were typed as compound symmetry for site and autoregressive for trip. Autoregressive is appropriate for time sensitive variables, such as trip because it assumes measurements that are farther apart have lower correlation, while compound symmetry assumes equal correlation between all measurements. Island was treated as a fixed variable.

For male aggression rates, we evaluated the influence of OSR, distance to nearest neighbor, territory size, site density, temperature, sea state on the Beaufort scale and the rate of female aggressions as independent variables. For female aggression rates, we used reproductive rate, temperature, sea state on the Beaufort scale, male aggression rates, and OSR as independent variables. For both models, we only included variables that were not correlated based on Pearson's correlation coefficients. Thus, because site density and reproductive rates were highly correlated ( $r = 0.89$ ,  $p < 0.05$ ,  $N = 507$ ), we used site density for our male model but reproductive rates for our fe-

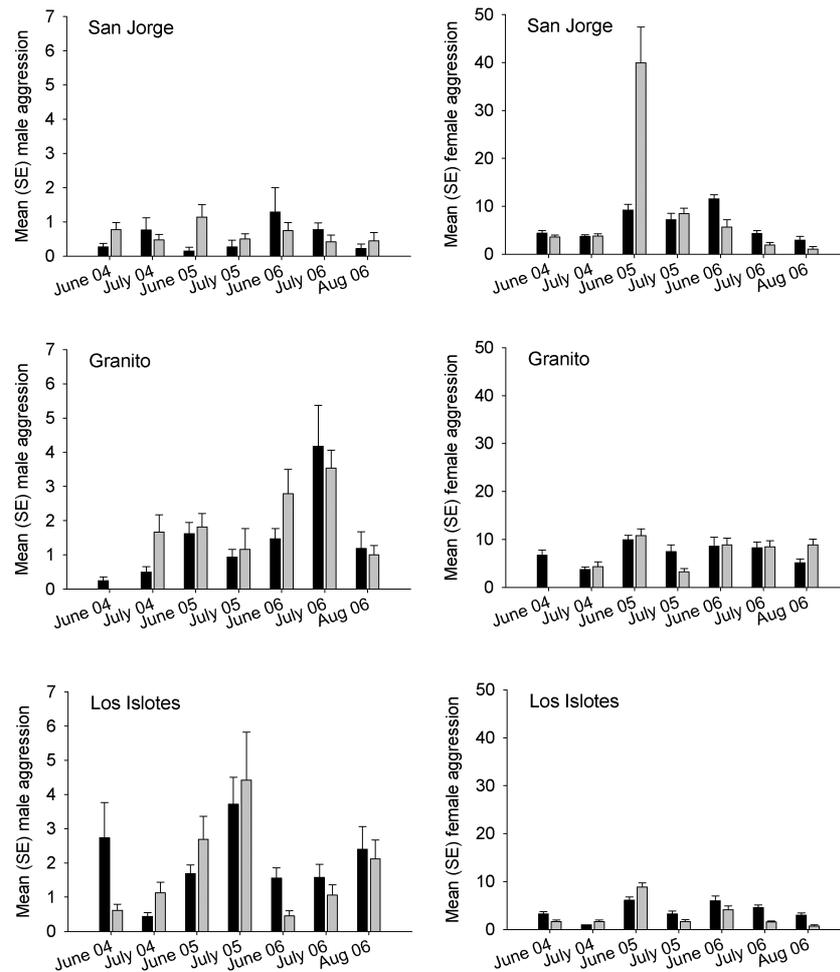
male model to best evaluate the biologically relevant variable for each sex. Because female aggression in June 2006 was extremely high at San Jorge and may represent an outlier (Figure 2), we excluded all June 2006 female interactions from San Jorge and repeated the analysis. Interactions were similar in direction and level of significance, so only results from our full data set are shown. Values are reported as mean  $\pm$  standard error, and statistical significance was defined as  $p < 0.05$ .

## Results

Male and female agonistic interactions were recorded for  $15.7 \pm 0.6$  h at each site during each trip. Significant differences in male ( $F_{2,11} = 11.07$ ,  $p < 0.002$ ) and female aggression rates ( $F_{2,11} = 7.78$ ,  $p < 0.008$ ) occurred across islands. In particular, males had significantly lower rates of aggression at San Jorge, while rates were similar between Los Islotes and Granito (Figure 2). Females showed lower hourly aggression rates at Los Islotes (a colony with an increasing, small population), but female agonistic rates at San Jorge and Granito were similar (Figure 2).

We found differences among islands for population densities ( $F_{1,36} = 73.36$ ,  $p < 0.001$ ), territory size ( $F_{1,35} = 6.25$ ,  $p = 0.02$ ), reproductive rate ( $F_{1,38} = 12.59$ ,  $p = 0.001$ ) temperature ( $F_{1,36} = 10.10$ ,  $p < 0.001$ ) and Beaufort sea state ( $F_{1,36} = 12.88$ ,  $p < 0.001$ ). Density was lowest at Granito ( $0.01 \pm 0.001$  individuals/m<sup>2</sup>) compared to Los Islotes ( $0.04 \pm 0.003$  individuals/m<sup>2</sup>) and San Jorge ( $0.04 \pm 0.004$  individuals/m<sup>2</sup>), and territory size was largest at Granito ( $210.1 \pm 35.3$  m<sup>2</sup>) compared to San Jorge ( $101.6 \pm 21.0$  m<sup>2</sup>) and Los Islotes ( $115.8 \pm 13.5$  m<sup>2</sup>).

Reproductive rates increased with latitude across islands ( $0.70 \pm 0.05$  pups/female at Los Islotes,  $0.90 \pm 0.08$  pups/female at Granito and  $1.19 \pm 0.14$  pups/female at San Jorge). Average temperature was highest at Granito ( $34.9 \pm 0.7^\circ\text{C}$ ) compared to San Jorge ( $32.5 \pm 0.5^\circ\text{C}$ ) and Los Islotes ( $32.0 \pm 0.6^\circ\text{C}$ ), but Beaufort sea state was highest at San Jorge ( $2.1 \pm 0.1$ ) compared to Granito ( $1.3 \pm 0.1$ ) and Los Islotes ( $1.5 \pm 0.1$ ). OSR ( $F_{1,37} = 2.64$ ,  $p = 0.11$ ,  $6.03 \pm 0.46$  females/male) and distance to nearest territorial neighbor ( $F_{1,38} = 0.08$ ,  $p = 0.78$ ,  $5.55 \pm 0.73$  m) were similar across islands.



**Figure 2.** Average hourly rate  $\pm$  SE of male and female California sea lion agonistic interactions at two study sites within three rookeries. For each island, study site 1 is represented by black bars and study site 2 by gray bars. Note different y-axis scale.

Our general linearized mixed model indicated that distance to nearest neighbor, territory size, ambient temperature, and sea state are strongly related to male aggression rates (Table 1). For males, we found inverse relationships between agonistic interaction rates and all significant parameters except territory size (Table 1). For females, our model indicated that all variables were influential except reproductive rate (Table 1). Rates of agonism

**Table 1.** Statistical results from generalized linear models to evaluate the relationship between male or female agonistic interactions and site specific parameters.

Sex	Parameter	$\chi^2$	<i>p</i>	Relationship
Male	Intercept	24.00	< 0.0001	+
	Territory size	26.22	< 0.0001	+
	Sea state	14.45	< 0.0001	–
	Temperature	14.34	0.0002	–
	Distance NN	6.23	0.0126	–
	Density	1.40	0.2359	–
	Aggression rate	0.05	0.8280	–
	OSR	0.00	0.9617	–
Female	Female intercept	430.76	< 0.0001	+
	OSR	68.57	< 0.0001	+
	Temperature	218.44	< 0.0001	–
	Sea state	126.77	< 0.0001	–
	Male aggression rate	28.30	< 0.0001	–
	Reproductive rate	2.47	0.1164	–

in females were greater with high OSR, but all other significant parameters were inversely related to agonistic interactions (Table 1).

## Discussion

Our results provide evidence that sea lions in the GoC exhibit variability in rates of agonistic interactions (Figure 2). This contrasts with female southern fur seals (*Arctocephalus australis*) that appear to have similar intensities of aggression at different colonies (Cassini, 2001). The variation may reflect sex-specific responses to environmental, behavioral, or demographic variables that also differed across islands. In fact, our results indicate that male agonistic interactions relate to environmental and spatial parameters, whereas female interactions relate to male interactions, OSR, and environmental parameters. Agonistic interactions between males may be related to spatial resources because males are typically attempting to gain or maintain reproductive territories. Successfully obtaining a territory may improve breeding success and the likelihood of obtaining territories in subsequent years (e.g., Renison et al., 2003, 2006). In our study, male aggression rates were higher in areas where male territories were larger but neighbors were

closer. Although apparently conflicting, these two relationships may reflect distinct consequences of male aggressive behavior: aggression is likely to be associated with larger territories and closer proximity to neighbors because aggressive males may be more often found in proximity to neighbors with which they interact frequently (Spritzer et al., 2006).

Females engage in agonistic interactions to establish locations for rearing offspring that likely result in higher offspring survival (Renison et al., 2003). Although we did not observe a relationship between reproductive rates and female interactions, female agonistic behavior occurred most frequently in areas with high female-biased sex ratios (high OSR). Resting and nursing sites are less available when the density of females is high and is likely to result in more interactions between females as they defend their space and their pups (Francis, 1987; Cassini & Fernández-Juricic, 2003).

Our results suggest that agonistic interactions do not relate to reproductive rates, unlike the relationship observed in other marine mammals (e.g., Boness et al., 1995). It is possible that interactions occurred at too low a rate to cause stress or injuries that would reduce reproduction. Although reproductive rates were not related to agonistic interactions, female agonistic interactions were positively related to OSR, suggesting a mechanism by which aggression may affect population dynamics. Investigating the relationship between population dynamics and behaviors with time lags may provide insight into this role (Gerber et al., unpublished data).

In this study, both male and female agonistic interactions were related to environmental conditions. As predicted, interactions occurred less frequently when temperatures were higher and sea conditions were rougher. Similarly, in male Hawaiian monk seals differences were related to differences in environmental variables across islands (Boness et al., 1998). Cassini (2001) noted that female southern fur seals were more likely to engage in aggression when thermoregulation needs were highest and a similar relationship is suggested for South American sea lions (Fernández-Juricic & Cassini, 2007). At high temperatures sea lions are likely to engage in fewer agonistic interactions to reduce their risk of thermal stress. The observed reduction in agonistic interactions under rough sea conditions also may reflect a reduction of overall activity levels associated with intense waves and wind in other pinnipeds (Bjorge et al., 2002).

In addition to environmental conditions, density and population trends may also influence or be influenced by rates of agonistic interactions. At low

densities, female southern elephant seals (*Mirounga leonine*; Baldi et al., 1996) and South American sea lions (*Otaria flavescens*; Fernández-Juricic & Cassini, 2007) engage in fewer agonistic interactions.

Overall behavioral patterns of male California sea lion behavior may be influenced by density (Young & Gerber, 2008). Our findings suggest an inverse relationship between density and agonistic interactions among males. However, aggression rates (female and male combined) also were highest at the colony with a declining population (Granito), suggesting that agonistic behavior may play a role in or be a product of current population declines in this area. Interestingly, the increasing populations at San Jorge and Los Islotes also exhibited high levels of aggression in one sex (females in San Jorge and males in Los Islotes) but these were accompanied by low levels of aggression in the other sex. That is, female agonistic interactions were highest in areas where male agonistic encounters were less frequent. This effect may be the result of a trade-off between male and female aggressive behavior such that intermediate to high levels of aggression in both sexes are not sustainable and lead to declines (such as those observed in Granito). Studies that include a larger sample of declining and increasing colonies could further explore the relationship between population trend and aggressive behavior, and investigate the possible trade-off between female and male aggression.

In conclusion, we that found male and female agonistic behaviors are related to weather conditions, density, and sex ratio, suggesting agonistic behaviors may be related to sea lion population dynamics. One caveat of our study is that we could not identify all individual sea lions, so some may be represented within the data set multiple times and biased our results so that agonistic interaction rates are lower than we report. This bias would lead to the conclusion that stronger interactions between demographic and environmental parameters and agonistic interaction rates exist. Our evaluation of known males at San Jorge suggests the majority of adults within each study site were represented, so individual biases are unlikely. However, future studies would benefit from identification of all individuals. Information on known individuals would also allow the explicit examination of the mechanistic relationships between agonistic behavior and additional population parameters for California sea lions. Understanding what determines agonistic behavior and how aggression affects population dynamics may provide useful insights for the conservation and management of imperiled populations.

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