

DETERMINANTS OF OUTCOMES OF AGONISTIC INTERACTIONS AMONG MALE CALIFORNIA SEA LIONS (*ZALOPHUS CALIFORNIANUS*)

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Agonistic behavior in territorial male California sea lions (*Zalophus californianus*) may be influenced by multiple factors, including who initiates an interaction and who owns the territory on which an encounter takes place. We studied predictors of the outcomes of agonistic interactions between territorial male California sea lions on 3 islands (Los Islotes, Granito, and San Jorge) in the Gulf of California, Mexico, during the 2005 breeding season. We evaluated both displays and fights among males to examine the hypotheses that initiators of agonistic interactions and that territory owners were more likely to win disputes. The outcomes of agonistic encounters (win or lose) were independent of the types of interaction (displays or fights) by the initiator and, hence, all agonistic interactions were pooled for analyses. We used an overdispersed binomial logistic regression to determine if initiators and resident males were more likely to win an interaction than noninitiators and nonresidents, respectively. We found that initiators of agonistic interactions were more likely to win agonistic disputes. Resident and nonresident males were equally likely to initiate agonistic interactions and were also equally likely to win agonistic disputes. Our results suggest that agonistic interactions among male California sea lions are influenced by which individual initiates the encounter and not by territory ownership.

Key words: agonistic behavior, displays, pinnipeds, territorial disputes

Identifying the factors that determine the outcomes of territorial disputes is central to understanding patterns of reproductive success of males in many mammals. In polygynous mating systems, sexual selection should favor physical and behavioral traits that provide males with a competitive advantage. In systems characterized by male territory defense, this may include traits that increase a male's chances of winning territorial disputes (Selander 1965). Several factors may explain why particular individuals tend to win such disputes (Andersson 1994; Emlen and Oring 1977). For example, the “resident always wins” hypothesis argues that territory ownership confers advantages, such as greater familiarity with the habitat, that lead resident males to win more confrontations (Davies 1978; Kemp and Wiklund 2004).

In contrast, the “initiator always wins” hypothesis predicts that males that incite agonistic interactions are more likely to win, perhaps because they only initiate encounters that they are likely to dominate (Martin et al. 1997). Although the specific predictions of these hypotheses differ, both are similar in suggesting that the outcomes of agonistic encounters are influenced by consistent, identifiable male attributes.

Studies of a wide range of species provide support for the resident advantage and initiator advantage hypotheses. For example, Bronstein and Brain (1991) found that in adult convict cichlids (*Cichlasoma nigrofasciatum*), initiators of agonistic interactions typically won encounters. Similarly, Martin et al. (1997) found that domestic chicken hens (*Gallus gallus domesticus*) were more likely to win interactions that they had initiated. At the same time, residency has been shown to affect the outcome of agonistic interactions in species such as the great tit (*Parus major*—Krebs 1982), speckled wood butterfly (*Pararge aegeria*—Davies 1978), and white rhinoceros (*Ceratotherium simum*—Rachlow et al. 1998). Thus, initiating encounters or being the resident animal appears to be associated with winning agonistic encounters in a variety of taxa.

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Our study examines the relative importance of the resident advantage and initiator advantage hypotheses in explaining the outcomes of agonistic interactions among male California sea lions (*Zalophus californianus*). California sea lions (hereafter referred to as sea lions) are polygynous and gregarious carnivores. Parturition and breeding occur between the 2nd week of May and middle of August, while the animals congregate in rookeries along the Pacific coast from British Columbia to Mexico and in the Gulf of California (García-Aguilar and Aurióles-Gamboá 2003). During this period, males attempt to defend patches of coastline occupied by females, with successful defense likely leading to increased chances of mating with females that use that patch for giving birth to and suckling young (Campagna and Le Boeuf 1988; Le Boeuf 1986; Peterson and Bartholomew 1969). To defend their territories, male sea lions engage in 2 different forms of agonistic interactions: displays (vocalizations with no physical contact) and fights (physical contact). The initiator advantage hypothesis predicts that the male that begins an aggressive interaction typically wins that encounter. In contrast, the resident advantage hypothesis predicts that the male who occupies the territory where the encounter occurs typically wins. If both factors contribute to interactions among male sea lions, then resident initiators may be particularly likely to win agonistic interactions. Determining how these factors shape agonistic interactions among male sea lions is important for understanding how intrasexual selection shapes the behavior of species with mating systems characterized by male territory defense.

MATERIALS AND METHODS

Study site and data collection.—Data were collected on male sea lions at Los Islotes, Granito, and San Jorge islands in the Gulf of California, Mexico (Fig. 1) during the summer breeding season in 2005. Two study sites per island were established (Granito: site 1 = 7,032 m², site 2 = 12,973 m²; San Jorge: site 1 = 1,918 m², site 2 = 3,500 m²; Los Islotes: site 1 = 2,203 m², site 2 = 1,505 m²). Estimated mean (\pm SD) numbers of adult males per island were 23 ± 3 for Los Islotes, 54 ± 14 for Granito, and 159 ± 25 for San Jorge. Behavioral observations were conducted during two 7-day trips to the islands on 15–22 June and 14–22 July 2005. Separate research teams recorded data at each site on each island during a given trip. Interactions among adult males were monitored during three 30-minute observation periods per day at each site. The number of adult males per island was variable and could only be estimated from a boat census conducted during each trip at each island ($n = 6$ at Granito, $n = 5$ at Los Islotes, and $n = 2$ at San Jorge) because not all males were successfully identified and, at any given point in time, males may have been underwater or absent from view. All field protocols were approved by the animal care and use committee at Arizona State University and follow guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

For each agonistic interaction observed, we identified the initiator and the recipient. The initiator was defined as the male that began the interaction, either by vocalizing or by making

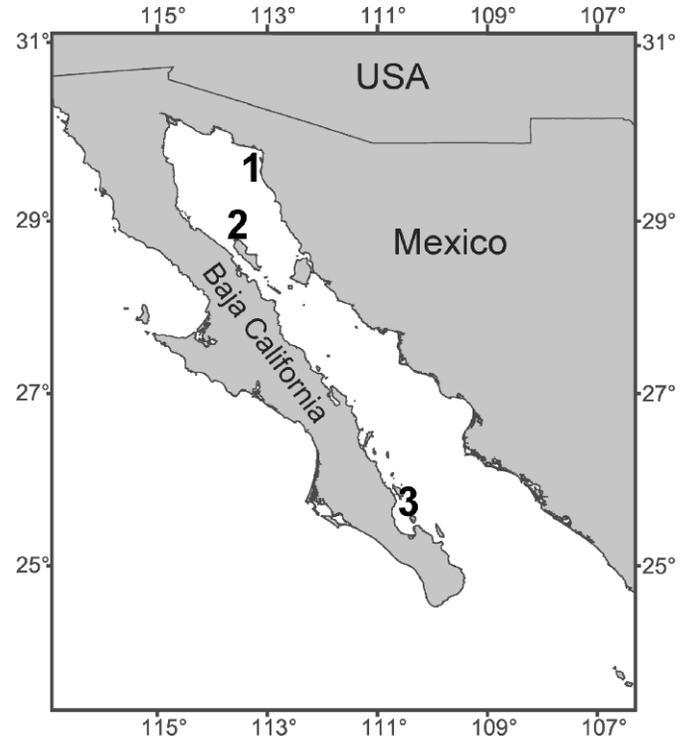


FIG. 1.—Map of the Gulf of California, Mexico. The locations of 3 islands where observations were conducted are indicated: 1) San Jorge, 2) Granito, and 3) Los Islotes.

physical contact with his opponent. The interaction was categorized as a fight if the males involved engaged in a physical confrontation, whereas the interaction was designated a display if it included aggressive components (e.g., calling or chasing) but no physical contact. Interactions for which the initiator was unknown (e.g., the encounter started before observations began) were excluded from subsequent analyses.

An interaction was considered as a discrete event if ≥ 3 min of nonaggressive behavior elapsed between agonistic encounters. Each interaction was treated as an independent sample and was included only once in our statistical analyses, with the outcome of the encounter determined from the perspective of the initiator. Although we could distinguish between the 2 males engaged in a specific interaction, we could not consistently identify individual males across interactions. Some males in the study population could be distinguished on the basis of unique natural marks. Analyses of this subset of known individuals revealed that some males were observed in multiple interactions (2.89 interactions \pm 0.37 SD per male; range = 1–9 interactions, $n = 28$ identifiable males). Thus, not all observations in our data set may have been strictly independent. However, assuming that repeated observations of unidentified males occurred at a similar rate, the total number of interactions documented during this study ($n = 102$) suggests that nonindependence of observations did not greatly bias the outcomes of our analyses.

Analyses of the initiator advantage hypothesis were based on data collected from all 3 islands. In contrast, the resident advantage hypothesis was evaluated using only data from Los

Islotes. We restricted analyses of the resident advantage hypothesis to this island because, unlike Granito and San Jorge, most males on Los Islotes could be individually identified based on natural marks, which allowed a much more accurate determination of the residency status of the animals monitored. We determined residency by conducting a census of the males present on the study site 3 times per day (morning, midday, and afternoon). During each census, we identified each male observed as resident (known individual previously observed on the same territory, with no other males present on that territory) or nonresident (unknown male, not observed previously on the territory in question). Residents occupied specific territories and were regularly observed patrolling areas of water with clearly defined boundaries, whereas nonresidents did not regularly occur in a specific area but were observed only periodically at the Los Islotes study site.

Classifying interaction outcomes.—For each male involved in an interaction, the outcome of the encounter was classified into 1 of 3 categories: remained at the location of the interaction (i.e., remained in the territory in the case of territorial males), left the interaction location but remained within the study site (i.e., lost access to the territory in question but not access to territories in general), or left the study site (i.e., lost access to any territory within the study site). We identified the winner and loser of each interaction by ranking these outcomes in the order described above. For example, if male A remained at the location of the interaction but male B moved away from the site, then male A was considered the winner. A tie occurred when the same outcome was assigned to both males (e.g., 2 neighboring territorial males remained at the interaction site). Because ties were ambiguous with respect to winning and because ties may be a form of boundary display (Stamps and Krishnan 1997), we excluded ties from the data set and analyzed only interactions with an asymmetric outcome (e.g., clear winner and loser).

Analyses of initiator advantage.—All statistical analyses were conducted with SAS version 9.1 (SAS Institute 2002). We used chi-square tests to determine if, for initiators, the outcomes of interactions (win or lose) were related to the type of interaction (display or fight). We used generalized estimating equations to determine if the tendency for known initiators to win encounters differed across islands and sampling sites within islands. Generalized estimating equation analyses allow examination of data sets that contain repeated observations of the same individuals and, hence, this approach was appropriate for assessing variation among males that may have been included in our data set more than once.

The outcome of an asymmetric interaction was a binary response (win = 1, lose = 0) and so we used an overdispersed binomial logistic regression (Williams 1982) to calculate the odds ratio for the proportion of interactions won by the initiator versus noninitiator and determine if initiators were more likely than noninitiators to win an interaction. This procedure accounted for overdispersion of data points resulting from variability among known males or groups of observations (each male considered a “group” that included several interactions), which often exceeds that explained by logistic regression models

(Williams 1982). To perform these analyses for each known male (group) we calculated the total number of interactions involving the male and the number of interactions won by that male. All unknown males were placed in a single group.

Analyses of resident advantage.—Chi-square tests (Zar 1999) were used to explore the relationship between initiating an agonistic interaction and residency on the territory where the encounter occurred. Because the outcomes of interactions were independent of the interaction type ($\chi^2 = 0.833$, *d.f.* = 2, $P > 0.05$, $n = 87$), fight and display agonistic interactions were pooled for further analysis.

As for our analyses of initiator advantage, we used an overdispersed binomial logistic regression (Williams 1982). For analyses of resident advantage, however, only data for known males from Los Islotes were examined, with the response variable being the probability of the resident winning. Although we assessed all interactions, only interactions involving a resident and a nonresident male were included in the logistic regression analysis to improve our ability to determine the effects of residency. Because the number of interactions per male was small for this analysis ($n = 21$ interactions involving 11 males), we 1st pooled resident males according to the number of interactions in which they participated (e.g., group 1 = 1 interaction per male and group 2 = 2 interactions per male).

RESULTS

Most (74%) of the 301 agonistic interactions documented at the 3 islands were displays. Only 54% of all interactions had asymmetric outcomes, meaning that a clear winner and loser could be identified. We observed 35 agonistic interactions at San Jorge (27 interactions with distinct win–loss outcomes, 6 ties, and 5 identifiable initiator males), 41 interactions at Granito (34 interactions with distinct win–loss outcomes, 7 ties, and 21 identifiable initiator males), and 225 interactions at Los Islotes (87 interactions with distinct win–loss outcomes, 138 ties, and 59 identifiable initiator males).

Effects of initiator status.—For males that initiated encounters, the outcomes of agonistic interactions (win or lose) were not related to interaction type (display or fight) on either San Jorge ($\chi^2 = 0.267$, *d.f.* = 1, $P > 0.05$, $n = 27$) or Los Islotes ($\chi^2 = 0.833$, *d.f.* = 1, $P > 0.05$, $n = 87$); the small number of interactions on Granito precluded similar analyses.

Generalized estimating equation analyses of data from known males revealed no differences between islands ($\chi^2 = 0.95$, *d.f.* = 2, $P = 0.62$, $n = 80$) or data collection trips ($\chi^2 = 2.67$, *d.f.* = 1, $P = 0.10$, $n = 80$) with respect to the tendency for initiators to win encounters (Fig. 2). Therefore, we pooled data across islands and trips for logistic regression analysis. For this pooled data set, the odds ratio for the proportion of interactions won by the initiator versus the noninitiator was 1.901, with a 95% confidence interval of 1.009–3.740. Because the odds ratio was >1 and the confidence interval did not include 1, we concluded that initiators were significantly more likely than noninitiators to win encounters.

Effects of residency status.—The tendency for known males to initiate interactions was independent of residency ($\chi^2 =$

3.73, *df.* = 1, *P* > 0.05, *n* = 66). The odds ratio for the proportion of fights won by residents versus the proportion won by nonresidents was 1.323, with a 95% confidence interval of 0.349–5.467 (*n* = 21). Because this confidence interval included 1, we concluded that residents were not significantly more likely than nonresidents to win encounters.

DISCUSSION

Our results support the prediction that initiators of agonistic interactions are more likely to win encounters. However, examination of our data does not support the prediction that residents were more likely to win interactions. We found a strong positive relationship between the tendency to initiate fights and the number of times that a male won; this pattern was evident for each island as well as when data for all islands were combined. Our results are consistent with previous work on a variety of species suggesting that initiators win more interactions (Bronstein and Brain 1991; Côté 2000; Hogue et al. 1996; Martin et al. 1997; Randler 2004; Rutte et al. 2006). However, similar studies have not been conducted for other marine mammals. Thus, our findings add to the taxonomic diversity of species for which it is possible to predict the outcomes of interactions based on who initiates them.

More interactions occurred at Los Islotes than San Jorge or Granito. This difference in the frequency of agonistic encounters between males may reflect other differences detected between the islands. For example, the operational sex ratio was lower at Los Islotes than Granito or San Jorge (Gerber 2006), potentially resulting in more competition among males for access to females at Los Islotes. At the same time, the availability of resources such as resting spaces was reduced at Los Islotes relative to the other 2 islands (Gerber 2006), which may have lead to increased competition for access to these resources and, hence, increased agonism among males on Los Islotes. However, the specific factors affecting the frequency of agonistic interactions between male California sea lions remain unclear.

Functional significance of initiator advantage.—Some non-contact behaviors (e.g., vocalizing by neighboring males) are commonly used to establish territorial boundaries (Stamps and Krishnan 1997). This tendency may help to explain why we observed such a large percentage of display interactions between resident males. Sea lions could be hesitant to engage in escalated interactions because such encounters increase the risk of severe injuries (Dunham et al. 1995). If outcomes are predictable to the individuals involved, then risky interactions should be avoided (Aragón and Pillar 2006; Stamps and Krishnan 1994). Male sea lions may use display interactions to gauge the size and competitive ability of a potential opponent, which may explain not only why most interactions were displays but also why most display interactions resulted in ties.

Males also may engage in displays instead of fights when territories are energetically costly to defend (e.g., Klatt and Paszkowski 2005). Evidence from song sparrows (*Melospiza melodia*) suggests that if males are familiar with their neighbors (Hyman and Hughes 2006) then displays may act as a ritualized

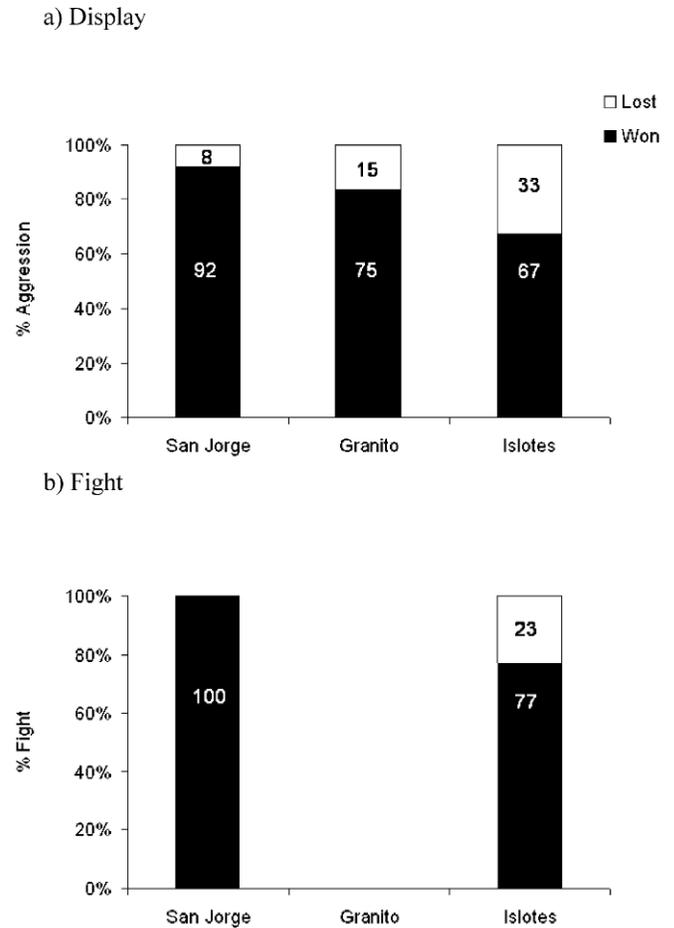


FIG. 2.—Outcomes of a) display and b) fight interactions by male California sea lions at San Jorge (*n* = 24 display and 3 fight interactions), Granito (*n* = 20 display and 0 fight interactions), and Los Islotes (*n* = 61 display and 26 fight interactions) islands in the Gulf of California, Mexico. For each island, the percentage of wins and losses are shown for males that initiated agonistic interactions.

behavior to maintain territorial spacing. Similarly, territorial male sea lions may become familiar with neighbors over a breeding season and rely on agonistic displays instead of fights to maintain boundaries. Although our results indicated no differences in rates of encounters between sampling trips, further studies that identify individual sea lions are needed to determine if familiarity with neighboring animals influences the nature of agonistic interactions among males. By excluding ties and only analyzing data with asymmetric outcomes, our findings likely emphasized male–male aggression that was involved in acquiring territories, thereby precluding comparisons of our findings with interactions between males that were familiar with one another.

Functional significance of resident advantage.—Although overall, resident males were no more likely to win encounters than nonresidents, we found that residents who initiated interactions were more likely to win. The high success rate of nonresident initiators may reflect the number of intruder males attempting to gain access to the resident’s territory. Campagna and Le Boeuf (1988) found that the number of

females on a territory determined the frequency of agonistic interactions by the male resident on the territory. Thus, males with a large number of females on their territory may face a greater number of intrusions by nonresidents. Indeed, nonresident males may seek out such territories and preferentially initiate interactions at such sites (Stamps and Krishnan 1995). We found no relationship between initiator status and residency (i.e., resident and nonresident males were equally likely to be initiators), suggesting that residency and initiator status are independent conditions that contribute separately to the outcome of an agonistic interaction.

Although our analyses indicated that initiating interactions influences the outcomes of agonistic encounters, other factors also may affect aggression by male sea lions. For example, resource-holding potential also may have contributed to the observed patterns (Rutte et al. 2006). Territorial male Magellanic penguins (*Spheniscus magellanicus*) exhibit varying levels of aggression based upon the value of the resource they are disputing (Renison et al. 2006); if sea lion territories also vary in quality, then the extent to which a male will defend his territory may vary depending upon the quality of the area in which he is resident. Body size also may be important. Specifically, larger males may be more likely to win interactions because they have more strength to fight and maintain territories during the breeding season (Le Boeuf 1974). In northern (*Mirounga angustirostris*) and southern (*M. leonina*) elephant seals, mating success of males was positively correlated with rank, which was directly related to size (Haley et al. 1994; Modig 1996); the mating system of sea lions is generally similar to that of these species, suggesting that body size also may influence interactions in the animals in our study. Finally, learning from previous encounters may influence the behavior of males (e.g., winner effect—Switzer et al. 2001). Hyman and Hughes (2006) found that neighboring territorial male song sparrows respond differentially to neighbors depending upon their history of interactions (winning or losing) with those individuals. Future research on agonistic behavior in sea lions should build upon data presented here to explore the possible effects of these additional factors on the outcomes of interactions among males.

RESUMEN

El comportamiento agonístico en machos territoriales de lobo marino de California (*Zalophus californianus*) puede ser influenciado por múltiples factores, incluyendo si un individuo es el que inicia una interacción o si el macho es dueño del territorio donde ocurrió la interacción. En este trabajo, estudiamos los factores que predicen el resultado de las interacciones agonísticas entre machos territoriales de lobo marino de California en 3 islas (Los Islotes, Granito y San Jorge) en el Golfo de California, México, durante la temporada reproductiva 2005. Evaluamos tanto despliegues agonísticos como peleas entre machos para explorar 2 hipótesis: los machos que inician una interacción agonística y los machos dueños de territorios tienen más probabilidades de ganar las disputas. El resultado de los encuentros agonísticos (ganar o

perder) fue independiente del tipo de interacción (despliegues o peleas) en los machos iniciadores y, por lo tanto, todas las interacciones agonísticas se agruparon para realizar los análisis estadísticos. Utilizamos una regresión binaria logística para determinar si los machos iniciadores y residentes (dueños de territorios) tuvieron mayor probabilidad de ganar una interacción que los machos no iniciadores y no residentes respectivamente. Los machos iniciadores de interacciones agonísticas tuvieron mayor probabilidad de ganar las disputas. Los machos residentes y no residentes tuvieron la misma probabilidad de iniciar una interacción agonística y de ganar las disputas. Nuestros resultados sugieren que las interacciones agonísticas entre machos de lobo marino de California son influenciadas por quién es el macho que inicia la disputa pero no por el estatus de los individuos (residente o no residente).

ACKNOWLEDGMENTS

This research was partially supported by a grant to LRG from the National Science Foundation (Animal Behavior, Biological Oceanography, and International Programs; award 0347960), by support to DFJ from the Arizona State University office of the Provost through the School of Life Sciences Undergraduate Enrichment Program, and a grant to CJH-C from Consejo Nacional de Ciencia y Tecnología. We thank the lobos field crew for field assistance, R. J. Fredrickson and T. Lalonde for invaluable statistical advice, and the Gerber laboratory and E. Lacey for insightful comments on this manuscript. Secretaría de Medio Ambiente y Recursos Naturales authorized data collection in the Gulf (Oficio NUM/SGPA/DGVS/05325).

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Submitted 4 June 2007. Accepted 27 March 2008.

Associate Editor was Eileen A. Lacey.