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South American sea lions in Peru have a lek-like mating system

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ABSTRACT

Five years of behavioral observations revealed significant effects of high air temperatures and breeding site topography on the mating system of South American sea lions in Peru. Unlike most polygynous mammals that defend females or fixed territories, male sea lions in Peru maintained positions along the shoreline where females passed each day to thermoregulate, and where most copulations occurred. Sex ratios (1 male per 17 females) and male mating success were extremely skewed (14% of males achieved 50% of the copulations, and 25% of them did not copulate at all). The mass daily movements of females toward the water and cool substrate of the shoreline, along with a highly skewed sex ratio, accentuated the difficulty for males to monopolize and restrict female movements. Females moved freely and chose their mates, unlike in temperate regions of their range where male South American sea lions control groups of females or access to tide pools. Our observations indicate that the South American sea lion in Peru has a lek-like breeding system. This is a rare alternative to the common male strategies of defending females and resources, and is likely an evolutionary product of their highly skewed sex ratio, protracted breeding season, and the extreme subtropical climate where they breed.

Key words: South American sea lion, *Otaria byronia*, mating system, mating success, lek, sex ratios.

Pinniped mating systems range from sequential to extreme polygamy, with females caring for the young and assuming most of the reproductive costs whereas males primarily contribute their gametes, devoting their energy to securing access to estrous females rather than caring for offspring (sequential polygyny; Emlen and Oring 1977, Stirling 1983, Boness 1991). Male pinnipeds compete intensely for mates and maximize their fitness by copulating with as many females as possible. Male mating success may thus vary greatly among individuals, further intensifying selection for those traits that confer an advantage in reproduction (Bartholomew 1970, Stirling 1983, Clutton-Brock 1989, Boness 1991).

Among the three pinniped families, all otariids (fur seals and sea lions) are polygamous with males defending females directly (female-defense polygyny), or males defending territories where females aggregate (resource-defense polygyny; Emlen and Oring 1977, Krebs and Davies 1978, Campagna and Le Boeuf 1988*b*, Boness 1991, Francis and Boness 1991). However, males of some species of sea lions (California sea lion and Hooker's sea lion) may adopt lek-like mating behaviors (Boness 1991). In contrast to otariids, the mating behavior of phocids (the true seals) ranges from controlling access to one or two females at a time (sequential polygyny; Boness *et al.* 1988) to defending large groups of females (female-defense polygyny; Stirling 1983; Le Boeuf and Reiter 1988; Hoelzel *et al.* 1999; Lidgard *et al.* 2004; Harcourt *et al.* 2007, 2008). Odobenids (walrus) on the other hand have a polygamous mating system where groups of males aggregate and monopolize access to females (Atlantic walrus, *Odobenus rosmarus rosmarus*) or display to attract females because they cannot effectively defend female groups or resources where females congregate (mobile lekking—Pacific walrus, *Odobenus rosmarus*; Fay 1982, Fay *et al.* 1984, Sjare and Stirling 1996).

Lekking is one of the least common and understood mating systems of all vertebrates (Bradbury 1981, Clutton-Brock 1989). Although few mammalian species exhibit classical lek mating systems, there are many that have leks that are intermediate between a resource defense system and classical leks (Bradbury 1981). Leks among pinnipeds are less clear and only a few species such as the harbor seal, *Phoca vitulina* (Hayes *et al.* 2004, Boness *et al.* 2006), the California sea lion, *Zalophus californianus* (Heath and Francis 1983), and the Pacific walrus *O. rosmarus* (Ray and Watkins 1975, Fay *et al.* 1984) are considered to have dispersion patterns and mating characteristics similar to those of true lek species.

Pinniped mating systems appear to be primarily a product of the type of substrate where males and females aggregate and breed (Stirling 1983). Species that breed in large aggregations on land can have males defending resources (*e.g.*, caves or tide pools) or groups of females (*e.g.*, sea lions, fur seals, elephant seals—*Mirounga leonina* and *M. angustirostris*, and gray seals—*Halichoerus grypus*), while those that breed in dispersed aggregations on ice can at best defend access to one or two females at a time (*e.g.*, harp seals, *Pagophilus groenlandicus*; ringed seals, *Pusa hispida*; and hooded seals, *Cystophora cristata*; Stirling 1983, Boness 1991), compared with those breeding in water that display to attract females (*e.g.*, Pacific walrus and harbor seals, *P. vitulina*; Fay *et al.* 1984, Hayes *et al.* 2004). However, substrate does not explain all of the variation in mating systems observed among pinnipeds (Stirling 1983, Boness 1991). Climate and its effect on thermoregulation have also shaped the evolution of pinniped mating systems through habitat choice and behavioral mechanisms that facilitate thermal balance at high and low air temperatures (Limberger *et al.* 1986, Campagna and Le Boeuf 1988*b*, Riedman 1990, Francis and Boness 1991, Gonzalez-Suarez and Gerber 2008).

Among otariids, climate and beach topography affect the movements and distribution of females at breeding sites (rookeries), which can in turn determine the degree of male competition and the extent to which males can monopolize mates (Emlen and Oring 1977, Boness 1991, Carey 1991, Francis and Boness 1991). This is particularly true in hot climates where thermoregulatory needs and cool substrates structure male breeding and social behavior, and ultimately determine mating success (Campagna and Le Boeuf 1988*b*, Riedman 1990, Francis and Boness 1991). Thus, male sea lions and fur seals commonly employ territorial strategies when females are distributed near resources for thermoregulation (*e.g.,* water pools, shade), or they will directly defend groups of females (Campagna and Le Boeuf 1988*b*).

The wide geographic range (encompassing temperate and subtropical conditions) of the South American sea lion (*Otaria byronia*) affords an opportunity to gain further insight into the evolution of mating systems and sexual selection in pinnipeds. Most of what is understood about the mating system of South American sea lions has come from studies conducted at two rookeries on the temperate Atlantic coast of South America (Argentina) where males defend both females and resources (Campagna and Le Boeuf 1988*b*, Cappozzo and Perrin 2009). At one of the sites (Puerto Piramide), males compete aggressively for territories on flat rocky shelves that contain tide pools where females concentrate to meet their thermoregulatory requirements. At the second site (Punta Norte), males directly defend and control the movements of females along a narrow wet strip at the high tide mark because the uniform pebble beach lacks tide pools and shade (see Campagna and Le Boeuf 1988*b*). These observations of sea lions along the Atlantic coast suggest that male sea lions breeding in the Pacific under higher ambient temperatures with no defendable resources for thermoregulation should also control the movements of females to and from the water. However, behavioral observations suggest a different sort of mating system in Peru (Soto *et al.* 2004, 2006).

The Atlantic and Pacific populations of South American sea lions differ substantially in many aspects. In the Pacific, sea lions at the subtropical Ballestas Islands (Peru) have the longest breeding season reported for the species (mid-December to mid-March; Soto *et al.* 2004). They are also exposed to extreme stochastic changes in the availability of prey due to El Niño events that adversely affect reproduction and survival rates (Soto *et al.* 2004). Females also move each day to the water's edge to avoid overheating (Soto *et al.* 2006). All of these factors are likely important determinants in the evolution of the South American sea lion mating system because they might differentially affect the distribution of males and females in the breeding areas and influence the way in which males monopolize mates.

We made detailed observations of South American sea lions during five breeding seasons (1997–2002) at the Ballestas Islands, Peru, to determine whether their mating system differs from that observed in most polygynous pinnipeds and other mammals. We were particularly interested in determining whether male sexual behaviors were similar to those of lekking species. We examined environmental and social factors that might favor a particular mating system from the range of systems exhibited by pinnipeds—and studied female behavior and the distribution of males and females on the rookery to better understand the potential for males to monopolize mates. Finally, we considered whether the apparent plasticity in the mating system of South American sea lions is an evolutionary product of climate, thermoregulation needs, female behavior, and onshore distributions of animals.

METHODS

Study Site and Species

Data were collected at the Ballestas Islands (13°44′S, 76°24′W), Pisco, Peru (Fig. 1). These islands are protected by the Peruvian Government as a guano bird reserve. The Ballestas Island contain one of the largest breeding concentrations in

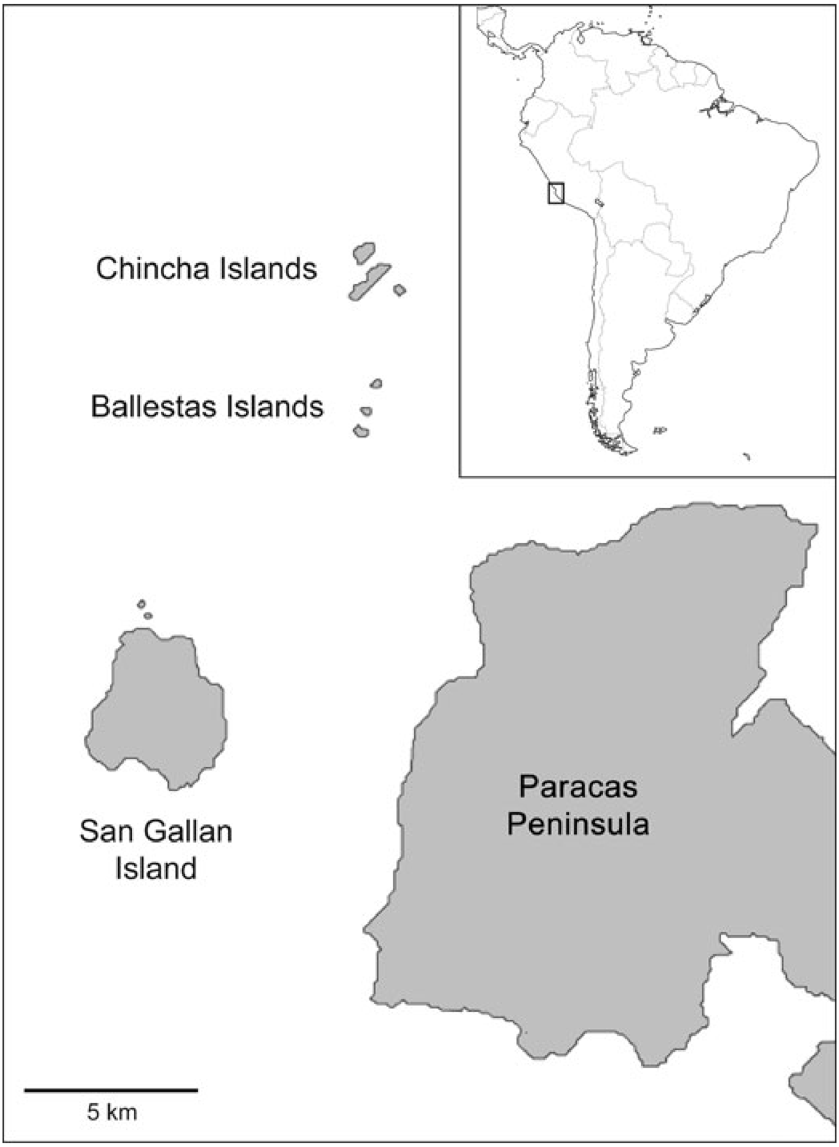

Figure 1. The study site "La Maternidad" located at the North Ballestas Island (13°44′S, 76°24′W) in Pisco, Peru.

South America (Arias-Schreiber and Rivas 1998). The study beach, La Maternidad (The Maternity), is the biggest breeding beach of the Ballestas Islands and is used annually. It is a narrow stretch of open flat sloping pebble beach without pools or shady areas allowing all sea lions on the beach to be observed at all times (Fig. 2). La Maternidad is bounded by open ocean to the north, a rocky 60 m cliff to the south, and small caves to the east and west.

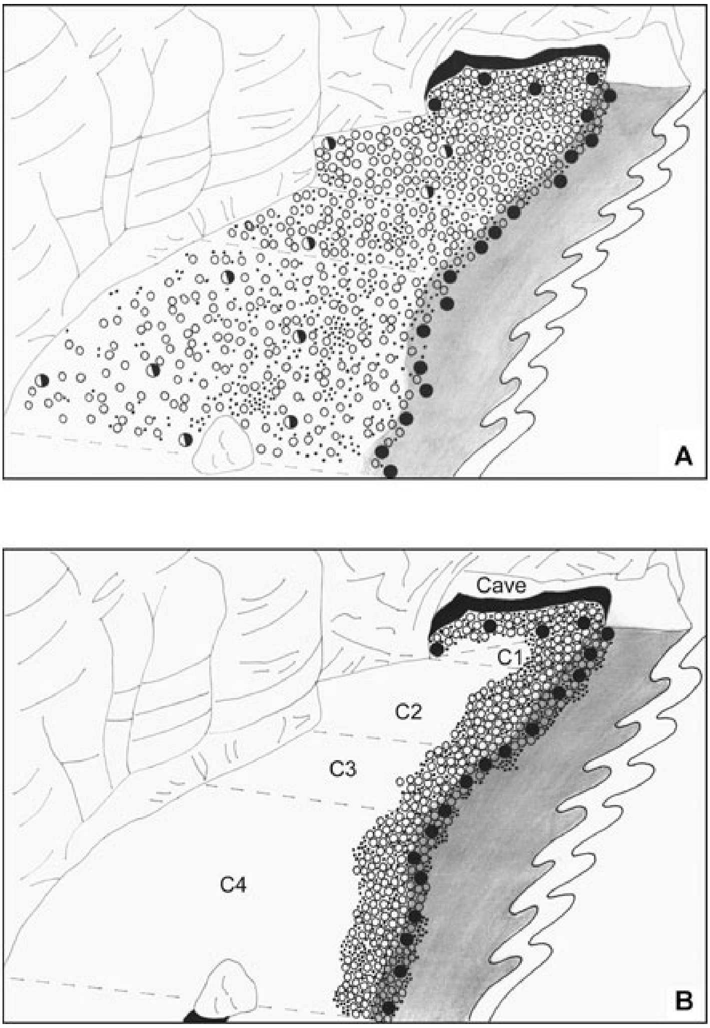

Figure 2. Typical distribution of South American sea lions at La Maternidad beach during (A) the cool shaded hours and (B) the hot sunny hours. Large solid circles on the shoreline denote resident bulls, half-filled circles correspond to nonresident bulls, open circles indicate females and small dots represent pups. Dashed lines indicate the limits between study zones. Gray substrate represents wet pebble and white substrate represents dry pebble.

We used conspicuous rocks along the rocky cliff to divide La Maternidad into five zones (Cave, C1, C2, C3, and C4) to facilitate behavioral observations (Fig. 2). The cliff limited the space perpendicular to the water and provided shade to sea lions during the afternoon hours. The Cave was the only zone that differed from the four others (Zones C1–C4). Its sheltered structure with no direct access to the water offered partial shade for the sea lions during the hot hours. The Cave and Zone C1 were the first zones to be shaded by the rocky cliff soon after midday (~1230).

Figure 3. A section of shoreline showing the linear arrangement of resident South American sea lion bulls along the wet substrate of the shoreline, and the distribution of females and pups that moved toward the water during the hot hours at La Maternidad beach.

Mean air temperature during the austral summer (January–March) from 1997 to 2002 (excluding 1998) was 22.8°C, with a minimum of 19.6°C and a maximum of 28.3°C. Relative air humidity was high and constant during this period (mean 73.5%). Wetting the flippers and fur at the shoreline was the main means for sea lions to avoid overheating on the open beach during the hottest hours. The pebble beach substrate sloped slightly toward the water due to continuous wave action. Thus, animals occupying the shoreline had continuous access to the cooling beach substrate throughout the day (Fig. 2, 3).

Breeding Season

We divided the breeding season from early January to mid-March into three periods: early, peak, and late according to the timing of copulations around the median date of copulations (MDC) for each year (see Majluf 1992). The peak season corresponded to the period encompassing the MDC ±25% of copulations. The early and late season corresponded to the first 25% and last 25% of copulations.

Behavioral Observations

Observations were conducted daily using binoculars and a spotting scope from a blind located on the top of the cliff approximately 100 m from the colony. Twelve consecutive hours of observation per day (0600–1800) were carried out by two observers per bout of 3 h each during five consecutive breeding seasons (January–March) from 1997 to 2002. Conditions were similar between years except in 1998 when the strong 1997–1998 El Niño event caused high mortality and the total abandonment of the beach before the end of the season (see Soto *et al.* 2004, 2006). We therefore excluded data from the 1998 breeding season from our analysis of breeding behavior. During the 1997 breeding season, field observers recorded daily numbers of copulations and pups born, but did not individually identify males or record whether copulations involved a resident or nonresident bull. These details were recorded in all other years (1999–2002).

A bull was considered to be a resident if he established himself onshore associating with females and defending his position from other males (Fig. 3). A nonresident bull was an adult male that did not defend any position in particular and normally abandoned the beach each morning. All resident bulls were individually identified ($n = 338$) within each breeding season from 1999 to 2002 using paint marking and natural scarring. Nonresident bulls were not individually identified. Daily presence and location of resident bulls were recorded on a map three times per day (0600, 1200, and 1800). Each map showed the location of each bull relative to the zones of the beach and the distance with respect to other males in the same zone (Fig. 2). We estimated the distance between males using body lengths as our measure of reference (Campagna and Le Boeuf 1988*a*). Male tenure was defined as the number of days that a resident bull defended a position on the beach (which equaled the number of days between arrival and departure dates). The shortest tenure was considered to be 1 d and males with tenures <24 h were removed from our analysis.

We recorded the number of copulations per male each day using continuous all-occurrence sampling (Altman 1974). A copulation was considered to be successful if a male mounted a female and exhibited rhythmic pelvic thrusting for more than 5 min after intromission was observed (see Campagna and Le Boeuf 1988*a*). Otherwise, we classified the copulation as a mating attempt.

A total of 501 females and their pups were marked on their day of birth or during the subsequent perinatal period (the time between parturition and first departure of mother to sea) with paint pellets fired from a CO_2 gun (Nelson Paint Co., Kingsford, MI, USA) and with paint-filled-eggs thrown approximately 35 m from the animals (1999: $n = 145$, 2000: $n = 143$, 2001: $n = 113$, 2002: $n = 100$). Paint markings and natural scarring of the study animals were drawn on individual identification cards, and site of parturition was drawn onto a map for each marked female.

The traditional model of resource or female-defense polygyny predicts high variance in male mating success, with a small proportion of males obtaining a disproportionate share of matings in a given year (Boness 1991). We used the rate of copulations as a proxy for male mating success to analyze whether differences between males were related to the mating site, the length of tenure, or portion of the breeding season when tenure was held. Male mating success may differ from reproductive success because the number of paternities per male was unknown.

We studied male–male competition by recording all agonistic interactions (AI) of resident bulls during the 1999, 2000, and 2002 breeding seasons. AI were defined as hostile contests between two males during which they threatened, chased, or fought (Campagna and Le Boeuf 1988*a*, Jacobs *et al.* 2008, Robertson *et al.* 2008). We marked the location of all females on a map during daily censuses at 0600, 1200, and 1800 to determine their distribution on the beach. Numbers of copulations as well as the number and locations where pups were born were also recorded by zones to determine whether females had preferred birthing and mating sites.

Mean values were calculated ±SE, and median values were calculated with interquartile ranges (25%–75%); while nonparametric Kruskal-Wallis tests were used for data that could not be normalized by transformation (presented in the results as medians and interquartile ranges, instead of means ± SE).

Sex Ratios and Degree of Polygyny

We calculated three sex ratios: (1) daily adult sex ratio (ASR), (2) daily operational sex ratio, and (3) seasonal operational sex ratio. The daily ASR was derived from the number of adult males and females counted each day at 0600, while the operational sex ratio reflected the number of females that were in estrus each day or over the entire breeding season relative to the numbers of males that were present. We estimated the seasonal ratio of fertilizable females to reproductively active males from the maximum numbers of pups and sexually mature males (resident and nonresident) counted during daily censuses (see Francis and Boness 1991), and used it as an empirical measure of polygyny and the degree to which males monopolized mates (Emlen and Oring 1977). In contrast, we derived the daily operational sex ratio from the maximum daily counts of males and the numbers of females we estimated were in estrus each day (by back calculating the number of pups born 6 d earlier to adjust for the postpartum period, see Campagna and Le Boeuf 1988*a*). This provided an empirical measure of the degree to which females might choose mates. Note however, that both calculations of operational sex ratios may underestimate the true values if all fertilizable females did not give birth.

RESULTS

Number and Distribution of Males

The resident bulls established themselves along the shoreline where they had continuous access to wet substrate and water spray to facilitate thermoregulation (Fig. 2, 3). Land-locked territories did not exist. Males maintained their linear alignment along the shoreline day after day through aggressive physical confrontation toward contenders that attempted to access the beach or gain a position along the shoreline. Nonresident bulls attempted to access the beach mostly during the afternoon hours when females and juveniles returned from the water or moved to the dry inland areas from the shoreline (data not shown). Nonresident bulls that tried to secure a position at the shoreline were rebuffed and attacked by the nearest resident bull. Those that managed to pass the fortified shoreline did not defend any particular position from other males on the inland beach and remained resting until the next morning.

The total number of resident bulls counted (January–March) averaged 84.5 bulls (±4.87), over a breeding season (1999–2002), but averaged only 20.0 bulls (±1.88) on any given day (1997–2002). The number of nonresident bulls per day was about half this number, and averaged 11.0 bulls (±2.56, 1997–2002). Distance between resident bulls fluctuated over the course of a day and depended in part on interactions with new arriving males. Mean distance between males was about 1 body length (mean: 2.3 m ± 0.1, see Fig. 3) and was similar during the peak breeding season in all years estimated (1999–2002), as well as independent of the zone that males occupied.

Resident bulls did not defend fixed territories. Mapping the location of the males on a daily basis revealed that resident bulls defended positions along the shoreline (*e.g.*, Fig. 2) that shifted slightly and overlapped with positions held by neighboring males within a day or between days (maps not shown). For example, it was not uncommon for a male to be plotted at one position at 0600 (*e.g.*, close to our dividing line between Zones C2 and C3), and at other locations at 1200 and 1800 (*e.g.*, as far as the middle of Zone C3, or back to their former spot in Zone C2). Male movements were in response to pounding waves or tidal changes, and all males moved relative to one another. Males maintained positions that were fixed relative to their order along the beach, but shifted slightly each day with varying degrees of overlap between the tightly distributed males. Neighboring bulls occurred in close proximity to each other (*i.e.*, often separated by less than one body length) and were able to rest and mate without engaging in AI with their neighbors.

While some individuals were more restrictive in their movements than others, all males moved over the wet pebbles in response to crashing waves (that enlarged or reduced the shoreline), but always maintained their linear alignment and small distances between each other. Such defense of position relative to other bulls rather than defense of a fixed territory was most evident when wave action forced all sea lions to move up the beach to avoid being washed off. Resident bulls never held an aquatic position, but maintained their linear alignment along the water's edge independent of how far they moved to escape the waves (up to seven body lengths or ~20 m inland). Males only moved inland if forced to do so by waves.

Male–Male Competition

We recorded 25,486 AI between resident bulls as they maintained and defended their positions along the water's edge. These interactions included fights, retreat displays, and threat vocalizations (with and without charges). Threat vocalizations without charging their nearest neighbor accounted for only 20.1% of the AI. Such threats typically consisted of a resident bull jumping suddenly to face his neighbor and produce a short vocalization showing his chest and directing his nose toward the sky. His opponent typically followed suit. These particular interactions between neighbors stemmed from misdirected provocation caused by one of the two having fought with a third male, or following the return of the provoked male to his beach position after having an AI with a nonresident male. All other AI (79.9%) were directed by resident bulls toward itinerant males passing near them.

During retreat displays, the charging attacker would stop abruptly before reaching his opponent face to face, whereupon the retreating bull would rapidly shake his head side to side with his mouth open. Charges consisted of a short rush toward the opponent with open jaws and an outstretched neck. Male charging behavior was the most frequent AI (41.7%) followed by retreat displays (35.5%), and never occurred between neighboring resident males. Male fights (violent biting of neck, chest, and flippers) were infrequent (2.7%) and only occurred when new males attempted to gain a position on the shoreline. Once a new male gained a position, fights or charges between neighbors were never observed.

Numbers of AI per male per breeding season did not differ among years (median of all years combined: 77.5 AI; interquartile range: 30.8–160.2 AI). However, significant differences occurred between the zones of the beach (Kruskal-Wallis: $\chi^2_4 = 37.58$ $P < 0.01$), with the highest number of interactions per male occurring in Zone C4 (median: 155 AI, interquartile range: 60–231 AI) and the lowest values in the Cave Zone (29 AI, 11–59.5 AI). High variability within a year occurred in the number of AI recorded per male, and was consistent between years (CV all years combined: 90.4%). We also found a significant positive relationship between the number of AI and the number of times a male copulated across years (Spearman correlation, $P < 0.01$). However, the correlation coefficients differed significantly among years ($\chi_3^2 = 10.84$, $P < 0.01$; 1999: $r = 0.60$; 2000: $r = 0.74$; 2002: $r = 0.56$). Mean number of AI per hour per male for all years combined was 0.72 ± 0.03 AI.

Adult Sex Ratio and Operational Sex Ratio

We noted significantly greater numbers of females to males in all years, even following the strong 1997–1998 El Niño event that killed significant numbers of adult females (Soto *et al.* 2004). The ASR from 1997 to 2002 averaged 19 females per male (Table 1), but varied over the course of the breeding season (variability was highest in 1997: CV = 41%, and lowest in 2001: CV = 12%). Greater numbers of adult females per bull occurred at the beginning of the breeding season, and was the highest in 1999 (51 females:1 male), and the lowest in 2002 (10 females: 1 male). The seasonal operational sex ratio was 17.5 females per resident bull, while the relative numbers of estrus females to bulls present on any given day was just 0.38 or about three males for every estrus female (Table 1). Thus, the operational sex ratios indicated a high degree of polygyny over a protracted breeding season (>2 mo) with the opportunity for considerable mate choice by the relatively small numbers of females that were in estrus on any given day.

Distribution of Females

Females occupied all areas of the beach (Fig. 2a), but their numbers and distribution varied according to changes in air temperatures and amount of direct sunlight, suggesting that female movements reflected thermoregulatory considerations. Females moved directly toward the shoreline or abandoned the beach in massive synchronous numbers as soon as the morning sunlight reached the beach (~0730). They and their pups would closely pack themselves along the shoreline, leaving the dry back parts of the beach completely empty of animals (Fig. 2b), and would not move back to their dry inland resting sites until after midday (~1230) when they would progressively occupy the areas shaded by the projection of the rocky cliff over the beach.

During mass female movements, resident bulls were never observed restraining or injuring the females as they moved about the beach, suggesting that females were free to move to the shoreline to thermoregulate. Variation in the number of females onshore throughout the day reflected their behavioral response to meet their thermoregulatory needs. Counts of females onshore during the hot hours (1200) yielded minimum numbers (1999: 357 ± 16.7 females, $n = 32$; 2000: 302 ± 8.9, $n = 62$; 2001: 344 ± 9.5, $n = 23$; 2002: 322 ± 13.8, $n = 36$) compared with counts at other times of the day. The highest numbers of females onshore occurred at 1800 h when most animals returned from the water (1999: 677 ± 32.6, $n = 31$; 2000: 533 ± 10.9, $n = 61$; 2001: 501 ± 11.5, $n = 23$; 2002: 451 ± 19.2, $n = 38$), followed by counts at 0600 (1999: 548 ± 18.6, $n = 63$; 2000: 470 ± 7.2, $n = 60$; 2001: 458 ± 7.4, $n = 43$; 2002: 390 ± 12.0, $n = 47$). The proportion of females that abandoned the beach during the thermoregulatory movements varied among years (1999–2002: $\chi_3^2 = 70.18$, $P < 0.01$), with the highest proportion occurring in 2000 (40.1% ± 1.3, $n = 48$) and the lowest in 2002 (17.9% ± 0.9, $n = 25$). In 1997, counts based

Table 1. Population data for South American sea lions breeding at La Maternidad beach from 1997 to 2002 showing the mean numbers of adult females and resident bulls counted onshore each day at 0600, total numbers of pups born, total number of copulations, operational sex ratios (daily OSR_d, and seasonal OSR_s), adult sex ratio (ASR) and median date of copulations (MDC). Counts and ASR are given ±SE and the number of counts in parenthesis. ASR was the mean of the daily ASR calculated from the daily numbers of adult males and adult females counted at 0600, while the seasonal operational sex ratio was estimated from the maximum numbers of resident bulls (from daily censuses) and pups born over the entire breeding season, and the daily operational sex ratio was estimated from the maximum daily counts of males and the numbers of females we estimated were in estrus each day (by back calculating the number of pups born 6 d earlier to adjust for the postpartum period).

Year	Females	Pups	Males	Copulations	OSR_d	OSR_s	ASR	MDC
1997	884.77 ± 98.97 (9)	1,229	25.02 ± 0.39 (52)	2,321	0.44 (33)	18.06	20.66 ± 2.83 (9)	7 February
1999	548.05 ± 18.64 (63)	406	15.54 ± 0.21 (65)	558	0.30 (58)	16.24	26.46 ± 1.08 (63)	10 February
2000	470.15 ± 7.23 (60)	561	17.40 ± 0.30 (62)	778	0.31 (54)	17.00	19.69 ± 0.72 (60)	27 January
2001	457.91 ± 7.43 (43)	729	20.24 ± 0.36 (45)	975	0.43 (39)	18.69	14.26 ± 0.26 (43)	25 January
2002	390.19 ± 12.01 (47)	799	19.19 ± 0.38 (63)	1,140	0.40 (57)	17.37	12.91 ± 0.29 (47)	2 February

on total number of sea lions onshore showed an average of 46.2% (±3.5, $n = 12$) of the sea lions abandoned the beach during thermoregulatory movements.

The importance of avoiding heat-related thermal stress in sea lions was evident during the afternoon when the distribution of sea lions always matched the shade provided by the rocky cliff. By ~1500 each day, the entire rookery was covered by shade and the sea lions were occupying all inland resting sites. Females did not make thermoregulatory movements during cloudy days, and did not abandon the beach as observed during sunny days—opting instead to increase the spacing between themselves and other females by at least one body length. Numbers of females during cloudy days, when mass thermoregulatory movements did not occur, were similar between counts at 0600 and 1200 (*i.e.*, counts at 1200 averaged just 0.5% [±1.1%, $n = 15$ d] fewer than at 0600).

Females had preferred birthing sites. In all years, the first pups of the season were born in two zones: the Cave and Zone C1 (Fig. 2). Although both zones represented only about 10% of the area occupied by females, 40.1% (±5.2%) of the pups were born here during the early breeding season. Newborns became more noticeable at other parts of the beach after pup densities peaked in Zone C1 and the Cave Zone (data not shown). In total, these two zones accounted for 29.2% (±4.0%) of all pups born at the rookery. Number of pups born per zone relative to the number of females counted per zone at 0600 was similar among all five zones (mean: 2.2 ± 0.2 pups per female, $n = 45$), with slightly, although not statistically significant, greater numbers of pups born per female observed in the Cave Zone (2.3 pups) and Zone C1 (2.8 pups) suggesting that more females tended to give birth there.

Pregnant females tended to give birth near or among females with newborns. The female-newborn groups were easily distinguished at several points along the beach, and increased in size as the season progressed until newborns occurred along the full length of the beach at the peak of breeding. Female clustering was more evident during the mornings at the peak of the breeding season when at least two or three females with newborns and fresh placentas were typically observed beside each other.

Birthing and mating were spatially segregated. Although most copulations occurred along the shoreline, most females (82.5%) gave birth on dry ground, with 17.5% of females giving birth on the wet substrate of the shoreline during the hot hours.

Female Mate Choice

Female South American sea lions at La Maternidad gave birth to single pups and remained onshore to nurse for 7.5 ± 0.07 d ($n = 260$ perinatal periods) before undertaken regular foraging trips. Females mated 6.0 ± 0.06 d ($n = 260$) after parturition and before making their first foraging trip. The sites and dates of parturition and copulation, as well as identification of mating partner(s), were obtained for 174 females. Of these females, 9.2% mated with both the male they were nearest after giving birth (birthplace male), as well as with another male. Only 54.6% of females mated solely with their birthplace males, with 45.4% opting to copulate with other males away from their birthing or resting sites. Of those females that mated with a nonbirth-place male, only four (2.3% of the total) mated with the nearest neighbors of their birthplace males, with the remaining copulating with males elsewhere along the shoreline (but not in their path to and from the beach). Overall, 83.9% of females mated with a single male and 16.1% had multiple partners. None of the males distributed along the shoreline made any obvious displays to draw further attention from the females.

In terms of mate choice by females, 63.8% of the females ($n = 111$) had a prior interaction with their mate, but 36.2% ($n = 63$) copulated with one or more males that they had not previously encountered. These females moved freely from where they remained with their pup after giving birth (which was close to their birth males) and walked toward males located as far as 10 neighboring males away. Females were observed to solicit mounting by exposing their genitalia to the chosen male. Males responded by smelling or licking the vulvae before mounting the females. After mating, females were observed rejoining their pups at their former location, and did not leave them again until departing on their first foraging trip.

Male Mating Success

We recorded 5,769 copulations and 913 mating attempts between 1997 and 2002 (Table 1). Excluding the 1997 breeding season when bulls were not categorized as residents or nonresidents, we found that as many as 3,284 (95.2%) of the 3,448 copulations we observed were achieved by resident bulls and 164 copulations (4.8%) were by nonresident bulls (1999–2002). Females resisted mating with resident bulls in 103 (3.2%) of the observed copulations and in eight (4.9%) of the copulations with nonresident bulls. Nonresident bulls interrupted 39 copulations attempted by resident bulls (1.2% of the total number of resident male copulations). In general, females appeared to mate willingly with resident and nonresident bulls.

Total number of copulations differed significantly among years (Kruskal-Wallis: $\chi^2_4 = 102.54$, $P < 0.001$) dropping from 2,321 observed copulations in 1997, to 558 in 1999 (after the 1997–1998 El Niño event), and rising to 1,140 in 2002 (Table 1, Fig. 4). The MDC also differed significantly among years (median test: $\chi^2_4 = 267.47$, $P < 0.001$; Fig. 4, Table 1) with as many as 17 d between the earliest peak (25 January 2001) and the latest peak in breeding activity (February 10, 1999). The peak period of breeding thus differed among years and overlapped on only 24% of the observed days (*i.e.*, 5 d from 31 January to 4 February). The peak season encompassed 52.0% ± 0.7% of total copulations observed during a period of 18.6 ± 0.8 d (all years combined).

The numbers of copulations per male differed significantly among years (Kruskal-Wallis: $\chi^2_3 = 13.15$, $P = 0.004$; median 1999: 4, $n = 71$; 2000: 3, $n = 94$; 2001: 6, $n = 88$; 2002: 7, $n = 85$), and varied significantly within each year of study (CV > 113%). Of 338 resident bulls, 84 (24.9%) were never seen mating, while the remaining 254 (75.1%) mated at least once. Only a small proportion of the males were responsible for most of the copulations (9.8 ± 2.6%, $n = 34$, >25 copulations), while 28.1% of the bulls (±1.7%, $n = 95$) accounted for up to five copulations (Fig. 5). These proportions of copulating males were consistent among years. However, the proportion of males that failed to copulate differed significantly between years ($\chi^2_3 = 9.33$, $P = 0.025$, mean: 24.9 ± 4.5%).

The maximum number of copulations achieved by a male was 75 during a 40 d tenure in 1999. The second most successful bull achieved as many as 61 copulations over 25 d in 2001. This significant skewing in mating success was apparent each year with 14% of all resident bulls achieving 50% of all copulations (median = 12, interquartile range: 9–14 males). During the peak breeding period, males defending

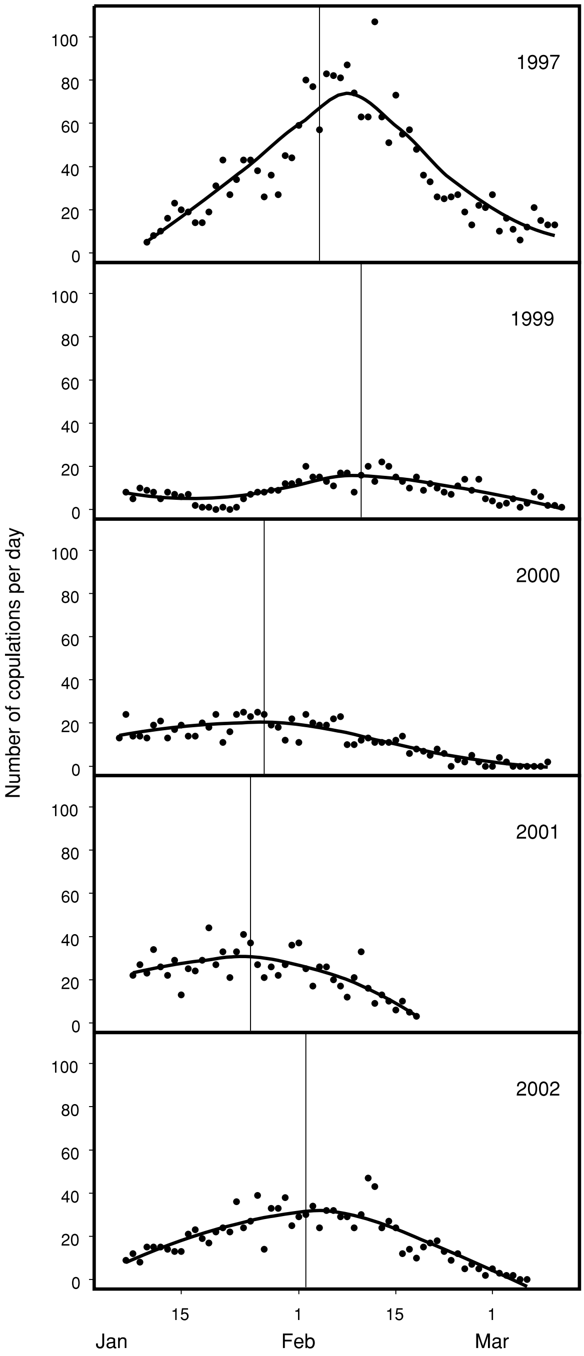

Figure 4. Total numbers of copulations per day by all South American sea lion bulls at La Maternidad beach from 1997 to 2002. Vertical lines indicate median date of copulations (MDC). Data were smoothed with LOESS curves.

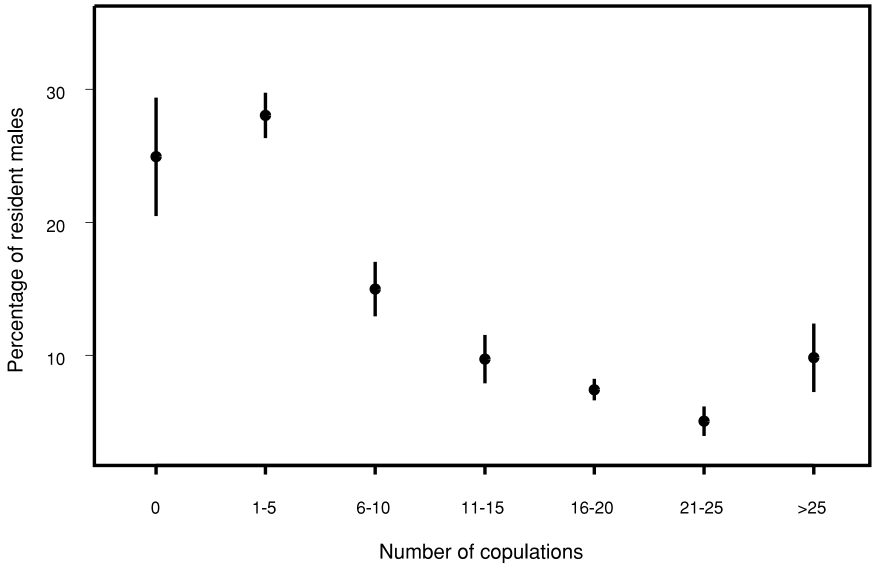

Figure 5. The percentages of resident South American sea lion bulls (mean ± SE) that achieved 0 to >25 copulations during a single breeding season from 1999 to 2002 at La Maternidad beach.

positions within the same zones for equal durations and dates achieved significantly different numbers of copulations (*e.g.*, Zone C2 in 2001: $\chi_3^2 = 11.42$, $P = 0.009$, range 6–23 copulations per tenure) suggesting a disproportional share of copulations among males. Differences between the numbers of copulations were also found among zones for males having equal tenures during the peak breeding season (2002: $\chi_7^2 = 22.42$, $P < 0.001$, range: 7–32 copulations per tenure; 2001: $\chi_{10}^2 = 35.77$, $P < 0.001$, range: 7–31; 2000: $\chi_8^2 = 16.52$, $P = 0.035$, range: 4–21; 1999: $\chi_{11}^2 = 51.00$, $P < 0.001$, range: 6–35). However, when considered over the entire breeding season, no significant differences were noted in the number of copulations per male among the five zones of the beach in each year of study (Kruskal-Wallis: $\chi_4^2 > 2.04$, $P > 0.25$).

Although female densities varied among the zones of the beach (mean: 87.2 ± 18.7 females), the mean number of females per zone (from daily counts, $n = 45$) relative to the mean number of resident bulls per zone (from daily mapping, $n = 45$) was consistent among zones ($\chi_3^2 = 4.48$, $P = 0.214$, 20 females per resident bull). Similarly, the total number of copulations per zone relative to the mean number of resident bulls per zone was also consistent among zones ($\chi_3^2 = 4.82$, $P = 0.185$; 29 copulations per male). Interestingly, the number of copulations relative to the number of pups born per zone did not differ among zones of the beach or years of study (Kruskal-Wallis: $\chi_3^2 = 3.78$, $P = 0.29$; mean 1.52 ± 0.1 copulations per pup born all years combined). In other words, males in all zones had the same potential to inseminate a similar number of females and did not increase their chances of copulating by having more females passing by them each day. However, variability in the rate of copulations by males within a zone was high in all years (CV > 88%) indicating a disproportional share of expected copulations between

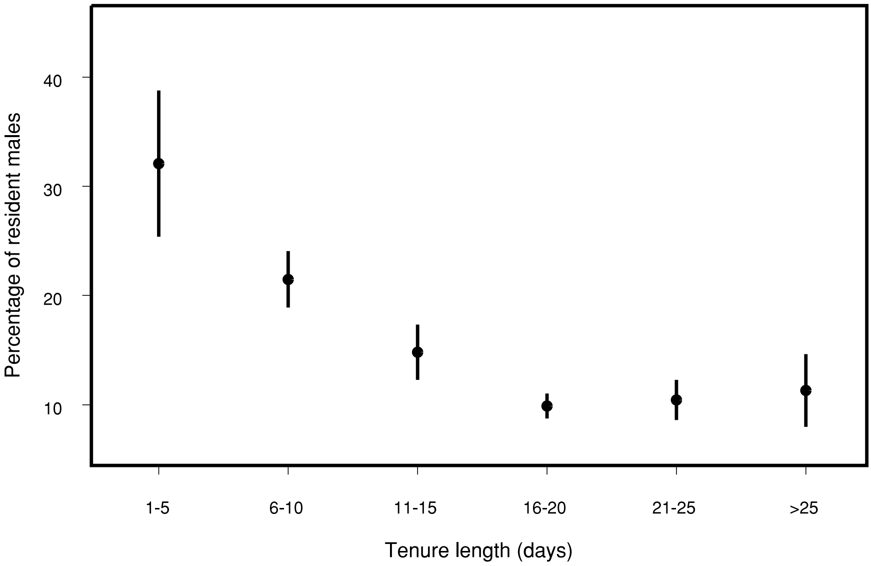

Figure 6. The percentages of resident South American sea lion bulls (mean ± SE) with tenures of 1 to >25 d onshore per breeding season from 1999 to 2002 at La Maternidad beach.

males (*i.e.*, the number of copulations achieved by neighboring males during the same day ranged from a minimum of 0 to a maximum of 7). High variability in mating success was also detected from one day to the next, with daily coefficients of variability in all years ranging from 69% to 219% during the peak of the breeding season.

Male Tenure

The tenure of males onshore differed significantly among years (Kruskal-Wallis: $\chi^2_3 = 20.57, P < 0.001$, median 1999: 11, $n = 71$; 2000: 7, $n = 94$; 2001: 7, $n = 88$; 2002: 12, $n = 84$), and was shortest in Zone C1 compared to the other zones of the beach in all years. Variability in tenure length of males was high in each year of study (CV > 113%) with most males having short tenures between 1 and 5 d (32.1 ± 6.7%, $n = 110$), and relatively few (9.8 ± 2.6%, $n = 37$) having tenures longer than 25 d (Fig. 6). These proportions were consistent among years except for males with short tenures (1–5 d, $\chi^2_3 = 19.24, P < 0.001$).

The number of copulations per male differed with the time of year that tenure was held (Kruskal-Wallis: $\chi^2_4 > 39.49, P < 0.001$). Males that held their positions during the early and peak season had a higher rate of copulations in all years (*e.g.*, median 2001: 25 copulations) compared with males that were onshore only during the early season (3 copulations), or only during the peak season (7 copulations), the peak and late season (14 copulations) or the late season (1 copulation). Most males started their tenure during the late breeding season (30.9%, $n = 105$), compared with 21.5% ($n = 7\ 2$) of males that held tenures through the peak season and early portion of the late season, 17.4% during the early and peak season ($n = 59$), 16.8%

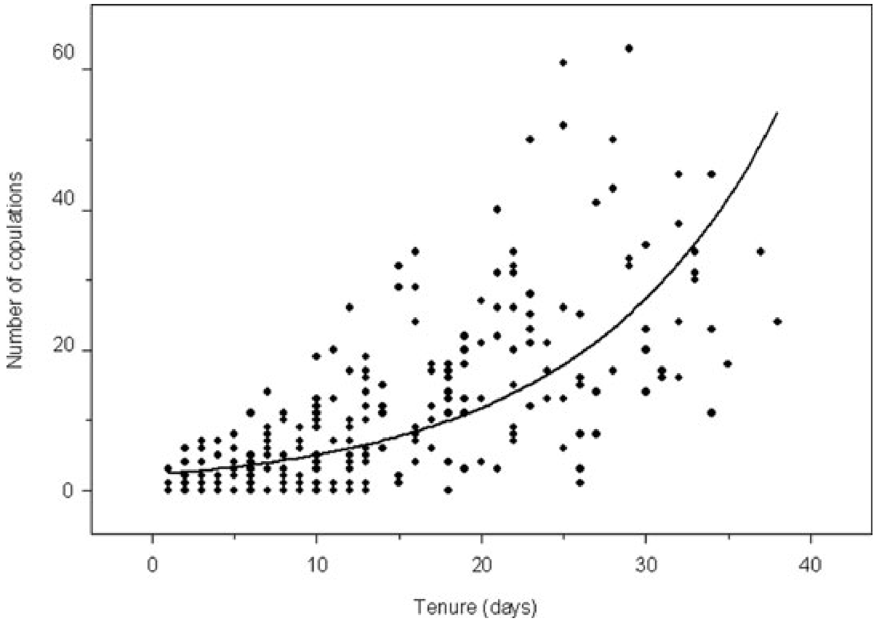

Figure 7. Numbers of copulations per resident South American sea lion bull as a function of tenure length (days) onshore during the 1999–2002 breeding seasons at La Maternidad beach. The data were best described by a nonlinear regression ($r^2 = 0.59$, $P < 0.001$).

only during the early season ($n = 56$), and 13.4% only during the peak season ($n = 46$).

Tenure length was positively correlated with numbers of copulations per male (Fig. 7) for each year of study, and did not differ significantly among years ($r = 0.77$, $P < 0.001$, all years combined). A large proportion (59%) of the variation in the number of copulations could be explained by the length of tenure. Males that were never seen copulating had the shortest tenures in all years (mean ± SE: 4.0 ± 0.4 d, $n = 83$), while males with more than 25 copulations had the longest tenures (24.7 ± 1.0 d, $n = 51$). Fitting a nonlinear regression to the relationship between numbers of copulations and length of tenure showed the number of copulations increased exponentially per day spent at the beach ($r^2 = 0.59$, $P < 0.001$, Fig. 7). Thus, the reproductive opportunity for males to mate increased exponentially with each additional day they stayed onshore.

Discussion

The mating system of South American sea lions at the Ballestas Islands differs from that reported for South American sea lions at more temperate breeding sites where males defend groups of females and fixed territories (Cappozzo and Perrin 2009). Instead of restricting the movement of females to tide pools or open ocean as expected, the South American sea lion bulls we observed positioned themselves along the waterline and allowed the free movement of females between the beach and water. Such behavior is more reminiscent of lekking behavior than the resource-defense polygyny commonly associated with pinniped mating systems.

Lekking Criteria

The minimal criteria to distinguish classical lek species from those with alternative mating systems are: (A) no male parental care, (B) males aggregate in a mating arena and defend small mating territories that do not fill the entire habitat used by females and where most mating occurs, (C) mating grounds contain no critical resources required by females, and (D) females can choose between potential partners (Bradbury 1981). Another important characteristic of leks is having (E) large variance in male mating success where few males may account for most of the matings (Bradbury *et al.* 1985, Höglund and Alatalo 1995). The mating system of the South American sea lion at our study site appears to satisfy all of these criteria with the possible exception of Criterion C.

A. *No male parental care*—The resident bulls at our study site provided no parental care to newborn pups, as is the case for all pinniped species (Le Boeuf and Campagna 1994). Only females nurtured and directly protected the pups. Resident bulls generally appeared to be indifferent toward pups, although their presence along the water's edge provided pups with indirect protection from attempts by subadult males to abduct and treat suckling pups as estrous females—often leading to their deaths (Soto 1999).

B. *Male aggregation and small mating sites*—The resident bulls at La Maternidad were not distributed evenly among the breeding females, but maintained positions that facilitated thermoregulation (Fig. 2, 3). Bulls showed a preference for being in zones that were superior for pupping (*i.e.*, C1 and the Cave) where they could access greater numbers of receptive females, particularly during the early part of the breeding season. The positions held by the resident bulls were dynamic (*i.e.*, they moved with the prevailing ocean conditions) and were not restricted to a fixed space associated with physical features of the environment as expected in most resource-defense polygyny systems (Twiss *et al.* 1994).

The aggregation of resident bulls at La Maternidad was much denser than at the temperate South American sea lion breeding sites in Argentina where spacing between territorial bulls guarding females is much greater (Campagna and Le Boeuf 1988*a*). However, there was no apparent increase in aggressiveness associated with the closeness of the resident bulls. The low rates of AI we observed at La Maternidad between the neighboring resident bulls were low, suggesting a relatively low degree of competition for preferred zones (*e.g.*, aggressive interaction in the Cave were lower than in any other zones of the beach). This suggests that position by itself relative to other males may not ensure breeding success. Thus, male South American sea lions at La Maternidad defended positions where most mating occurred but did not fill the entire habitat used by females.

C. *No critical resources required by females*—Pregnant females require a safe place to give birth that is free of predators and protects the pups from harmful tides, wave action, or other dangers (Mesnick and Ralls 2009). In a hot sunny climate, they must also ensure that they and their offspring do not become too hot and die of heat exhaustion. The sloping pebble beach at La Maternidad combined with the shade and terrestrial protection of the cliffs satisfies many of the female requirements, as does the cooling effects of the water and wet intertidal substrate.

The resident bulls at La Maternidad attempted to remain as close to the estrous females as possible while ensuring that they too did not overheat. Given their much larger body size than females, the bulls had no choice to avoid overheating but to stay out of the sun (*i.e.*, in the Cave) or position themselves along the water's edge. They defended their positions from other males on the shoreline where wet substrate was a dynamic and critical resource used by both males and females. Males had continuous access to females on the shoreline and did not restrict or prevent them from using the cooling substrate or moving over it.

Defensible patches of resources must exist for resource defense to be a viable reproductive strategy (Emlen and Oring 1977). However, the availability of wet pebbles and water was uniformly distributed along the shoreline of the beach and was equally available to all females. Unlike a tide pool or a cave, there was no limited resource that males could defend to attract females (Campagna and Le Boeuf 1988*b*). Resident bulls prevented nonresident males from using the wet substrate near the breeding females, but were unable to influence where females chose to give birth. The apparent small size of male sites (and the proximity between resident bulls) relative to the size of the female breeding area, and the small size of the mating grounds relative to the resources critical to their survival suggest that males were not using resource defense as a reproductive strategy.

D. *Female choice*—Males with equal tenure duration had differential mating success, which we could not explain by time of season, numbers of females, or beach position. While more detailed fine-scale movement and location data on individual females and males with which they mate might yet reveal an importance of location, our observations suggest that the difference in numbers of copulations attained by different males reflected female mating preferences for male characteristics that we were unable to recognize. About half of the females only mated with the resident bull closest to where they had given birth, while over one-third only mated with a different male further along the beach. Females that copulated with their birth-place males might have chosen them prior to giving birth given that some marked pregnant females were known to have visited the beach before settling down to pup. The absence of harassment and the free movement of females we observed between males added further credence to the possibility that females chose partners on the basis of male phenotype rather than male locations (Clutton-Brock *et al.* 1989). The fact that male mating success was independent of the locations where males held tenure on the shoreline also suggested that females actively chose between potential partners.

Female choice is generally thought to be a particularly important determinant of variable male mating success (Gemmell *et al.* 2001, Lidgard *et al.* 2004, Lancaster *et al.* 2007, Negro 2008). However, the extent to which females at our study site selected males based on location or phenotype was unclear due to the difficulty of distinguishing between female choice for a top male *per se* and choice for a prime location that top males may coincidentally prefer (Birkhead and Moller 1993). Some male characteristics such as the ability to keep intruders away from the mating grounds may attract females and may differ between individuals (Clutton-Brock *et al.* 1993). Levels of male competition may also be reflected in the frequency of AI associated with gaining and maintaining a position along the shoreline, which in turn might be a sexual display to attract females and improve male fitness (Boness 1991). Such male agonistic behavior has been reported in other species of pinnipeds as a mechanism of sexual selection that promotes female mate choice (Cox and Le Boeuf 1977, Boness *et al.* 1982).

E. *Variance in male mating success*—The large variance we observed in male mating success is consistent with that found in several lek-breeding mammals where few males account for most of the copulations (Bradbury 1981, Bradbury and Gibson 1983, Clutton-Brock *et al.* 1988, Clutton-Brock *et al.* 1989, Wiley 1991, Apollonio *et al.* 1992). A few of our resident sea lion bulls accounted for most of the matings and the large variance we observed in male mating success as observed in polygynous systems. In fact, one-quarter of all the resident bulls we observed did not mate, while only 14% of them accounted for half of all copulations. Mating success was extremely skewed, with one male achieving 75 copulations during a 40-d tenure. Most males had short tenures between 1 and 5 d, with relatively few having tenures longer than 25 d. Those that stayed longer succeeded in copulating with more females. Location of male sites on the shoreline failed to explain the variation we observed in mating success, as seen in true territorial species where the location and quality of the territory determine the magnitude of male mating success (Campagna and Le Boeuf 1988*b*).

Male mating success assessed from behavioral methods can reflect true reproductive success determined genetically in some polygynous mammals (Pemberton *et al.* 1992, Hoelzel *et al.* 1999, Fabiani *et al.* 2004, Twiss *et al.* 2006). In terms of mating success, we recognize that copulations do not necessarily equate with paternity but nevertheless believe that it was a good proxy given that most females (>83%) observed over 4 yr of study copulated with only one partner, and few (<18%) had two or more partners. Further confirmation of mating success will require molecular studies that may increase understanding of male mating success and the role of female mate choice in polygynous mammals.

A True Lek or a Resource-Defense Variant?

Grouse are probably the best known example of lekking species where males aggregate and display close together in one area, while females freely choose to mate with any males in the lek before leaving the males to continue displaying toward other females (Höglund and Alatalo 1995). Among mammals, fewer species display lek-like mating behaviors (*e.g.*, some ungulates and bats; Bradbury 1977, Clutton-Brock *et al.* 1988, Clutton-Brock *et al.* 1989, Apollonio *et al.* 1992, Balmford 1992, Balmford and Blakeman 1992, Deutsch and Nefdt 1992, Deutsch 1994, Sachteleben and Von Helversen 2006). A few of the pinnipeds (most notably harbor seals, California sea lions and Pacific walrus) are also thought to have lek-like mating systems (Heath and Francis 1983, Fay *et al.* 1984, Hayes *et al.* 2004, Boness *et al.* 2006), which contrasts sharply with most species of fur seals and sea lions that employ resource-defense mating strategies (Campagna and Le Boeuf 1988*b*, Francis and Boness 1991).

Lek-breeding has been proposed to occur as a default strategy when males cannot successfully monopolize mates by defending female home ranges, stable groups or predictable resources patches (Balmford 1992, Deutsch 1994). Under these circumstances, males may be forced to establish small mating territories and advertise for females (Emlen and Oring 1977, Deutsch 1994). It has also been suggested that leks originate from placing male territories in "hotspot" areas where females are highly concentrated (Bradbury and Gibson 1983). This we believe captures the sea lion mating behavior we observed at La Maternidad in Peru.

Our observations of the South American sea lion in Peru are consistent with typical lekking species that have long breeding seasons, highly skewed operational sex ratios and an inability of males to economically monopolize resources necessary to acquire mates (Emlen and Oring 1977). Male South American sea lions at our study site did not defend females or rigid territories, and allowed females to freely pass by them, which is in marked contrast to the often intense herding effort of male otariids directly defending females or fixed areas (reviewed in Boness 1991). The resident bulls in Peru obtained their positions to optimally encounter females, which meant that females never went far to choose between potential partners.

Mating systems encompass an enormous range of behaviors and strategies within and between species that are optimized to increase the reproductive success of males and females (Höglund and Alatalo 1995, Shuster and Wade 2003, Oliveira *et al.* 2008). Some of this apparent plasticity in behaviors and strategies makes it difficult to definitively classify many of the mating systems that have been studied. At our study site, the South American sea lion appeared to display a lek-like breeding behavior consistent with the five criteria outlined above to distinguish lek species from those with alternate mating systems (Bradbury 1981, Bradbury *et al.* 1985, Höglund and Alatalo 1995). However, it might be more accurate to classify the sea lion mating system in Peru as a resource-based lek-like system given the dependence of males to remain on cool wet substrate to maintain thermoregulatory control.

South American Sea Lion Mating Systems

To date, the mating system of South American sea lions has been described as a polygynous female-defense system where males defend positions on the central breeding area beginning in mid-December, and later defend and copulate (sometimes forcefully) with females until early February (Campagna and Le Boeuf 1988*b*, Cappozzo and Perrin 2009). These descriptions are largely based on observations of South American sea lions in the temperate waters of Argentina (see Campagna and Le Boeuf 1988*b*), and differ significantly from those we made in the subtropical waters of Peru where the breeding season is much longer and the mating system is not a female-resource based defense. Such geographic differences in breeding behavior exhibited by South American sea lions are likely explained by the ratio of breeding males to females, a protracted breeding season, and the thermoregulatory selective pressures associated with climate and rookery topography.

Among the most notable differences between the Peruvian breeding population and the southern populations is the low rates of threat display per male at our study site (0.7/h) compared to a rookery of South American sea lions with a female-defense system in Argentina (9.0/h) (Campagna and Le Boeuf 1988*a*). This relatively low level of aggressive activity at La Maternidad may reflect the "dear enemy" phenomenon, when tolerance or familiarity exists between neighbors (Heath 1989). Less aggression between neighbors would reduce mating costs between males, and could theoretically increase reproductive success in females by reducing fatal injuries to them and their pups. In addition, the virtual wall of closely spaced males that border the shoreline of the Peruvian rookery presumably prevents groups of male raiders from storming ashore to abduct females and force them to mate as reported in Argentina (Campagna *et al.* 1988). The massive thermoregulatory movements of females each morning to the water, combined with the low ratio of males to females at La Maternidad accentuates the difficulty of female defense and might further help explain some of the intraspecific variation in mating systems between rookeries.

Differences in the ASR between the breeding colonies of South American sea lions are particularly striking with an average of 17 females per male at La Maternidad—the highest observed for the South American sea lion throughout its range. Prior to our study, South American sea lions were considered to be one of the otariids with the lowest level of polygyny (see Boness 1991). The number of females per male observed at other rookeries rarely exceeded 8 in Uruguay (Vaz-Ferreira 1975) and fluctuated between 9 and 12 females per male in Chile (Paves *et al.* 2005)—a value that corresponds to the minimum value we found. In Argentina a rookery with a similar topography and substrate to our study site had males defending female harems with fewer than four females on average per male during the peak season (Campagna and Le Boeuf 1988*a*).

The high ratio of females to males at our study site might have occurred because there were few males in the population or few males were prepared to reproduce, or because there was insufficient shoreline to accommodate greater numbers of resident bulls. The high density of adult males we observed in 1997 is consistent with the limited shoreline theory. However, the strong 1997–1998 El Niño event also killed a significant portion of the adult population (Soto *et al.* 2004), such that only a few males defended positions along the shoreline. This suggests that the low numbers of males we observed likely reflected a lower proportion of males in the population, but we cannot say with certainty why the ASR observed in Peru differs markedly from that observed elsewhere in South America.

Differences in the duration of pupping (and therefore the synchronicity in numbers of females in estrus) may explain some of the differences in the degree of polygyny observed among species (Boness 1991). In the case of South American sea lions, the duration of the breeding season varies across their range. Pups in Argentina, for example, are generally born from mid-December to early February, with most pups born during January (Campagna 1985). However, pups in Peru are born from mid-December to mid-March, with a peak or concentration of births that is either less defined than in Argentina, or shifts between years (Soto *et al.* 2004). The end result of a longer breeding season in Peru is a low ratio of estrus females to bulls on any given day (0.38:1.00, our study) compared to a high potential ratio of estrus females per bull across the entire breeding season (17.50:1.00, our study). Thus, the energetic costs for bulls in Peru to stay on land and maintain control over the small numbers of females that come into estrus at any one time may simply be too great to support the polygamous mating system observed in Argentina. This inability of males to defend protracted numbers of estrus females may well be the deciding factor that affords females the opportunity to choose potential mates.

The Peruvian marine environment is potentially a significant driving force underlying the mating success of males and the evolution of the sea lion mating system at La Maternidad (Soto *et al.* 2004). The interannual differences we noted in numbers of copulations and MDC appear to be linked to the major stochastic and contrasting episodes of high and low availability of the Peruvian anchovy—the main prey of the sea lions. The 1997–1998 El Niño was the strongest on record and had severe short-term effects on sea lion reproductive ecology through high adult male mortality (~40% died), massive numbers of abortions (~95% of the expected pups), and the loss of entire young cohorts (Soto *et al.* 2004). In contrast, the 1999–2001 La Niña resulted in a high abundance of prey, which sea lions failed to capitalize upon due to the lagged effects of the exceptionally strong El Niño that preceded it (Soto *et al.* 2006).

Lek-like Pinniped Mating Systems

Lek-like mating systems are not generally associated with pinniped mating systems. Yet, lek-like dispersion patterns and mating characteristics have been reported to date for 4 of the 34 species of pinnipeds—harbor seals, California sea lions, Pacific walruses, and with our study, the South American sea lion (Ray and Watkins 1975, Heath and Francis 1983, Fay *et al.* 1984, Hayes *et al.* 2004, Boness *et al.* 2006). Hooker's (New Zealand) sea lions have been classified as a lek breeder (Boness 1991, Mesnick and Ralls 2009), but closer inspection of their breeding system reveals that it is in fact resource-defense polygyny (Gentry 1998, Auge *et al.* 2009, Gales 2009). Additional cases of lek-like breeding behavior may increase with time as the lesser known species of pinnipeds become better studied. The lek-like mating systems reported to date reveal a wider repertoire of pinniped breeding behavior than generally recognized, and point to a number of common factors that may help explain the evolution of pinniped mating systems.

Heat stress, population density, female movements, ASR, breeding season duration, and the topography and stability of pupping sites appear to be the key factors that shape the extent to which the pinniped mating system is skewed toward female-resource defense or toward lek-like behavior. For example, male Atlantic walrus monopolize access to female herds (female-defense polygamy) in contrast to male Pacific walrus that form small groups near female herds and make intricate vocal and visual displays to attract females (Ray and Watkins 1975, Fay *et al.* 1984, Sjare and Stirling 1996). The difference in behavior between the two species of walrus presumably reflects the need for male Pacific walrus to display because they cannot control the movement of estrous females resting on moving ice flows as they can with females using land-fast ice. Male harbor seals that also mate in water, occupy strategically chosen aquatic display sites where they make vocal displays to attract mates swimming to foraging areas from dispersed pupping sites (Hangii and Schusterman 1994, Van Parijs *et al.* 1997, Boness *et al.* 2006). California sea lions and South American sea lions also appear to exhibit lek-like behaviors at some sites where males are unable to restrict the daily mass movement of females seeking water (Heath and Francis 1983, Heath 1989, our study). In both cases, male California and South American sea lions appear to have adapted their mating strategies to gain access to females rather than hold them captive because topography, climate, and sex ratios prevent them from controlling the movements of females. The energetic and reproductive cost of successfully defending large numbers of females may simply be too high (Emlen and Oring 1977).

Female pinnipeds appear to actively choose mates when certain combinations of climate, topography, or population density allow them to move freely among males. Male mating success may thus vary greatly among individuals, further intensifying selection for traits other than size and threat displays that confer an advantage in reproduction. We found that length of tenure was directly related to male mating success, as has been shown in several pinniped species (Campagna and Le Boeuf 1988*a*, Twiss *et al.* 1994, Arnould and Duck 1997), and that mating success was higher for males located near preferred pupping areas. Unfortunately, it is difficult to unambiguously demonstrate female choice among pinnipeds and the male characteristics they favor (Hoffman *et al.* 2007).

Conclusions

Our findings add to a growing body of literature showing that pinnipeds have greater plasticity in their mating systems than commonly recognized. In particular, our observations reveal that the South American sea lion at the Ballestas Islands has a lek-like mating system that differs markedly from South American sea lions in temperate climates, as well as from the common systems observed in most polygynous mammals. Thermoregulatory requirements and the absence of suitable places to prevent overheating inland were important determinants of the spatial distribution and behavior of the breeding sea lions we observed in Peru. Massive daily thermoregulatory movements of females to cope with hot environments, along with the protracted breeding season and large number of females relative to males, likely shaped their lek-like mating system by reducing the ability of males to monopolize mates.

Most research of pinniped breeding systems has focused on the abilities of males to defend females or monopolize resources that result in the more commonly reported polygamous mating strategies. Our research points to the need to better understand the relationship between sex ratios and sex-specific behaviors to control or attract each other, as well as the important role that female choice may play in male reproductive success. Exploring such relationships will help to further elucidate the selective forces that have shaped the evolution of mating systems of pinnipeds and other species.

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