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Plasticity in the agonistic behaviour of male California sea lions, *Zalophus californianus*

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Environmental conditions may influence mating behaviour in otariids breeding in areas with elevated temperatures and intense solar radiation. Although they have evolved morphological and physiological adaptations to prevent overheating while breeding on land, under extreme temperature conditions, they must adjust their behaviour in order to thermoregulate. The California sea lion mating system is based on male competition and displays that occur while defending their territories when females are present. We studied the agonistic behaviour of adult males at two breeding colonies in Mexico with contrasting environmental characteristics: Isla Santa Margarita (ISM) (Pacific coast) and Isla San Esteban (ISE) (Gulf of California). The goal of this study was to determine which variables influence where (i.e. on land or in the water) aggressive interactions between adult males occurred using logistic regression analysis. We analysed three scenarios: (1) both islands, (2) only ISM and (3) only ISE. The best model for the first scenario included the air temperature, density of females and type of aggression. The second scenario involved the density of females, and the third scenario included the rate of female interactions. Although the California sea lion mating strategy involves monopolizing critical resources, our results indicate that density of females and rate of female interactions have a significant impact on where male aggressive interactions occur. Our results highlight how changing environmental conditions affect the behavioural plasticity of this species' mating system. Most notably, males inhabiting high-temperature environments use the thermoregulatory strategy of defending territories adjacent to the coast while remaining immersed in the water. This strategy may result in decreased polygyny in the Gulf of California colonies relative to those on the Pacific coast.

Aggressive interactions are an expression of individuals competing for different kind of resources, such as shelter, territories, food or mates (among others). According to sexual selection theory, aggressive interactions between individuals of the same sex are mechanisms aimed at excluding competitors from areas occupied by potential mates in order to increase the individual's reproductive success (Darwin, 1871). This aggressive behaviour is defined by the spatiotemporal distribution of females (Emlen & Oring, 1977), which in turn is influenced by the distribution of resources and the risk of predation (Boness, 1991; Leutenegger & Kelly, 1977; Lindenfors, Froberg, & Nunn, 2004). Male reproductive success is limited by the number of females that males can successfully mate with (Clutton-Brock & Harvey, 1978). Thus, the mechanisms of sexual selection depend upon the competitors' ability to exclude adversaries (Boness, 1991; Harcourt, Harvey, Larson, & Short, 1981; Puts, 2010).

Because of their marked sexual dimorphism, pinnipeds have been used to test sexual selection hypotheses (Lindenfors, Tullberg, & Biuw, 2002). The large body size of otariid males appears to have evolved as a response to intrasexual competition for territory acquisition and the ability to control a particular territory over the long term (Bartholomew, 1970). Although male and female California sea lions reach sexual maturity at the same age (±5 years), males do not hold breeding territories with females until they reach physical maturity (= 2–2.5 m in length, = 250–400 kg, with fully developed secondary sexual characteristics) at approximately 9–10 years of age (Peterson & Bartholomew, 1967; Schusterman & Gentry, 1971). Females invest a greater amount of energy in the care of their offspring, at the expense of somatic growth. In

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contrast, because they do not aid in caring for pups, males can use their energy for physical growth (Lindenfors et al., 2002).

California sea lions have a resource defence polygynous mating system with some additional characteristics similar to those found in lek mating systems (Boness, 1991; Heath, 1989). As part of their mating ritual, California sea lion males compete for territories when females are present on land or in the water and engage in agonistic interactions that include ritualistic displays (vocalization and chasing) and/or physical aggression (hitting, biting or pushing). The principal body regions involved in such interactions are the neck, jaw, frontal and dorsal regions of the head, and the flippers. In the latter, vascularization can lead to excessive bleeding or even limit the injured animal's mobility (Heath, 1989; Jacobs, Hernández-Camacho, Young, & Gerber, 2008; Robertson, Runcorn, Young, & Gerber, 2008). California sea lion males engage in aggressive behaviour in front of females not only to obtain and maintain their territories, but also to control the movement and distribution of adult females within them, by either monopolizing the birthing sites or physically restraining females until they enter oestrus (Heath, 1989). In otariids, sexual selection acts upon the male attributes and behaviours that help them attract and control breeding females. Thus, females play a major role in sexual selection within this group and influence the aggressive behaviour between males (Miller, Ponce de León, & DeLong, 1996).

California sea lions are distributed from the southeast coast of Canada (British Columbia) to the southeast coast of Mexico (Tres Marias Islands), including both coasts of the Baja California Peninsula (Lowry & Forney, 2005). There are 8–10 California sea lion rookeries on the Pacific coast of the Baja California Peninsula (Lowry & Maravilla-Chavez, 2005) and 13 in the Gulf of California (Aurioles-Gamboa & Zavala-González, 1994). There are significant environmental differences between the coasts because the Baja California Peninsula mountain system and the Baja California and Sonoran deserts act as physical barriers, reducing the marine influence of the Pacific Ocean and creating a more tropical climate in the Gulf of California (Roden, 1964). These temperate/tropical environments are characterized by high air temperatures, particularly during the summer when air temperatures in the Gulf average 32 ± 10 °C (Castro, Lavín, & Ripa, 1994; Roden & Emilsson, 1980; Ulloa, Torre, Bourillón, Gondor, & Alcantar, 2006). In contrast, summer air temperatures along the Pacific coast of Baja California range from 18 °C to 22 °C (Ramírez & Fleischer, 1987). Summer is also the California sea lion breeding season, making thermoregulation particularly challenging during this important period.

In this species, thermoregulation limits some reproductive activities, including confrontations between males, as these agonistic interactions increase body temperature. California sea lions can physiologically maintain and control their body temperature when the ambient temperature is between 10 °C and 18 °C (Whittow, Matsura, & Lin, 1972). However, when California sea lions are exposed to temperatures above 30 °C they are unable to achieve physiological thermal equilibrium (Whittow et al., 1972). To address these physiological restrictions, California sea lions decrease the flow of blood to the skin via vasoconstriction to reduce heat loss and maintain thermal equilibrium at lower temperatures. California sea lions possess no physiological mechanisms, such as perspiration, panting or rapid and laboured breathing ('thermal polypnea'), to maintain their body temperature when exposed to higher ambient temperatures (Whittow et al., 1972). Thus, this species relies on external mechanisms (e.g. adjusting behaviour) to control body temperature when exposed to warmer ambient temperatures.

Physical, environmental and behavioural characteristics may influence male California sea lion mating behaviour in different ways (e.g. level of activity, time of day, when and where certain behaviours occur; Heath, 1989; Young, González-Suárez, & Gerber, 2008), leading to different reproductive strategies and, ultimately, differences in the breeding system. In particular, because of the environmental differences in the areas inhabited by California sea lions, we examined the effect of different variables on where (on land versus in the water) male confrontations occur. Our goal was to better understand the use of behavioural plasticity by this species as a response to varying environmental conditions. The variables selected for analysis describe the spatial and temporal differences between the sampling areas (island, area ID = replicate site, month). We also considered the thermoregulatory abilities of the species, including both physical (air temperature, time interval) and behavioural variables (type of aggression, duration of the encounter), as well as some variables that relate to the mating system (female density, rate of female interactions).

We hypothesized that temperature and female density would be the most important variables in terms of determining where male aggressive interactions occur due to the thermoregulatory restrictions of this species, the different environmental and physical characteristics of each area, and the fact that the presence of females influences male aggressive behaviour in polygynous species. Thus, we expected that, given the lower temperatures and the higher density of females on land at Isla Santa Margarita (Pacific coast of Baja California), the probability of aggressive interactions between males occurring on land would be higher there than at Isla San Esteban (Gulf of California), which is characterized by higher temperatures and fewer females on land.

METHODS

Study Area

We recorded behavioural data during the reproductive season at two colonies with relatively large California sea lion populations and contrasting environmental characteristics (Fig. 1). One colony was located on Isla Santa Margarita (ISM) to the southwest of the

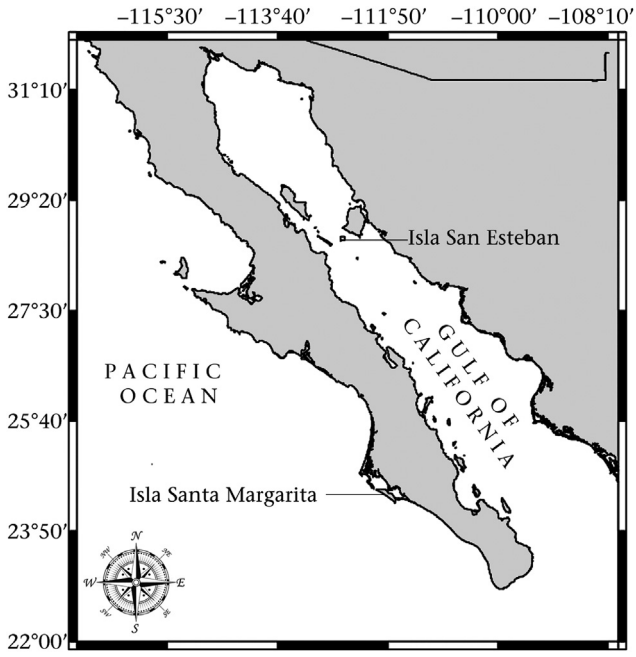

Figure 1. Map of the study area showing the two California sea lion colonies considered in this study: Isla San Esteban in the mid-Gulf of California and Isla Santa Margarita on the southwest coast of Mexico's Baja California Peninsula.