Seasonal Changes of Vocal Rates and Their Relation to Territorial Status in Male Galápagos Sea Lions (*Zalophus wollebaeki*)

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Abstract

Male vocal displays play an important role in sexual selection through both male–male competition and female choice. While this is supported by numerous studies in birds, much less attention has been paid to the role of such displays in mammals. We investigated the function of vocal displays in a polygynous mammal, the Galápagos sea lion (*Zalophus wollebaeki*). In our study population a large proportion of mature males are unable to establish a territory, providing the opportunity to compare the vocal behaviour between territorial and non-territorial males. We examined how seasonal patterns of vocalizations differed between territorial and non-territorial males and how the number of females present in a territory influenced behaviour of territorial males. We found that territorial males vocalized at higher rates than non-territorial males, and territorial males vocalized more at the onset than towards the end of territory tenure. During the onset of territory-tenure vocalizations of territorial males were directed more often towards other males than females. Furthermore, we found that vocalizations of territorial males were not only given in male–male interactions, but were also actively directed towards females. Territorial males vocalized at higher rates when more females were present in their territory. Our results suggest that vocalizations are important in male–male interactions, are relevant in territorial disputes and are used as a proxy for females to assess a male's quality.

Introduction

Sexual selection has led to the evolution of elaborated ornaments, such as vocal displays, which are important in both male–male competition and female choice (Andersson 1994). A male's display may correlate with its mating success by influencing other males, and also through direct or indirect effects on females (Wiley 1991). In many species, a pre-requisite to reproduce successfully is for males to establish and maintain a territory using vocal displays (e.g. Slater 1981; Reby et al. 1999), and females often base their mate choice on vocalizations (e.g. McComb 1991; Lode & Le Jacques 2003; Reid et al. 2004).

Thus, vocal displays may be an indicator of male quality (Andersson 1994). Across taxa it has been shown that the structure of vocalizations can encode information about the size, condition, quality, fighting ability or rank of an individual (e.g. Davies & Halliday 1978; Clutton-Brock & Albon 1979; Reby & McComb 2003; Fischer et al. 2004). These vocal displays often consist of repetitions of the same vocalization or call, throughout the breeding season (e.g. Gibson et al. 1991; McComb 1991; Gerhardt 1994; McElligott et al. 1999), suggesting that the rate and

the time spent vocalizing encode information about an individual. Although the function of vocal displays and their seasonal changes have been studied intensively in birds, anurans and insects (reviewed in Catchpole & Slater 1995; Gerhardt & Huber 2002), relatively little is known about seasonal changes of vocalizations in mammals (e.g. Fernandez-Juricic et al. 1999; McElligott & Hayden 1999; McElligott et al. 1999).

Galápagos sea lions (*Zalophus wollebaeki*) are endemic to the Galápagos islands (see Wolf et al. 2007a for recent taxonomic status) where they maintain large, sexually mixed colonies throughout the year (Trillmich 1979). Males are highly polygynous and compete intensely during the reproductive season for territories. In these territories, the majority of females give birth to one pup every second season, and are in oestrus briefly after giving birth (Trillmich & Wolf 2008). During the reproductive season, males use stereotyped vocalizations when interacting with each other. Serious fights rarely occur, suggesting that vocalizations are important to regulate territorial disputes among males. In our study population, a large proportion of mature males are unable to establish and maintain a territory (Wolf et al. 2005). This provides us with the opportunity to compare the vocal behaviour between males that are successful in establishing a territory and therefore having access to females (territorial males) and those males that remain unsuccessful throughout the mating season (non-territorial males).

Our aim was to determine the potential functions of vocal displays in the context of male–male competition and female choice in Galápagos sea lions. First, to determine the relevance of vocalizations in territory establishment and maintenance, we compared seasonal patterns of vocalization rates in territorial and non-territorial males. We hypothesized that, if the main function of vocalizing in males is territory establishment and maintenance, territorial males should vocalize more at the onset than towards the end of territory tenure, and territorial males should vocalize more than non-territorial males. Secondly, to determine to whom vocalizations are directed, we determined the recipients of vocalizations given by territorial males: other males, females, unspecific, i.e. to a group of individuals with no clear recipient. Furthermore, if acoustic signals provide information about male quality for females, we predicted that vocalization rate and the number of females present in a territory should be positively correlated.

Materials and Methods

Study site and study species

We studied Galápagos sea lions during their reproductive season between September and November 2004 on Camaño (0°45′S, 90°16′W), a small island close to Santa Cruz, Galápagos. About 120 adult males and 450 adult females use the island during the reproductive season (Wolf & Trillmich 2007). The reproductive season can last up to half a year, and over the course of the season the number of born pups and thus the number of receptive females is relatively constant (J. Wolf pers. obs.). Males compete for approx. 15 territories, the location and size of which remain rather stable across years (Wolf et al. 2007b).

We captured individuals in the rookery using hoop-nets (Fuhrman Diversified Inc., LaPorte, TX, USA) and restrained them briefly (for full details see Wolf & Trillmich 2007). We limited captures to the hours around dusk and dawn to prevent overheating of the animals and tagged individuals on both front flippers (numbered ear tags of size 0, Allflex, UK) for later identification through binoculars. Monitoring individuals over several years, we never observed animals to pay any attention to the tags and no inflammations were observed. We observed occasional tag loss (about 2% per year), mostly by flexible tag being pulled through the well-healed hole. Rarely, tags ripped out when applied by mistake too close to the body in the more fleshy part of the flipper. We recaptured several animals that had lost a tag and never found any infections or changes around the hole or the rip that would indicate inflammatory reactions.

Males that were too large for capture were either individually recognized by natural marks or bleached with a mixture of 12% hydrogen peroxide (Glynt; Swiss Formula, Konzen Cosmetic, Germany) and powder bleach (Frey-Cosmetic, Germany). To do so we approached sleeping males and applied the hair lightener from a plate connected to a pole. As many males slept throughout marking, this procedure caused minimal disturbance. We started data collection after we were able to recognize each male individually.

Data collection

We observed males shortly after sunrise when they are most active (our personal observation). To determine the territory boundaries of territorial males,

we conducted two surveys twice a day throughout the season (for details see Wolf et al. 2005). To allow comparisons between territorial males and non-territorial males at the onset of a territory tenure (3–7 days after a male has taken a territory) and towards the end of a territory tenure (1–5 days before a male lost its territory), we observed non-territorial males on the same morning as territorial males nearby and assigned these observations to the same period (for a similar approach see Amrhein et al. 2004; Kunc et al. 2005, 2006, 2007). In four cases, focal territorial males had already established their territory before we arrived on the island and six males still maintained their territory when we left.

We observed territorial and non-territorial individuals for 30 min at the onset and towards the end of territory tenure. In each observation period, we counted the number of vocalizations, i.e. the overall vocalizations rate of territorial and non-territorial males. Males emit vocalizations in bouts, which are separated by silent intervals. Each bout consists of a rapid succession of short calls. We counted each of these short calls as one call. For territorial males, we also noted the recipient of each call distinguishing between short range and long range communication (for a similar approach see Fernandez-Juricic et al. 1999; Phillips & Stirling 2001). Short range (directed) communication was classified as either the proportion of vocalizations (1) given in close range interactions with other males, i.e. the focal male was moving towards another male or males were vocalizing at the territory boundary at each other or (2) given in the vicinity of females, i.e. the male was moving towards a single female or a group of females. We could clearly assign these behaviours to the specified categories, since in male–male interactions the non-focal male responded to these calls immediately either by approaching the focal male or moving more towards the centre of the own territory, whereas in male–female interaction females responded either with vocalizations, head movement or with aggression towards the male by biting it in the snout. The long range communication, more undirected communication (3) includes the proportion of unspecified vocalizations which have no obvious single recipient. To investigate the correlation between vocalization rates of territorial males and females present in a territory we counted the number of females present in a territory at the end of each observation period. Because it is impossible to predict when a territorial male will lose its territory, we observed territorial males every 5–8 days and included the observed session closest to a male's territory loss as the end of territory tenure.

Statistical analyses

Analyses were performed using R 2.0.1 (R Development Core Team 2005). To analyse the correlations between vocalization rate, stage of territory tenure and whether male was territorial or not we used the lme function in 'MASS' (Venables & Ripley 2002). We analysed the vocalization rate as a function of whether a male was territorial or not, and whether a male was at the onset or end of territory tenure. To account for repeated sampling of the same individuals, and thus, the non-independence of data points, we included individual identity as a random factor. Furthermore, we analysed the number of females present in a territory as a function of vocalization rate of territorial males and stage of territory tenure. Individual identity was again fitted as a random factor. Non-significant interactions were dropped from the initial full interaction model according to Engqvist (2005). After graphical inspection, using a paired t-test, we compared whether the proportion of vocalizations directed to females and males differed at the onset of territory tenure, and whether males decreased the proportion of calls directed to other males between onset of territory tenure and end of territory tenure. We included in the analysis 17 territorial males and 19 non-territorial males sampled at the onset and the end of territory tenure. Assumptions for normality and homogeneity of variances were fulfilled. All results are given as mean ± SE. All reported tests are two-tailed.

Results

Territorial males vocalized at higher rates than non-territorial males (Fig. 1; $F = 44.44$, $df = 1,34$, $p < 0.001$), and vocalization rate differed between the onset and the late stage of a territory tenure (Fig. 1; $F = 16.31$, $df = 1,34$, $p < 0.001$). This difference is mainly due to the high vocalization rates of territorial males during territory establishment (interaction between stage of season and male class: $F = 22.48$, $df = 1,34$, $p < 0.001$). Territorial males that lost their territory usually left the island. In six cases, however, males stayed on the island but were unable to establish a territory again. These males vocalized significantly less than during their previous tenure time (Wilcoxon test: territorial end of tenure: 19 ± 11.1, non-territorial period: 0.17 ± 0.17, $n = 6$, $Z = -2.2$, $p = 0.028$).
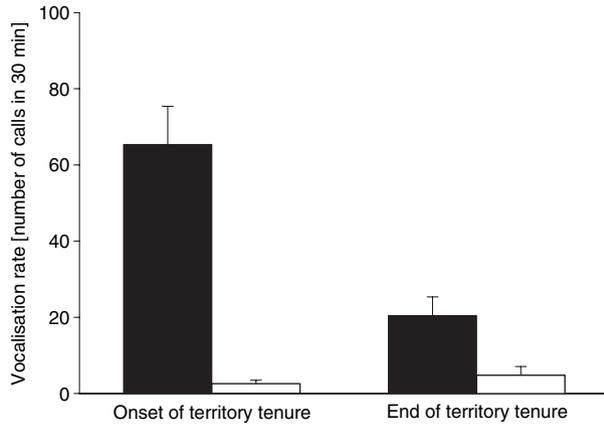
Fig. 1: Vocalization rate ($\bar{x} \pm$ SE) of male Galápagos sea lions at the onset and at the end of their territory tenure (black bars, n = 17). Non-territorial males were observed on the same morning as territorial males (white bars, n = 19).
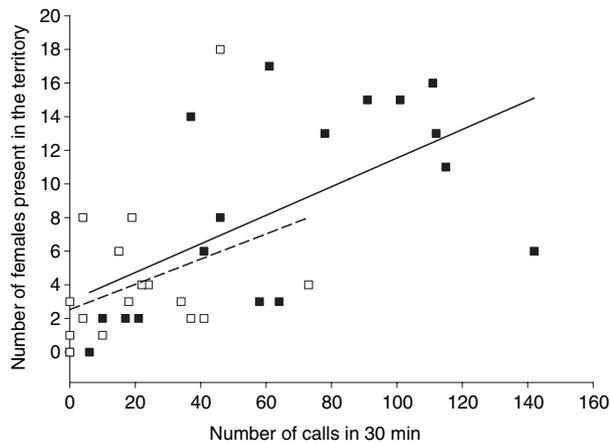

Fig. 2: Correlation between the vocalization rate of territorial males and the number of females present in the territory (filled squares and straight line: onset of territory tenure; open squares and dashed line: end of territory tenure).

In the following section, we restrict our analysis to territorial males. Territorial males vocalized at higher rates when more females were present in their territory (Fig. 2; F = 26.03, df = 1,15, p = 0.001) in both, the onset and the end of territory tenure (F = 0.44, df = 1,15, p = 0.52). Males directed most vocalizations to the colony (Fig. 3, F = 139.4, df = 1,82, p < 0.0001) in both, the onset and the end of territory tenure (F = 0.002, df = 1,83, p > 0.99). A small proportion of vocalizations, however, were specifically emitted either towards females or other males in both stages of their territory tenure. During the onset of territory tenure short range vocalizations were directed more often towards other males than
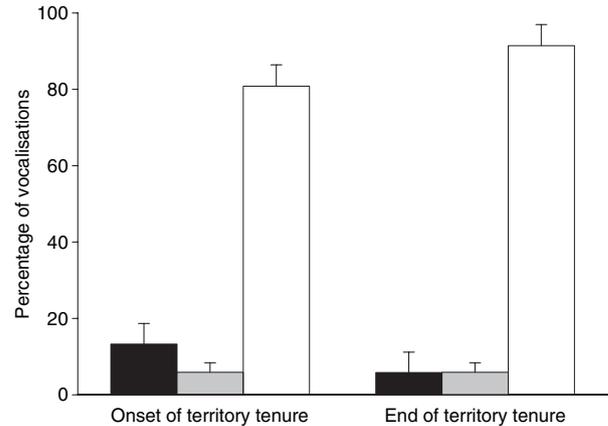

Fig. 3: Percentage of vocalizations ($\bar{x} \pm$ SE) directed to other males (black bars), females (grey bars) and with no clear addressee (white bars) at the onset and at the end of males' territory tenure.

females (Fig. 3; Paired t-test t = −2.38, df = 16, p = 0.022). Moreover, males decreased vocalizations that were directed to other males between the onset of territory tenure and end of territory tenure (Fig. 3; Paired t-test t = −2.42, df = 16, p = 0.029).

Discussion

Territorial male Galápagos sea lions vocalized more than non-territorial males. The vocalization rate of territorial males was higher at the onset than towards the end of territory tenure. Most of the vocalizations were given as a long range, undirected signals. Nonetheless, a small proportion of vocalizations were directed to both other males and females. In the onset of territory tenure more vocalizations were directed to males than to females. At the onset and at the end of territory tenure, male vocalization rate was significantly higher when more females were present in their territory. After loosing a territory, former territory owners had significantly decreased their vocalization rate.

Vocalization rate correlated strongly with whether a male was territorial or not. Vocalizing appeared to be particularly important to announce territory ownership at the onset of territory tenure. If vocalizations are an indicator of male quality, they should be costly to produce, otherwise cheating by low-quality males would be a viable strategy (Johnstone & Grafen 1993; Payne & Pagel 1996). To our knowledge the physiological costs of vocalizations in mammals have not been directly measured, but recent evidence in birds suggests that vocalizations entail rather low energetic costs (Ward et al. 2003, 2004 but see Vehrencamp et al. 1989; Gaunt et al. 1996).

As otariid males fast during territory tenure (Peterson & Bartholomew 1967), the main costs for a territorial male might be the permanent presence in its territory and the costs associated with male–male conflict rather than the vocal display itself.

Vocalizations may, however, represent an indirect cost for its sender. Vocalization rates could indicate a male's current ability or motivation to fight and only males that are able to compete with other males would vocalize regularly, which would explain the differences found between territorial and non-territorial males' vocal behaviour. This is also supported by our finding that territorial males vocalized significantly less after having lost the territory and that body condition (and thus fighting ability) is significantly lowered as a result of fasting (Peterson & Bartholomew 1967). The function of these vocalizations might therefore be to avoid costly confrontations with other males, since males might use vocalizations as well as visual signals to assess each other's current condition and fighting ability (e.g. Krebs et al. 1978; Clutton-Brock & Albon 1979; Reby et al. 2005). Thus, these vocal displays may not be energetically costly but they still may be an honest signal of quality where cheating is not a viable option.

The decrease in vocalization rate of territorial males towards the end of their territory tenure could further be interpreted that individuals learn to recognize neighbours via acoustic cues. Galápagos sea lions, as other otariid species, probably show individual vocal characteristics (e.g. *Arctocephalus tropicalis,* Roux & Jouventin 1987; *Otaria flavescens*, Fernandez-Juricic et al. 1999; *Arctocephalus australis,* Phillips & Stirling 2001) and the cognitive abilities for individual recognition (e.g. *Arctocephalus tropicalis,* Charrier et al. 2001; *Zalophus californianus,* Schusterman et al. 2000). Thus, males that occupy territories over a longer period might learn to recognize neighbours by their calls and therefore cease vocalizing with tenure time. This "dear enemy effect" (Fisher 1954) could explain the decrease in vocalization rate and the decreased aggression (our personal observation) among territory neighbours. This saves time, energy and reduces the risk of injuries, which is especially important in species where males can inflict serious wounds to one another. Similarly, male of other pinniped species were found to respond less often to the vocalizations of neighbouring males than to those of stranger males, or to decrease the duration and rate of boundary displays with a neighbour over time (Gentry 1975; Boness 1979).

In polygynous species with highly skewed male reproductive success (Bartholomew 1970), sexually selected ornaments are likely to play a role in both intra- and inter-sexual context at the same time (Berglund 1996), particularly so, when access to mating opportunities is related to fighting success (Gosling 1986; Gross 1996; McElligott et al. 2001). In the Galápagos sea lion, the social behaviour of males during the reproductive season resembles a lek rather than a female defence system typical for most other otariid seals (Boness 1991). Therefore, the mating system may best be described as resource defence polygyny, since males defend territories in areas where females rest, and females prefer to mate and probably also to rest inside rather than outside territories to avoid harassment by non-territorial males (our personal observation).

In the Galápagos sea lion, female home ranges stretch across several male territories (Wolf et al. 2007b) which opens the opportunity for mate choice. Females might use information encoded in the vocalizations of territorial males to decide with whom to mate. Because males addressed vocalizations specifically to females, and males had a higher vocalization rate the more females were present in a territory, suggests that females might base their choice of mate on vocalizations. Vocalizations are common in all otariids (Miller 1991; Hanggi & Schusterman 1994; Coltman et al. 1997; Van Parijs et al. 1997, 1999; Phillips & Stirling 2001), and vocalization rates were primarily directed towards males (Schusterman & Dawson 1968; Schusterman 1977) and were also found to increase not only with the number of females, but also with the number of male–male interactions (Campagna & Leboeuf 1988; Fernandez-Juricic et al. 2001). Thus, territories with many females present might attract non-territorial males as well as other females, and males defending these territories might be involved in more agonistic encounters (Campagna & Leboeuf 1988). However, the causality in such relationships is unclear, because vocalization rates could affect mating success either directly by influencing females, or indirectly by influencing other males. Our finding that territorial males who lost their territory vocalized significantly less after loosing a territory in comparison to the time when they were in the end of their territory tenure, a period where rates were already lower than at the onset of territory tenure, emphasizes the function of vocalizations in the maintenance of territorial status.

In a species such as the Galápagos sea lion, where temporal harems are formed and where males invest time and energy in defending a territory, vocalizing with high rates might be a reliable cue of male

quality. Such repetitive display behaviour may have evolved to elevate the costs of displaying so that high quality individuals may be discriminated from lower quality individuals (Payne & Pagel 1997). Thus, in species where males vary substantially in body condition over the season females might be selected to monitor current condition and/or other characteristics of males that indicate their overall 'quality' (Kodric-Brown & Brown 1984). Indeed, territorial males indicated their presence vocally throughout the entire period of territory tenure and immediately ceased vocalizing after territory loss. Vocalizations may thus serve as an honest signal for females indicating a male's fighting ability. Individual recognition based on acoustic signals is common in mammals (Rendall et al. 1996; Reby et al. 1998; Vannoni & McElligott 2007). As individual recognition has been shown for female-pup recognition in Galápagos sea lions (Trillmich 1981), females may be additionally able to discriminate between males by means of vocal characteristics and thereby monitor a male's ability to establish and maintain a territory and use it as a cue for mate choice.

In conclusion, our findings suggest that vocal displays in Galápagos sea lions have both an intra- and inter-sexual function. The clear difference in vocalizing behaviour between territorial and non-territorial males suggest that vocalizing in Galápagos sea lions is primarily important in male–male competition. The positive correlation between the number of females and vocalization rate suggests that either females shift their activity to territories where males vocalize at high rates or that males have to vocalize more to keep other males away since these territories are the most attractive and most vigorously intruded by non-territorial males.

Acknowledgements

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