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Variations in the arrangement of South American sea lion (*Otaria flavescens*) male vocalizations during the breeding season: patterns and contexts

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Abstract

We analysed whether South American sea lions (*Otaria flavescens*) varied the syntax or arrangement of vocalizations (the order in which calls were produced) according to different social contexts. Three male calls that formed a progression of increasingly aggressive displays (growl<bark<high-pitched call) were studied in a breeding colony at Península Valdés. We found that: (a) growls and barks had higher probabilities of emission than high-pitched calls, (b) vocal bouts generally were initiated by growls, (c) the transitions most likely to occur were growl-bark and bark-growl, and (d) the number of male-male agonistic interactions (high-pitched call after growl, bark after growl) and the number of neighbour males (growl after high-pitched call) affected some transitions between call types. The baseline vocal display of males consists of a sequence of growls and barks given in succession (e.g., growl–bark–growl–bark), which can incorporate high-pitched calls during highly aggressive male-male interactions. Vocal arrangement variations could be a strategy to modulate agonistic behaviour during vocal displays and to increase the chances of being detected in noisy breeding colonies.

Key words: male interactions, *Otaria flavescens*, South American sea lions, vocal arrangement, vocalizations, syntax.

Introduction

Breeding colonies are acoustically constraining environments for pinnipeds because of the high levels of background noise (e.g., Miller & Job, 1992; Robisson *et al*., 1993; Mathevon, 1997; Jouventin *et al*., 1999). Pinnipeds may use several strategies to increase the signal-to-noise ratio of their vocalizations and increase the chances of being detected by the recipient of calls (Miller & Job, 1992). In the case of males, different types of vocalizations can be used in different contexts (male-female or male-male interactions, e.g., Fernández-Juricic *et al*., 1999; Phillips & Stirling, 2001), individual distinctiveness can increase by variations in frequency, intensity and temporal vocal parameters (e.g., Shipley *et al*., 1981; Sanvito & Galimberti, 1999), and the number of calls per unit time (vocal rates) can vary according to different social contexts (e.g., Schusterman, 1977; Turbull & Terhune, 1993; Van Parijs *et al*., 1999).

A strategy that has received relatively little consideration is the variation in the syntax or arrangement of distinct vocalizations (but see Morrice *et al*., 1994). We investigated whether South American sea lion (*Otaria flavescens*) males followed some pattern in the order in which different call types were emitted, and whether such patterns were correlated with social contexts during the reproductive season. Basically, this study, unlike previous ones on the same species (Fernández-Juricic *et al*., 1999, 2001), intends to infer syntax in breeding male vocalizations.

South American sea lion males produce four types of vocalizations during the breeding season (Fernández-Juricic *et al*., 1999): growls, barks, high-pitched calls (HPC), and exhalations. The latter call type is rarely produced and consists of an expiration of breath through the nostrils, with no specific recipient. We concentrated our study on the other three vocalizations because they are produced when males defend territories and females against neighbour and non-neighbour males. The specificity of the context of emission increases from growls to

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barks and from barks to HPCs. Generally, growls are given in broad contexts, such as close-range interactions with females and agonistic interactions with adult and sub-adult males. Barks are emitted from upright alert postures during the establishment and maintenance of territories, and are usually not directional. HPCs are highly directional calls used specifically during male-male fights. The degree of vocal individuality is low in growls, high in HPCs, with barks having intermediate values (Fernández-Juricic *et al*., 1999).

The contexts of emission of these three calls resemble a graded system used during the escalation of animal conflicts (reviews in Huntingford & Turner, 1987; Bradbury & Vehrencamp, 1998). Actually, it has been suggested that they form a progression of increasingly aggressive displays (growl<bark<HPC, Fernández-Juricic *et al*., 1999, 2001). Males tend to use the least aggressive vocalizations (growls and barks) during the maintenance of their positions, and reserve the most aggressive calls (HPC) to situations that could involve the loss of females or the territory (e.g., increasing number of non-neighbour males, Campagna & LeBoeuf, 1988).

As a result, the arrangement of calls is expected to start with growls, which would be followed by barks, and finally by HPCs, under certain social contexts.

First, we determined the probability of occurrence of the three call types during the breeding season. Second, we compared the probabilities that vocal bouts were initiated with different vocalizations. Third, we assessed transition probabilities for different combinations of vocalizations to find out arrangement patterns, but controlling for the frequency of calls. Finally, we analysed the effects of different social contexts involving males and females on the transition probabilities. We considered social factors related to the number of individuals involved in the interactions (females, neighbour, and non-neighbour males) and number of interactions per unit time (male–male and male–female interactions).

Materials and Methods

Study animal

The breeding system of South American sea lions has been characterized as female defence polygyny (Campagna & LeBoeuf, 1988).

Males employ different strategies to increase their chances of mating.

Dominant males defend a position in the area where most females group and attempt to guard them against neighbour and non-neighbour males (Campagna & LeBoeuf, 1988; Campagna *et al*., 1988, 1992; Fernández-Juricic *et al*., 2001). Males with no established positions in the breeding area gain access to females by means of fighting with and defeating males that already hold a position. Another strategy involves group raids, where groups of males that have been ousted from the breeding area invade the positions where females are with the intention of seizing them (Campagna *et al*., 1988).

Study area

We conducted this study at Punta Norte, Península Valdés, Argentina (42°04′S and 63°47′W) during January 1995. The substrate of this breeding colony is homogenous, lacking tidepools or vegetation (for a detailed description see Campagna, 1985).

Study individuals and behavioural observations

We studied 24 males holding positions in the Punta Norte colony with about 100 adult males and 500 females. Most males were marked with paint pellets, but four of them were identified by natural marks (following Campagna & LeBoeuf, 1988). We carried-out 30-min focal observations (Altmann, 1974) on 6–8 marked males per day, and daily recorded their presence and position in the colony. Observations were spaced out in such a way that each marked individual had a similar weekly sampling effort.

In a typical 30-min focal observation, calls were arranged in bouts separated by periods without vocal activity (silence). A bout was defined as a series of vocalizations emitted in sequence, such that the time interval between call types was lower within than between bouts. We registered the order in which individual calls (growl, bark, and HPC) were produced. For the sake of clarity, let us consider the following examples: sample 1=growl–growl–growl–*silence*–bark–bark–bark–*silence*–HPC–HPC–HPC; and sample 2=growl–bark–HPC–*silence*–growl–bark–HPC–*silence*–growl–bark–HPC. Both samples have the same number of bouts (3), and the three call types have the same frequency (number of times a call type occurred) in each sample (three repetitions per call type). However, they differ in arrangement. In sample 1, there is no variation in the ordering of calls within bouts; whereas in sample 2, bouts are arranged in a consistent pattern, where growls initiate, barks follow, and HPCs are given at the end. In this study, we assessed the average arrangement of call types within bouts, which represent a natural unit to circumscribe vocal behaviour in response to different contexts (see also Hailman & Hailman, 1993).

We recorded other variables during focal observations: number of male-male agonistic interactions of the target males (chases, fights, attack and retreat displays; Campagna & LeBoeuf, 1988), interactions

with females (genital investigation, fights, mounts, and copulations), number of females defended per male, and number of neighbour and non-neighbour males surrounding the focal animal. We followed previous criteria to assign females to breeding groups; females were considered associated with a male when they were at less than two female body lengths from the focal animal (Campagna & LeBoeuf, 1988). A male was considered a neighbour when he had defended an adjacent position to a study male for at least three days. Non-neighbour males were individuals that had lost their positions in the breeding area or had never established one.

Statistical analyses

To assess patterns in the arrangement of male vocalizations, we employed a transitional analysis based on Markov chains (see Hailman *et al.*, 1985). All analyses were conducted with UNCERT software (Hailman & Hailman, 1993), which has been used previously to analyse syntax patterns of avian vocalizations (e.g., Armstrong, 1995). Our approach was to determine whether the emission of a certain call type would predict the next call type; that is, we dealt with first-order transition probabilities between one vocalization and the next. Higher order transitions (e.g., between two preceding call types and the next) were not considered because longer chains of previous events generally do not increase predictability substantially (Hailman & Hailman, 1993). We did not take into account repetitions of the same call type within bouts and only focused on switches in call types to increase the statistical accuracy of the analyses (see also Armstrong, 1995). Therefore, we analysed the arrangement of call types controlling for variations in their frequency within bouts. We included in the analyses only focal observations with at least two bouts of at least two different call types and 10 calls, totalling 81 samples. This sample size included similar numbers of focal observations (3–4) per marked male.

The probability of occurrence (P_i) of a call type i was calculated as $P_i = F_i/n$; where F_i was the frequency of occurrence of that call type in a focal observation, and n the total number of vocalizations in a focal observation.

We assumed that sea lion male vocalizations had natural boundaries, as they were emitted in response to social conditions (Fernández-Juricic *et al.*, 1999). Such assumption allowed us to calculate the probability that each of the three call types initiated a vocalization bout (Hailman & Hailman, 1993). First order transitional probabilities between call types were calculated as conditional probabilities of a certain call type provided another type already occurred (Hailman & Hailman, 1993).

ANCOVA analyses were used to assess the variations in the probabilities of occurrence of call types, the probabilities of initiating a vocal bout, and first-order transition probabilities. We included day as a covariate to control for possible temporal variations in the probabilities of occurrence of different vocalizations during the breeding season. We used planned comparisons to examine contrasts between pairs of call types. We analysed the effects of social factors on the first-order transition probabilities (growl–bark, growl–HPC, bark–growl, bark–HPC, HPC–growl, HPC–bark) with stepwise multiple-regressions (forward selection procedures). The following variables were included as independent factors: number of male-male agonistic interactions in 30 min, number of male-female agonistic interactions in 30 min, number of neighbour and non-neighbour males, and number of defended females. The normality and homogeneity of variances of the data were checked by means of a Shapiro–Wilk's test and a Cochran's C test, respectively.

Results

Probability of occurrence

The probability of occurrence of the three male vocalizations varied significantly ($F_{3,239}=61.31$, $P<0.001$, $R^2=0.43$, covariate: day, $F_{1,239}=0.14$, $P=0.702$, Fig. 1). There were no differences in the occurrence probabilities between growls and barks ($F_{1,239}=1.29$, $P=0.256$), but these calls were more likely to be emitted than HPCs during the breeding season ($F_{1,239}=182.21$, $P<0.001$, Fig. 1).

Initiation of vocal bouts

We found significant differences in the type of call that usually initiated a vocal bout (probabilities of occurrence, growl $=0.65 \pm 0.37$, bark $=0.17 \pm 0.28$, HPC $=0.17 \pm 0.30$, $F_{2,239}=58.44$, $P<0.001$, $R^2=0.33$), with growls being more likely to occur than barks and HPCs ($F_{1,239}=116.87$, $P<0.001$). There was no difference in the probability that barks or HPCs would initiate vocal bouts ($F_{1,239}=0.001$, $P=0.973$). Temporal variations in the probability of initiation of vocal bouts were not significant (covariate: day, $F_{1,239}=0.02$, $P=0.891$).

Transition probabilities

Controlling for temporal variations (covariate: day, $F_{1,479}=0.36$, $P=0.546$), the first order transition probabilities differed between different call types ($F_{5,479}=42.07$, $P<0.001$, $R^2=0.31$, Fig. 2). After initiating a vocal bout with growls, the probabilities that males vocalized barks were higher than those of HPCs ($F_{1,479}=143.37$, $P<0.001$, Fig. 2). Moreover, the transition between barks and

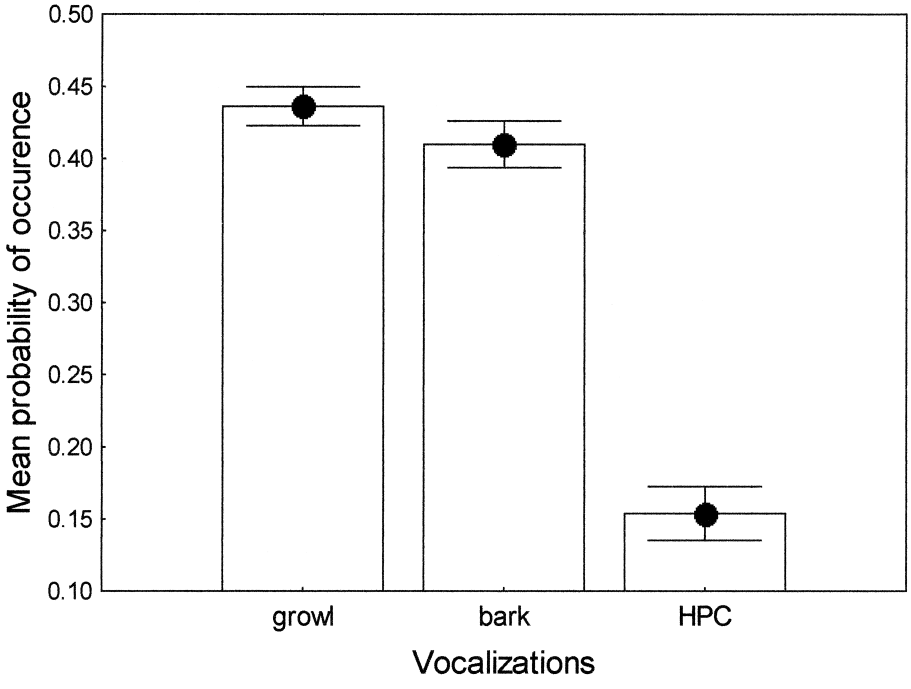

Figure 1. Mean probability of occurrence (±SE) of three South American sea lion male vocalizations (growl, bark, and HPC, high-pitched call) during the breeding season.

growls was more likely than between barks and HPCs ($F_{1,479}=53.38$, $P<0.001$, Fig. 2). Therefore, South American sea lion males usually produced alternating sequences of growls and barks (e.g., growl–bark–growl–bark . . .). After emitting a HPC, there were no significant differences in the probabilities of vocalizing growls or barks ($F_{1,479}=1.87$, $P<0.173$, Fig. 2).

Social factors

We found that the only social factors that affected the transitions between call types were the number of male-male agonistic interactions and the number of neighbour males (Table 1). As the number of agonistic interactions increased, males had higher probabilities of emitting HPCs after growls (Table 1). However, the probabilities of a transition from growl to barks decreased with the number of agonistic interactions (Table 1). The amount of variability explained by these models was rather low (5–6%). Males were more likely to emit a growl after a HPC when the number of agonistic interactions and the number of neighbour males increased (Table 1). This model accounted for 15% of the variability. The other transitions (bark–growl, bark–HPC, HPC–bark) were not affected by any of the factors considered in this study.

Discussion

This study is a new contribution to our general understanding of South American sea lion vocalizations (Fernández-Juricic *et al.*, 1999, 2001). In Fernández-Juricic *et al.* (1999), we characterized the structural and contextual variability of the different call types. In Fernández-Juricic *et al.* (2001), we assessed the variation in vocal rates in relation to different contexts, and found that male vocal rates were affected by social conditions relevant to territory and female defence. In the present study, we found that males arranged the order of emission of growls, barks, and HPCs and that some transitions between call types occurred in specific contexts. Our main results were that: (a) growls and barks had greater probabilities of occurrence than HPCs, (b) growls usually initiated vocal bouts, (c) growls and barks were generally alternated before emitting HPCs, and (d) transitions between growls and barks, growls and HPCs, and HPCs and growls were influenced by the number of male-male aggressive interactions and the number of neighbour males. Previous quantitative studies identified similar syntactical arrangements in the underwater vocalizations of Weddell seal, *Leptonychotes weddellii* males, (Morrice *et al.*, 1994) and in the airborne calls of harp seals, *Phoca groenlandica*, (Miller &

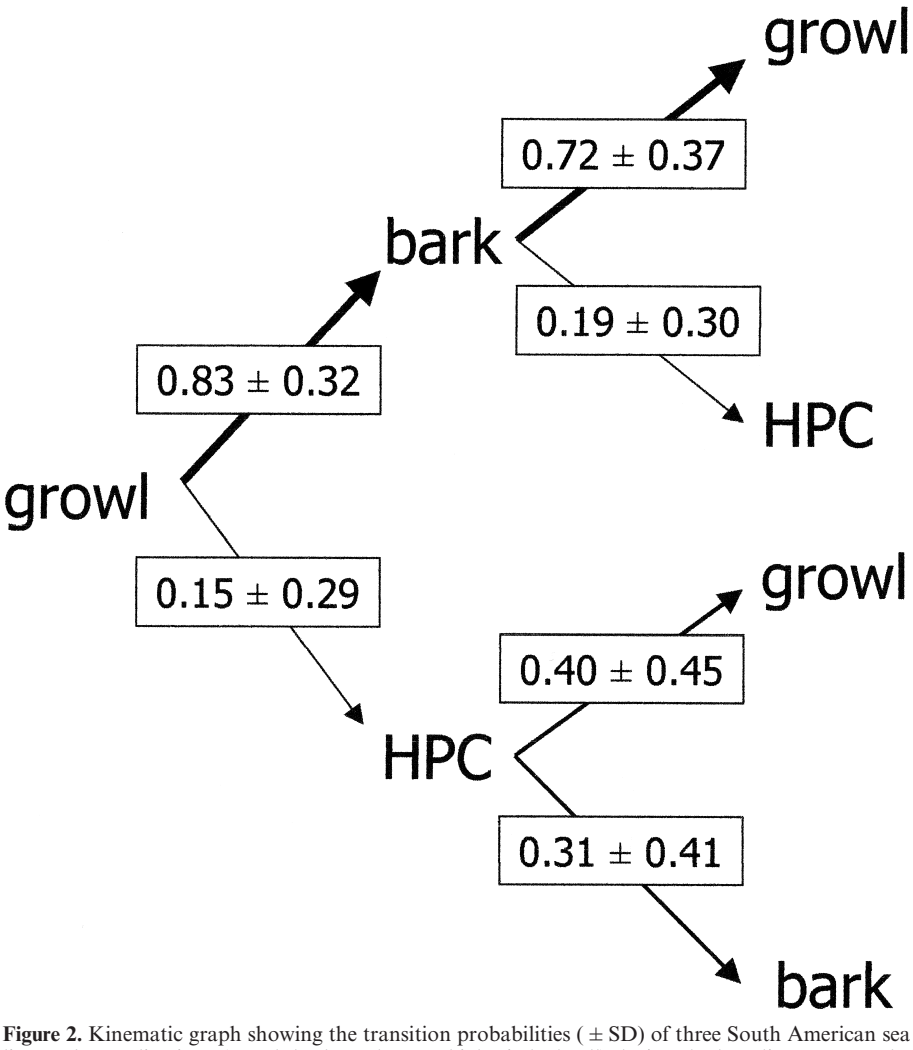

Figure 2. Kinematic graph showing the transition probabilities (± SD) of three South American sea lion male vocalizations (growl, bark, and HPC, high-pitched call) during the breeding season. The arrows represent the first-order transitions from one call to the next and their width is proportional to the probability of transition.

Murray, 1995). However, to our knowledge, this is the first study to report some sort of syntactical vocal organization in otariids.

Growls and barks seem to be fundamental calls during vocal displays, having three times as much probabilities of occurring as HPCs. The prevalence of these calls could have to do with their emission contexts: male–female and male–male interactions (growls) and establishment of territories (barks). Their emission, in combination with physical displays such as approaches to females and boundary displays (Miller, 1991), could allow males to maintain the territorial status against neighbour males.

Growls are usually the first call type males give when vocalizing a sequence of calls. After the emission of a growl, males are more likely to vocalize a bark than a HPC. Likewise, barks are generally followed by growls instead of HPCs. Consequently, the baseline vocal display of South American sea lions during the breeding season consists of a sequence of growls and barks given in succession (e.g., growl–bark–growl–bark). From this basic pattern of switching between call types, males can modify their vocal behaviour by incorporating HPCs under specific contexts. Growls and barks are less hostile than HPCs (Fernández-Juricic *et al.*, 1999), suggesting that males could

Table 1. Social factors affecting transition probabilities of different combinations of South American sea lion male calls (growl, bark, and HPC, high-pitched call).

Transition	F	d.f.	P	R^2	Number of AI's	Number of neighbour males
Growl–bark	4.19	1, 79	0.043	0.05	− 0.03	
Grow–HPC	5.25	1, 79	0.025	0.06	0.04	
Bark–growl	*NMF*					
Bark–HPC	*NMF*					
HPC–growl	6.95	2, 78	0.002	0.15	0.06	0.12
HPC–bark	*NMF*					

Results from multiple regressions showing the F statistic for each transition, its degrees of freedom (d.f.), its associated probability, the amount of variability explained (R^2), and the b-coefficients of the significant factors.
AI's, number of male–male agonistic interactions; NMF, no model fitted (the contribution of each factors was less than 1% and as a result no factor was included in the model).

modulate their agonistic behaviour during vocal displays and reduce excessive energy expenditure (Gentry, 1975; Boness, 1979 cited in Miller, 1991). For instance, a previous study found that South American sea lion males used HPCs and chases differently when defending their territories against different types of competing males (Fernández-Juricic *et al*., 2001). Established males tend to spend more time in aggressive displays (vocalizing more HPCs and chasing more frequently) when defending their positions against non-neighbour than neighbour males. Non-neighbour males are riskier because they can disrupt male harems and seize females, with consequences for male tenure and mating success (Campagna *et al*., 1988).

The transitions between some calls were associated with certain contexts relevant to male mating success. The chances of vocalizing a HPC, instead of a bark, after a growl increased with the rate of male-male agonistic interactions. Disputes among males trigger a series of physical interactions (attack and retreat displays, fights, Campagna & LeBoeuf, 1988) usually accompanied by highly directional and individually distinctive HPCs. The transition between growl and bark is more likely when the rate of male–male agonistic interactions decreases, suggesting that when males are not engaged in agonistic encounters, they maintain their positions, and monitor females and competing males through a sequence of growl–bark vocal displays. The contexts of these transitions support the prediction that the three vocalizations form a progression of increasingly aggressive displays (growl<bark<HPC) and that the transition from growl–bark to HPC occurs in highly agonistic situations. Finally, the transition between HPC and growl is more likely when the rate of agonistic interactions and the number of neighbour males increase. One possible explanation is that after aggressive encounters involving HPCs, males turn to females vocalizing growls. In this way, males might potentially assess changes in the number and positioning of females before resuming agonistic displays.

Although some transitions were associated with particular contexts, the amount of variability explained was rather low, and three of six transitions could not be accounted for by any of the factors studied. This lack of association could result from the fact that the transitions convey very general information or that the level of analysis was not appropriate. Observations were gathered in 30 min and associated to relatively stable contexts over that period: number of females defended, number of neighbour males, etc. However, our sampling period was not sensitive to highly variable contexts; for instance, if males modified the order of vocalizations in response to subtle social conditions (e.g., the receptivity of females, female–female interactions). Future studies considering in more detail contextual information within shorter time periods could shed more light into the social contexts associated to call transitions.

The study of how animals solve the problems of high levels of background noise in breeding colonies has been focused upon long-distance calls, such as the ones used by parents and offspring for recognition (Balcombe & McCracken, 1992; Aubin & Jouventin, 1998; Jouventin *et al*., 1999; Phillips & Stirling, 2000). However, otariid male vocalizations are generally used in short-range signalling towards females and competing males (Miller, 1991). Because environmental masking is lower at short ranges, male vocalizations can be more variable to convey different types of information (Tyack & Miller, 2002). So far, we have found that South American sea lion males make use of different strategies to improve social communication in

breeding colonies. First, they employ different call types associated to territory/female maintenance and male-male agonistic disputes (Fernández-Juricic *et al*., 1999). Second, the acoustic properties of some vocalizations (barks and HPCs) make them suitable for individual recognition (Fernández-Juricic *et al*., 1999), which could enhance the identification of competitors that may risk territorial tenure (Fernández-Juricic *et al*., 2001). Third, males increase the temporal redundancy of vocalizations (vocal rates) in contexts that could convey a relative advantage in breeding performance, such as when the number of defended females or non-neighbour males increases (Fernández-Juricic *et al*., 2001). Finally, males also arrange the order in which different call types are emitted following certain syntactical patterns, and this order could be related to the degree of aggressiveness of the social context (this study). All these strategies could increase male mating opportunities, by improving the ability to defend territories and females, and reducing the chances that females stray away because of disturbances (e.g., group raids).

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