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VOCAL RATES AND SOCIAL CONTEXT IN MALE SOUTH AMERICAN SEA LIONS

During the breeding season reproductively active South American sea lion males (*Otaria flavescens*) compete aggressively against other males to defend a position along the shoreline, where most females group (Campagna and Le Boeuf 1988*a*). Vocalizations are a conspicuous component of male behavior: high pitched calls (HPC) are highly directional sounds used at the beginning of a fight, barks are given during the establishment and maintenance of territories and in relation to female defense, and growls occur mainly during interactions with females (Fernández-Juricic *et al.* 1999).

Despite the importance of vocal displays, it is not known if males adapt their communication signals to different social contexts. Vocal rates (number of calls per individual per unit time) are considered a good indicator of vocal behavior, since temporal and spatial variations in vocal rates may convey different messages in pinnipeds (Schusterman 1977, Shipley and Strecker 1986, Miller and Job 1992, Van Parijs *et al.* 1999). In this study we assessed the change in vocal rates in relation to social variables of crucial importance for male mating success within a breeding colony (Campagna and Le Boeuf 1988a): (1) tide level; (2) location of the target animal in the breeding colony; (3) presence of females in the vicinity, number of them, and interactions with them; and (4) presence of and interaction between competing males (neighbor and non-neighbor) in positions adjacent to the target animal (Table 1). Tidal level has an indirect social effect because it modifies the area utilized by breeding sea lions and, as a result, individual distances (Campagna and Le Boeuf 1988*a*).

Table 1. Statistical analysis conducted to assess relationships between male South American sea lion vocal rate and social context. Marked with (*) are significant results.

Context studied	Type and number of analyses	Dependent factor/sec	Independent factors and levels
1. Variation in vocal rates in relation to tide and position in the colony	ANCOVA (3)	HPC rate Bark rate Growl rate	Tide (high, mid, low) (*) Location in the colony (CBA, PBA)
2. Variation in vocal rates in relation to (a) type of context and (b) degree of stimulus within that context	(a) ANCOVA (3)	HPC rate	Presence/absence of females Presence/absence of non-neighbor males (*)
		Bark rate	Presence/absence of females defended by a male (*) Occurrence of agonistic interactions between males (*)
		Growl rate	Presence/absence of females defended by a male Occurrence of agonistic interactions between male and females (*)
	(b) Correlation (7)	HPC rate	Number of females defended by a male (*) Number of non-neighbor males (*) Number of neighbor males
		Bark rate	Number of females defended by a male (*) Rate of agonistic interactions between males (*)
		Growl rate	Number of females defended by a male (*) Rate of interactions between male and females (*)
3. Simultaneous variation in vocal and agonistic interaction rates during the approach of neighbor and non-neighbor males	(a) MANOVA (1)	HPC, bark, and growl rates	Occurrence of neighbor and non-neighbor males (*)
	(b) MANOVA (1)	Chase, attack and retreat display, and fight rates	Occurrence of neighbor and non-neighbor males (*)

Study animals were 35 marked males in a group of about 600 adult breeding sea lions (~100 males) at Punta Norte, Península Valdés, Argentina (42°04'S, 63°47'W), in January 1996. Rookery substrate is a uniform pebble beach, lacking tidepools or vegetation (Campagna 1985). The social system is female defense polygyny, in which males defend a position where most females group and attempt to remain close to them (Campagna and Le Boeuf 1998*a*, *b*; Campagna *et al.* 1988). A male that does not hold an established location along the shoreline takes over a position and gains access to females in the breeding colony by fighting with and defeating males that already hold a position. Groups of males that have been ousted from the colony also seize females from established harems during group raids (Campagna *et al.* 1988).

Males were identified by natural marks or were marked with paint pellets (Campagna and Le Boeuf 1988*a*). Their presence and position in the colony were recorded daily, and 30-min focal animal samples (FAS; Altmann 1974) were conducted on six to eight marked individuals per day. Male positions were categorized as either in the area of highest female density (central breeding area, CBA, as described in Campagna and Le Boeuf 1988*a*) or in the periphery of the colony (peripheral breeding area, PBA). During FAS, we recorded and classified all vocalizations by the target males. Male calls are acoustically different from each other and were easily distinguished by the observer (Fernández-Juricic *et al.* 1999). For most statistical analyses, the number of vocalizations of each type in 30 min was defined as the vocal rate, and was used as the dependent variable (Table 1, objectives 1–2). Other variables recorded during FAS were: number of agonistic interactions of the target males (chases, fights, attack and retreat displays; Campagna and Le Boeuf 1988*a*), interactions with females (genital investigation, fights, mounts, and copulations), number of females defended per male, and number of neighbor and non-neighbor males surrounding the focal animal. Females were considered associated with a male when they were less than two female body lengths from the focal animal (Campagna and Le Boeuf 1988*a*). A male was considered a neighbor when he had defended an adjacent position to a study male for at least three days; non-neighbor males were individuals that had lost their positions in the breeding area or had never established a position.

To examine the effect of the presence of neighbor and non-neighbor males on vocal rates, we used an alternative unit of time to define vocal rates: the number of vocalizations of each type displayed by the marked individual during the first 10 sec of an agonistic interaction triggered by the approach of a competitor (Table 1, objective 3a). In the same period of time we also recorded the number of three types of agonistic interactions (fights, attack and retreat displays, and chases) to assess the male physical reactions that supported vocal behavior (Table 1, objective 3b). The threshold distance to define an approach between the target animal and a non-neighbor male was three male body lengths. The definition of the rate and the threshold distance was based on the duration of agonistic interactions and on the average distance of males in the colony (Campagna and Le Boeuf 1988*a*). Male fights last about 10–15 sec, and HPC, being the most common vocalization associated with this context, is always displayed at the start of an agonistic interaction. Thus, recording data during the first 10 sec covered all vocal activity associated with a male-male interaction.

Statistical analyses were performed on a similar number of FAS per individual obtained during different days to produce balance designs (Underwood 1997). The normality and homogeneity of variances of the data were checked by means of a Shapiro-Wilk test and a Cochran C test, respectively.

The effect of tide and position of focal animals in the colony on vocal rates was analyzed with an ANCOVA test (Table 1, objective 1). Tide level was used as an indirect measure of colony density (Campagna and Le Boeuf 1988a). Independent factors were three tide levels (high, mid, low) and two location categories (CBA and PBA). Tide levels were grouped into four-hour intervals of the daily tidal cycle. Day was included as a covariate as vocal activity varied throughout the breeding season (Fernández-Juricic *et al.* 1999). Each combination of treatments included 15 FAS of different males recorded throughout the breeding season. We assessed independent effects of tide and position in the colony in a single analysis to detect possible interaction effects (*e.g.*, vocal rates increase only within the CBA and during high tides).

The relationship between focal male vocal rates and variables related to other competing males and females was studied with ANCOVA's and Pearson product-moment correlations, depending on whether the context was considered a binary variable (defined as a type of context, *e.g.*, presence/absence of females) or a continuous variable (the degree of stimulus within that context, *e.g.*, number of females present), respectively (Table 1, objective 2). Variation in vocal rates in relation to context and degree of representation of each context can be considered measures of the degree of contextual specificity of a certain call (Macedonia and Evans 1993, Blumstein 1995, Blumstein *et al.* 1997). The specific contexts for each vocalization were selected according to prior information on male behavior during the breeding season (Campagna and LeBoeuf 1988*a,* Fernández-Juricic *et al.* 1999). ANCOVA tests were conducted for each type of vocalization (HPC, bark, growl), using day as the covariate. Each ANCOVA included two independent factors (Table 1, objective 2a). The presence/absence of females defended by the target male was an independent factor in all three types of vocalizations studied. Additional independent factors were: presence/absence of non-neighbor males (for HPC), occurrence of agonistic male interactions (for barks), and occurrence of interactions between male and females (for growls). Presence/absence of neighbor males was not included as an independent factor because most FAS involved males with neighbors. Using correlation analyses, we assessed how vocal rates were associated with the degree of stimulus of the same factors analyzed in the ANCOVA tests (Table 1, objective 2b). Correlations included 128 focal observations. Dependent variables (vocal rates) were $\log_{10}(x + 1)$ transformed to meet normality requirements.

A MANOVA test was used to analyze the simultaneous variation in vocal rates of three male calls (HPC, bark, and growl rates) towards neighbor and non-neighbor male approaches (Table 1, objective 3a). We also conducted a

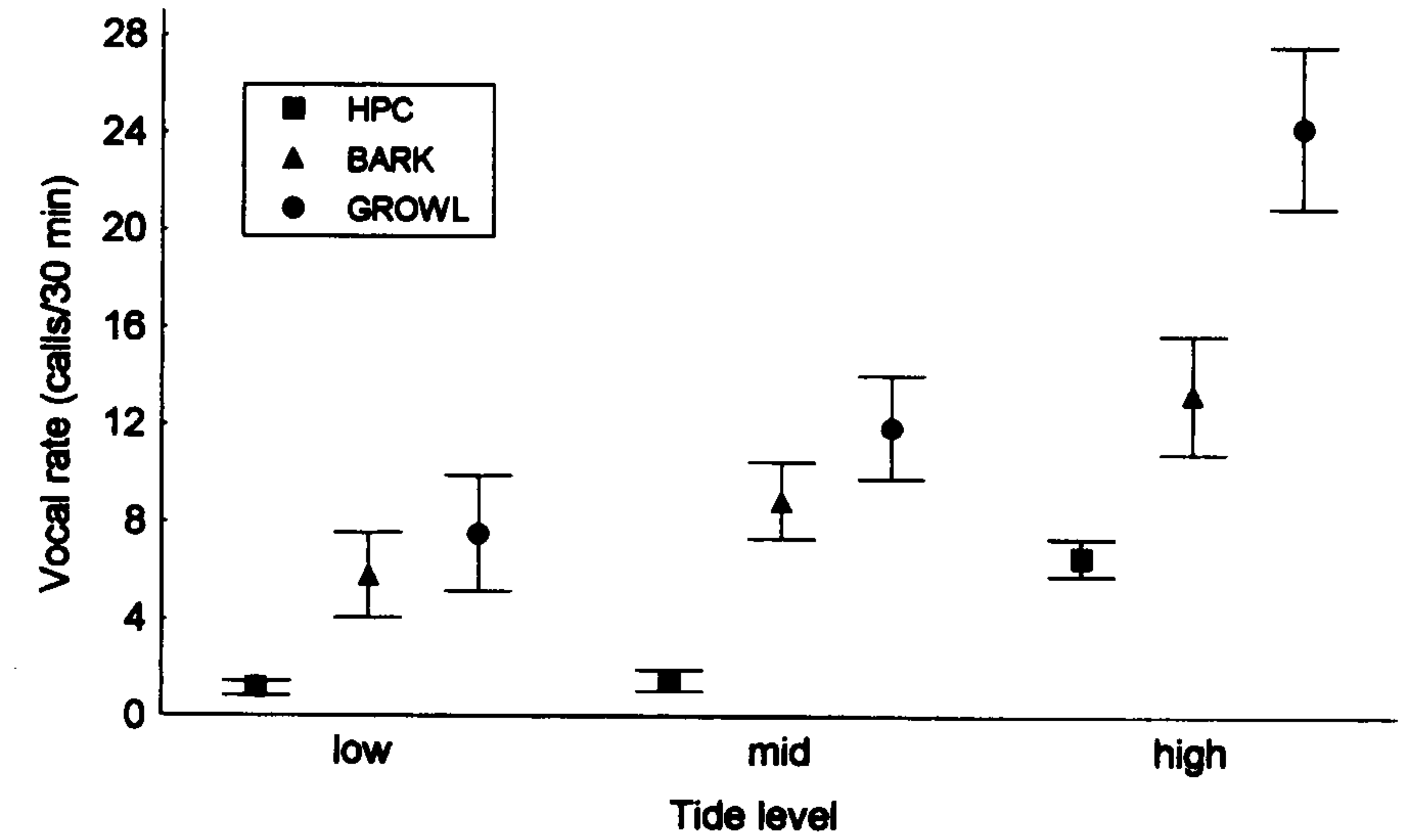

Figure 1. Male South American sea lion vocal rates for three call types (HPC, bark, and growl) as function of three tide conditions. Observations from Punta Norte colony, Península Valdés, Argentina in 1996. Error bars represent SE.

MANOVA test to determine the simultaneous variation of agonistic interactions (chase, attack and retreat display, and fight rates) supporting vocal displays (Table 1, objective 3b). For these analyses, we randomly chose 100 out of 307 recorded agonistic interactions (no more than 1 observation per FAS per animal).

The rate of all three vocalization types increased from low to high tide (Fig. 1), and the increase was particularly marked for high tides (HPC, $F_{2,83}$ = 34.93, $P < 0.001$; Bark, $F_{2,83}$ = 5.18, $P < 0.01$; Growl, $F_{2,83}$ = 16.75, $P < 0.001$). Vocal rates were not, however, significantly different for subjects located in the CBA *vs.* those in the PBA (HPC, $F_{2,83} = 0.13$, $P = 0.87$; Bark, $F_{2,83} = 0.01$, $P = 0.98$; Growl, $F_{2,83} = 1.54$, $P = 0.22$). There was no significant interaction between tide and position within the colony (HPC, $F_{2,83} = 0.5$, Bark, $F_{2,83} = 0.66$, Growl, $F_{2,83} = 0.23$; $P > 0.05$).

HPC rate increased when non-neighbor males were present, and did not vary with presence or absence of females in close vicinity of a target male (Table 2). Bark rate increased when females were within the area of control of a male, and during agonistic interactions between males (Table 2). Interactions with females increased growl rate, but the presence of females defended by a male did not apparently have a significant influence on growl rate (Table 2). No interaction effects were detected between the factors considered in each analysis (Table 2).

HPC rate was significantly associated with the number of females defended by a focal male ($r = 0.54$, $P < 0.05$) and non-neighbor males in the vicinity ($r = 0.53$, $P < 0.01$). Similar associations were found for the other two vocalizations: bark rate and number of females ($r = 0.33$, $P < 0.001$); bark rate and rate of male agonistic interactions ($r = 0.31$, $P < 0.001$); growl rate and number of females ($r = 0.25$, $P < 0.01$); growl rate and male-female interaction rate ($r = 0.42$, $P < 0.001$). There was no relationship between the number of neighbor males and HPC rate ($r = 0.07$, $P = 0.83$).

Table 2. Relationships between type of social context and male South American sea lion vocal rates (HPC, bark, and growl). The table displays results from three ANCOVA tests (one per vocalization), with mean of each level of factor in parenthesis (vocal rates = number of calls in 30 min). Each test has same degrees of freedom (2, 123).

	F	*P*
HPC		
Presence/absence of females: presence (3.14), absence (2.7).	0.64	0.43
Presence/absence of non-territorial males: presence (5.21), absence (1.56).	14.92	<0.001
Interaction	1.64	0.2
Bark		
Presence/absence of females: presence (9.32), absence (3.5).	10.91	<0.001
Occurrence of agonistic interactions between males: yes (9.82), no (2.96).	14.04	<0.001
Interaction	0.87	0.42
Growl		
Presence/absence of females: presence (13.72), absence (12.76).	1.67	0.19
Occurrence of interactions between males and females: yes (19.04), no (7.45).	6.85	<0.01
Interaction	0.18	0.84

The HPC rate of males defending females increased when non-neighbor males approached, whereas the bark rate decreased in the same circumstances (Fig. 2a, Table 3). Growl rate for males defending females did not differ significantly in relation to the approach of non-neighbor *vs.* neighbor males (Fig. 2a, Table 3). Regarding agonistic interactions, males more often chased non-neighbors approaching them than neighbors (Fig. 2b, Table 3). Non-neighbors were less inclined to engage in attack and retreat displays, and would flee after agonistic displays by established males.

In summary, this study showed that vocal rates: (1) changed in relation to tides, (2) were influenced by females and competing males, and (3) changed according to the type of competing males approaching (neighbor or non-neighbor males). High tides affect colony density by reducing high quality space at the beach. Space constraints arise as animals prefer to locate near the watermark, close to the spray zone, to reduce heat stress (Campagna and LeBoeuf 1988*b*). A temporary increase in density facilitates social interactions among males and females, increasing vocal rates (Campagna and LeBoeuf 1988*a*, Campagna *et al.* 1988). Similar results were found for male South American fur seal *Arctocephalus australis* (Phillips 1998), and for male harbor seals *Phoca vitulina* (Van Parijs *et al.* 1999).

Defending a position where most females group offers a better expectation of mating than being in the periphery of the colony (Campagna *et al.* 1988, 1992). However, differential expectation of mating does not apparently reduce

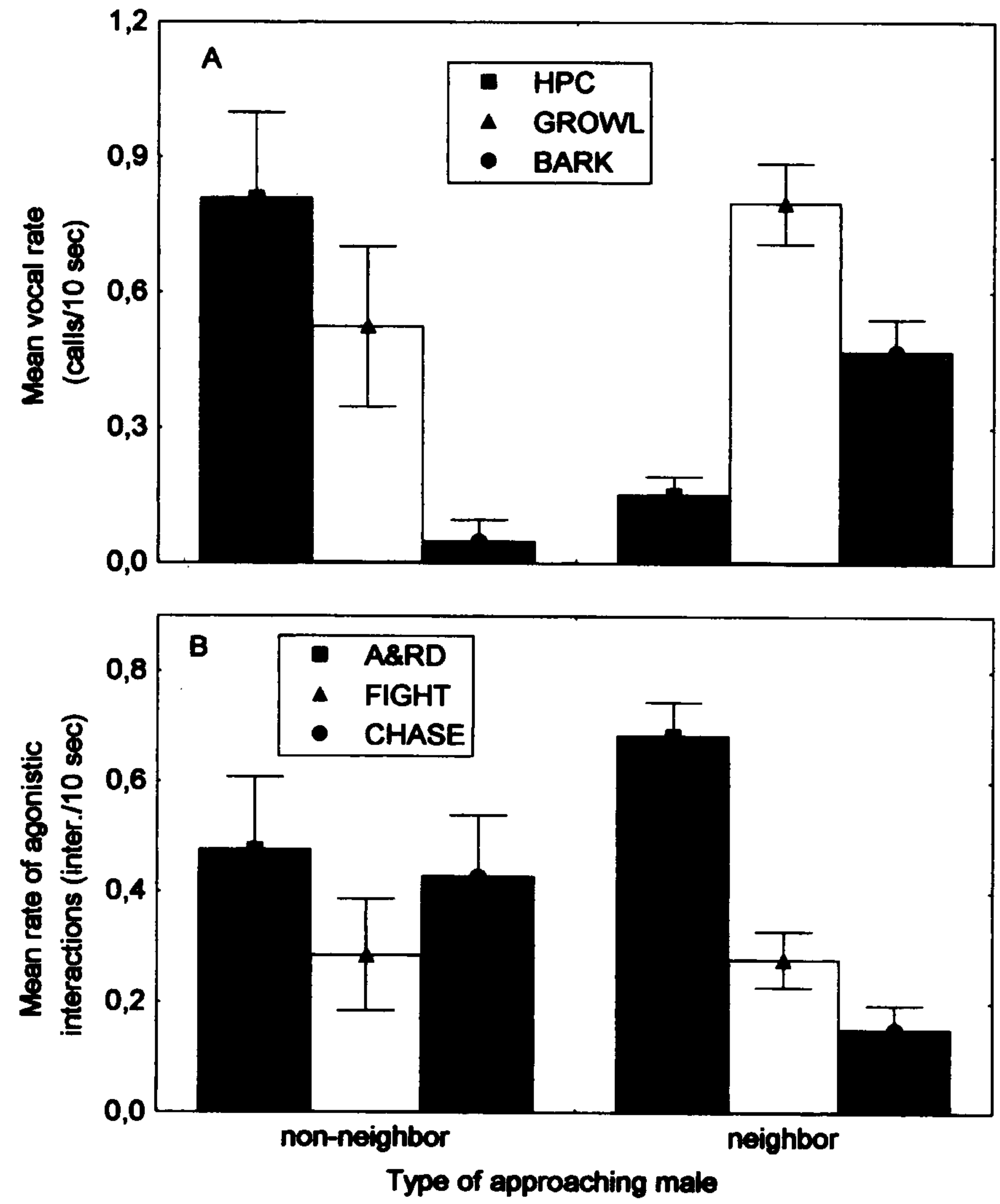

Figure 2. Vocal (A) and behavioral (B) responses during male agonistic interactions with neighbor and non-neighbor males. Shown are rates of three male vocalizations (HPC, bark, growl) and of three agonistic interactions (chase, Attack and Retreat Display, fight) by territory holders during first 10 sec of interaction. See also Table 3. Error bars represent SE.

the intensity of position defense, as is reflected by vocal rates. Male positions are highly vulnerable in a South American sea lion colony (Campagna *et al.* 1988), thus a male in the periphery may gain access to the CBA, making a second-rate place a step towards a better condition.

Vocal rates increase with the type of context and the degree of stimulus within each context. Thus, there is a high degree of association between male vocal behavior and the factors that influence male mating success, such as availability of females and interaction with competing males. HPC rates increase as males monopolize a larger number of females. Areas of high female densities attract males, and an individual defending a position among many females is exposed to more agonistic encounters (Campagna *et al.* 1988*a*). Similarly, bark rates increase with the number of females defended and the number of agonistic interactions among males. This relationship emphasizes the role of barks in the maintenance of the territorial status against competing males (Miller 1991). Growls apparently convey information directed toward

Table 3. Vocal and agonistic responses of established male South American sea lions during approach of neighbor and non-neighbor males. Results of a MANOVA test, using vocal rates (HPC, bark, growl) and agonistic interaction rates (chase, attack and retreat display, fight) occurring within first 10 sec of interaction. See also Figure 2a, b.

	df	*F*	*P*
Vocal response	Rao *R* (3, 96)	= 10.87	<0.001
HPC	1, 98	27.67	<0.001
BARK	1, 98	8.82	<0.01
GROWL	1, 98	1.96	0.16
Agonistic response	Rao *R* (3, 96)	= 2.71	<0.05
CHASE	1, 98	7.19	<0.01
ATTACK AND RETREAT DISPLAY	1, 98	2.31	0.13
FIGHT	1, 98	0.004	0.95

females (Fernández-Juricic *et al.* 1999), as evidenced by an increase in growl rate with the number of females within the harem. Males growl to females mainly during mountings and copulations and when females interact aggressively with one another. It is possible that this vocalization may serve to reduce disturbance within harems (Miller 1974, Harcourt 1991, Phillips 1998). Female movements attract the attention of ousted males (Campagna *et al.* 1988). Reducing female movements may decrease the number of male agonistic encounters.

The lack of association between HPC rates and the number of neighbor males, and the selective vocal and agonistic responses towards non-neighbors are compatible with the expected behavioral consequences of the "dear enemy effect" (Fisher 1954). Efforts invested in female defense could be reduced by recognizing neighbors' boundaries and focusing upon non-neighbor competitors (Getty 1987, Temeles 1994). Non-neighbor males disrupt male harems and seize females either individually or in groups, affecting male tenure, mating success, and the distribution of females within the CBA (Campagna *et al.* 1988). However, conclusive evidence of a "dear enemy effect" would require playback tests such as those conducted on subantarctic fur seal, *A. tropicalis* (Roux and Jouventin, 1987). Males of this species responded less often to the calls of neighbor males than to those of strange males, supporting the habituation response. Similarly, in Steller's sea lions, *Eumetropias jubatus,* and gray seals, *Halichoerus grypus,* neighbor males decrease the duration and rate of occurrence of boundary displays as their familiarity with one another increases during the breeding season (Gentry 1975, Boness 1979).

Otariid breeding colonies are noisy places where airborne communication may be interfered with or masked (Riedman 1990, Miller and Job 1992). Several acoustic features have been described that may enhance signal detection against background noise. These include an increase in loudness (Miller and Job 1992), time-frequency variation of vocal traits (Schusterman 1977, Trillmich 1981, Hanggi 1992, Insley 1992, Schusterman *et al.* 1992), and redundant repetition of vocalizations (Schusterman 1977). Variation of vocal rates of males, as described in this study, may improve the effectiveness of acoustic signals in social relations (Schusterman 1977, Shipley and Strecker 1986, Miller and Job 1992) that play an important role in male mating success.

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