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Barking, Dominance, and Territoriality in Male Sea Lions

Abstract. *Experiments in which male sea lions* (Zalophus californianus) *were removed and reintroduced into a social group demonstrate that barking by larger males restricts movement and barking by other smaller males. Barking and aggression were primarily directed toward animals of most nearly equal size. Two 6-year-olds seeking to establish and maintain territorial status used aggressive tactics similar to those observed in breeding males in the field.*

Aggressive behavior in vertebrate social groups is controlled by social structure, territoriality, and vocal signaling (*1*). Field observations made during the breeding season of several species of pinnipeds suggest that breeding males signal and defend territorial possessions primarily by means of a highly stereotyped series of vocalizations (*2*). Vocal signaling is thought to reduce actual fighting during the establishment and maintenance of territories.

Underwater sounds (barks, clicks, bangs, buzzes, and growls) produced by the sea lion (*Zalophus californianus*) are apparently a function of its social and investigatory responsiveness (*3*). Barking by individual males appears specifically related to the group social structure and territoriality (*4*). Manipulation of the social structure should therefore change the amount of barking by individual male sea lions in the group. On this hypothesis, a series of experiments was conducted in which group composition was modified by removing and reintroducing individual animals and recording the frequency of barking and attack by 10-second intervals on a time-ruled check sheet.

All experiments were conducted in two outdoor rectangular compounds enclosed and separated from each other by a cyclone wire fence. Compound 1 (where the animals were usually housed) contained a pool and a long concrete slide; there was a graded rocky slope running along one side of both compounds. The fence separating the two compounds had three gates. Six male *Zalophus,* living together for at least 3 months, and a seventh animal (G), introduced during the last experimental sessions, were observed from above the rocky slope (Table 1). All but one (S) of the sea lions were fed before the sessions which usually took place between 1300 and 1900 hours. On all but one occasion, sea lions were removed from compound 1, placed in compound 2, and reintroduced one at a time. Observations and recordings usually began approximately 30 seconds after an animal's removal or return. Living with the sea lions were three other species of pinnipeds: two young elephant seals (*Mirounga angustirostris*; one yearling and one 2-year-old), two adult harbor seals (*Phoca vitulina*), and two yearling Stellar sea lions (*Eumetopias jubata*).

During the first experiment, the most mature animal (M), which was removed and reintroduced, barked the most; when M was removed to compound 2, the next largest sea lion (W) barked the most. Further experiments substantiated this trend (Fig. 1). In another series of experiments, to determine the frequency of barking by individuals in both compounds, we removed sea lions M, W, and P (in that sequence) and then returned each one in reverse order (Fig. 2). In general, these results are similar to those previously obtained. The wire fence served as a signal to younger animals that barking and other aggressive displays by M could not be followed up by physical attack. The amount of individual barking always depended on the nature of the group's dominance structure.

The relation between barking and dominance is shown by the analysis of attack-withdrawal scores (Table 1), which represents the total number of 10-second intervals in which one sea lion was in the process of attacking another during the entire series of experiments. The most mature sea lion attacked, on a discriminative basis, usually the next largest sea lion in the group. Less mature animals never attacked larger individuals; the more mature sea lions rarely attacked the two smallest individuals.

Removal or reintroduction of a dominant or alpha animal dramatically affected the behavior of the (beta) individual next in line in the social hierarchy. A dominant sea lion usually maintained a position in the pool, either swimming around the perimeter or holding a quadrupedal stance at the shallow edge while producing a rather continuous series of barks. The beta animal was usually positioned at or near the top of the rocky slope. This spatial relationship between alpha and beta animals was stereotyped: when the beta animal moved from the top of the rocky slope he was usually attacked and pursued by the alpha animal until the beta individual resumed its former position. Usually, when it returned to compound 1, a dominant individual immediately set up a barking pattern and locomoted directly to the pool, while the beta animal immediately fell silent and

Table 1. Attack-withdrawal scores and characteristics of the male sea lions (*Zalophus californianus*) in the social group.

Age (yr)	Wt (kg)	Attacking animal	Withdrawing animal						
			G	M	W	P	K	S	T
5–6	136	G	–	8	1	0	0	0	0
5–6	153	M	0	–	42	1	0	0	0
3	68	W	0	0	–	104	54	6	4
3	58	P	0	0	0	–	6	3	1
2	50	K	0	0	0	0	–	10	1
2	40	S	0	0	0	0	0	–	2
2	38	T	0	0	0	0	0	2	–

scrambled out of the pool (*5*). However, in two instances [1858 hours on 22 June 1967 (Fig. 1) and 1704 hours on 23 June 1967 (Fig. 2)], instead of moving directly to the pool upon his return, M hauled out and rested in a shady corner of compound 1. A dominant individual usually attacked the beta animal by pursuing it. The beta retreated up the rocky slope, occasionally turning to face its attacker and displaying an openmouthed counterthreat while still withdrawing, but never barking. The attacking animal emitted a constant series of barks, and occasionally gave a rapid head lunge and a hard bite. The intensity of these agonistic encounters was directly related to the maturity or size of the animals involved.

In terms of vocal and agonistic behavior patterns, the youngest sea lions were least affected by modifications in the social hierarchy (Figs. 1 and 2; Table 1). The social activities of these animals were play-fighting and sexual play. When social play patterns increased in intensity, and these young animals began barking, a dominant animal would bark at them, rapidly moving between them. The smaller animals stopped barking and nuzzled the head and neck region of the dominant animal, and then they dispersed for a short time. When dominant animals were removed, play patterns of smaller ones increased in intensity, with correspondingly more barking. The decrease in K's barking during the last four experiments (see Fig. 2) was due to this sea lion's reacquiring a rocking and head-banging stereotypy not unlike those described for captive primate species (*6*).

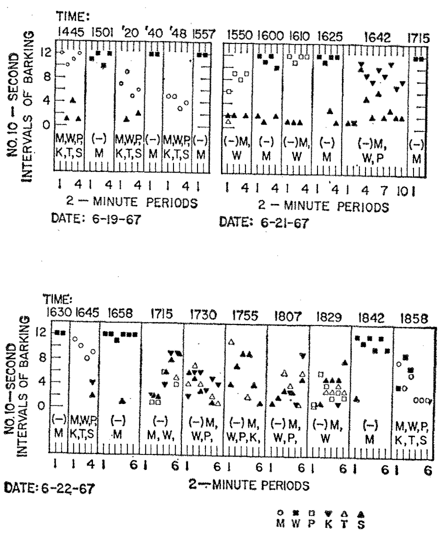

Fig. 1. Barking by male *Zalophus californianus* as a function of group composition in compound 1. Letters after minus signs refer to sea lions removed from compound 1 and placed in compound 2. Times refer to start of each experimental period.

On 18 June 1967, G was returned to compound 1 after an absence of about 6 months (Table 1). Just before his release into the compound, G remained silent while M barked continuously. Upon release of G, the combatants rushed forward and stood chest to chest; both emitted rapid series of barks. The violent fight which ensued lasted about 8 minutes and consisted primarily of chest and shoulder pushing, interspersed by whiplike head lunges, and hard biting. The struggle terminated when G pushed M into the pool. After grappling in the pool, M ceased barking, leaped from the pool, and fled up the rocky slope. A few minutes later, G was removed from the compound. Examination of M revealed several bloody cuts and wounds around the neck and flanks.

Except for a reduction in the duration and severity of the battle between G and M, reintroduction of G on 29 June 1967 led essentially to the same outcome as before. However, the center gate was left open and, when M fled silently through the gate entrance, G terminated the chase at the gate threshold. Some minutes later, M and G rushed toward the open gate and displayed a "stereotyped boundary ceremony" (*7*) in which little contact was made as the two combatants challenged each other with openmouthed threats while staring sideways or obliquely at one another, barking rapidly, wagging and shaking the head, arching the neck, and falling prostrate. After nearly 2 hours of almost continuous barking by M and G, data were collected on barking and attack behavior as before.

The results presented in the bottom pair of bar graphs of Fig. 2 agree essentially with the results from the previous six experimental sessions. However, three aspects deserve special mention: (i) M and G barked and displayed at one another continuously while the gate was open. (ii) No fighting broke out when M was returned to compound 1. (iii) G's forced presence in compound 2 eliminated M's original territorial defense. Reopening of the center gate resulted in renewed territorial displays by G and M. Although both animals were active in territorial maintenance during most of July, on several occasions M moved silently through the entrance from compound 2 and into the pool while G was resting or sleeping. Moreover, in several instances, G did displace M in compound 2.

Despite the great differences between captive and natural settings, there is a striking similarity between our observations of aggressive displays and the field observations (*7*) on the establishment and maintenance of territorial status of breeding males. Some examples of these similarities include: (i)

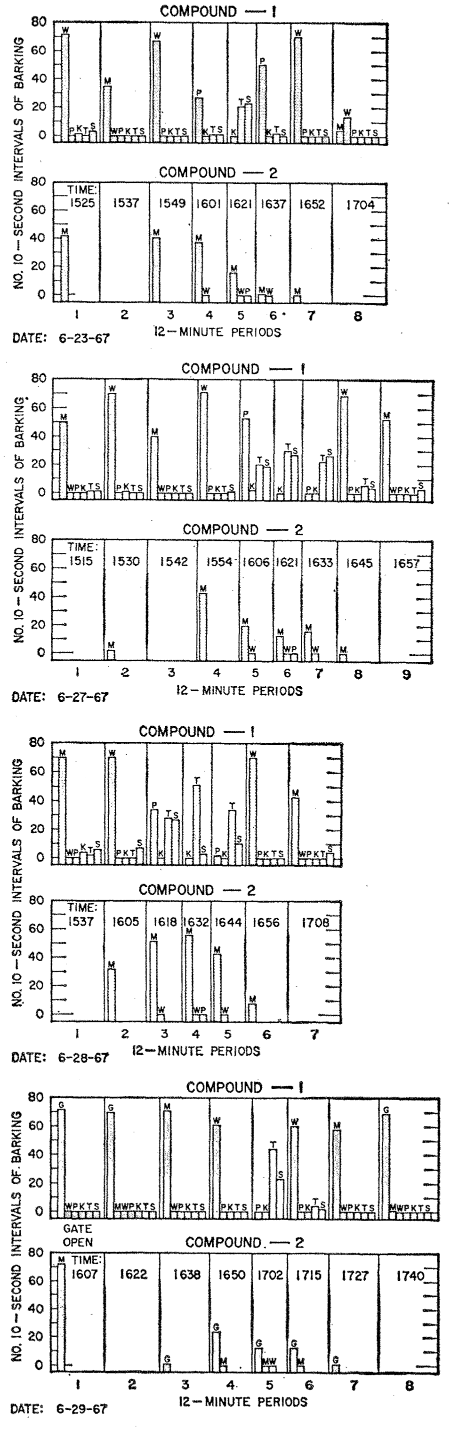

Fig. 2. Barking by male *Zalophus californianus* as a function of group composition in compounds 1 and 2.

establishment of partly aquatic territories; (ii) fights limited to two males; (iii) incessant barking by established territorial males; (iv) the use of physical force for displacement of an opponent; (v) the stereotyped boundary ceremony; (vi) the intrusion of smaller males into the resident male's territory so long as they maintain silence and remain visually inconspicuous; and (vii) interference by a dominant bull in "noisy squabbles" of females and pups.

Thus these experiments demonstrate that during its breeding season barking by a large *Zalophus* male serves as a cue for restricting movement and barking by other smaller males in the vicinity and accessible to attack. Intraspecific status or class recognition was demonstrated by the fact that, among the three more mature sea lions, barking and attack were primarily directed toward animals of most nearly equal size. The cues for identification among individual males are both visual and auditory. Although size is certainly an important cue, males also develop with growth a clearly discernible head crest as well as a lower-pitched bark.

Our experiment and recent field observations (*7*) demonstrate that barking by immature *Zalophus* males (in this study, 3 to 6 years old) is highly significant in the development of social communication patterns leading to adult displays of aggressive and sexual behavior. There is experimental evidence that *Zalophus* can learn to inhibit or emit its underwater click vocalizations in the presence of exteroceptive cues (*8*). That barking may also come under the control of exteroceptive cues, which are social in nature, is suggested by the finding that the sight and sound of a larger animal often suppressed vocalization and movement by the male of the next smaller size, when a larger male was capable of physically attacking and punishing smaller males.

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Selective Advantage of the Sickle-Cell Trait

Wiesenfeld's article "Sickle-cell trait in human biological and cultural evolution" (*1*) showed how a change in cultural practices may have far-reaching effects on the genetic composition of a population. His mathematical analysis, however, contains a common error which causes him to understate the importance of the effect.

In examining the relationship between intensity of endemic malaria (sporozoite rate) and selective advantage of the "sickler" heterozygote, Wiesenfeld derived an equation,

$$w_{12} = 1.075 + 1.289s$$

based on the estimated values for these variables; w_{12} is the selective advantage and s is the sporozoite rate.

If this equation is taken at face value it indicates that the sickle-cell trait confers a substantial selective advantage even when the sporozoite rate is zero. If this were true the trait would be common even in areas or among ethnic groups with no history of malaria. This, of course, is contrary to the known facts. What *is* known is that the gene results in significantly increased mortality among homozygotes and is associated with a number of deleterious conditions in heterozygotes (*2*). The selective advantage is only one of comparison, in that, on the average, persons with the sickle-cell trait are not as badly affected by the malarial parasite as persons lacking the trait are.

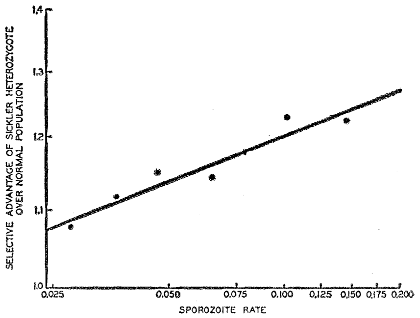

Fig. 1. Relationship between the intensity of endemic malaria (the sporozoite rate) and the selective advantage of the "sickler" heterozygote over the normal population.

The error in analysis which leads to this inconsistency is the assumption that the relationship is linear. Actually, logarithmic scales are almost always more appropriate for describing biological dose-response relationships (*3*). In this case, logarithmic scales not only give a visibly better fit (compare Fig. 1 given here with Fig. 4 of Wiesenfeld's article) but also yield a relationship in better conformity with known facts (*4*):

$$\log_{10} w_{12} = 0.1571 + 0.0774 \log_{10} s$$

Extrapolation of this result indicates that the selective advantage disappears at a sporozoite rate of 0.009; at rates below this the heterozygote is at a relative disadvantage. This is consistent with what is known of this condition.

This result adds weight to Wiesenfeld's argument by showing quantitatively how the rising prevalance of malaria, resulting from changes in agricultural practice, has caused a potentially harmful characteristic to become selectively advantageous. It further indicates that present and future efforts to control the incidence of malaria will have a long-term effect on the gene pool; when the sporozoite rate is reduced below approximately 0.009, the sickling trait will become disadvantageous and should be reduced to very low levels in a relatively few generations (*5*).

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