

Pinniped Vocal Communication: Form and Function

R. J. Schusterman, B. L. Southall, D. Kastak, and C. Reichmuth Kastak

*University of California Santa Cruz, Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, CA 95060 USA
(email rjschust@cats.ucsc.edu)*

Our study of pinniped vocal signaling emphasizes that an individual's vocalizations primarily operate to capture the attention of other individuals in the group. For example, the most basic function of a pup attraction call produced by a female is to draw the pup's attention to its mother's voice. Through its association with subsequent suckling behavior this vocalization eventually evokes a strong approach response when the pup is hungry. Conversely, threats typically arouse fear or aggressive responses in others due to their abrupt onset and their pairing with behavioral events such as pushing and biting. These observations, combined with our findings that the production and structure of vocalizations of pinnipeds can be altered with food reinforcement, suggests that non-imitative learning plays an important role in the vocal behavior of pinnipeds.

APPROACHES TO ANIMAL VOCAL COMMUNICATION

During the first three quarters of the past century animal vocal communication emphasized the delineation of stimulus variables influencing the emotional and aroused state of the signaling animal and a search for the neurophysiological mechanisms related to signal production. In contrast, the last quarter century has seen research and theory about animal vocal communication being greatly influenced by human information processing theory, particularly in terms of the human linguistic model (that is, semantics and syntactics). In particular, some primatologists and some marine mammalogists have tended to focus their efforts on the cognitive state of both the actors or senders and the recipients; they have emphasized the importance of the meaning of the signal while de-emphasizing the importance of signal structure and the identity of the signaler. However, with the advent of selfish gene theory, interest has been renewed in how the actors' signals function to govern the behavior of recipients to the benefit of the actor (and possibly, but not necessarily, to the benefit of the recipient as well). At the turn of the twenty-first century we are seeing a renewed emphasis on ethological principles and receiver psychology in the evolutionary and ecological study

of animal signaling, including sound production [1, 2]. Our approach to the study of pinniped vocal communication looks at the identity of the individual producing the signal (sex, age, emotional state within a social context, experience, etc.), the structure of the signal, and how the signal exerts an influence and guides the behavior of the recipient.

Pinniped Vocalizations

Natural Settings

Pinnipeds are among the most vocal of all mammalian taxa. Of the pinnipeds, the sea lions and fur seals vocalize most in air, the seals underwater, and walruses in both media. Sea lion females leave their pups to forage and then reunite with their pups after exchanging signature vocalizations at long range. Calls attracting females to their pups and visa versa are diverse, but are marked by sharp onsets and are frequency and amplitude modulated. Figure 1 shows a California sea lion mother-pup reunion; upon returning to shore, the mother emits her characteristic pup attraction call while simultaneously guiding her pup vocally around a physical barrier. Like sea lions, seals that breed on land in crowded rookeries also



FIGURE 1. California sea lion mother and pup exchanging calls while the mother controls the pup's locomotory behavior. The interaction terminates in a ritualized nose-to-nose greeting.

vocalize more in air. However, with the exception of elephant seals, there is no evidence of mutual vocal recognition between mother and pup in seals. In all pinnipeds, threats and alarm calls are structurally similar across sexes and species. Pinniped males have individually recognizable calls that they produce in the context of aggressive exchanges. They are repetitive, broadband pulses with rapid onset. The main function of pinniped vocalizations appears to be to elicit the attention of recipients and to guide their behavior in a way that is most beneficial to the signaler.

Artificial Settings

A variety of experimental approaches show that although pinniped vocal behavior is likely under strong hormonal control, the calls also have some degree of plasticity. For example, we have repeatedly found in the laboratory that male California sea lions, male harbor seals, and a female elephant seal are highly vocal during the breeding season and relatively quiet at other times of the year. Despite these strong annual cycles, it is relatively easy to condition the vocalizations of these and other captive pinnipeds [3]. Figure 2 shows spontaneous vocalizations produced in captivity during the breeding seasons of two seals. Although these calls were not spontaneously produced outside of the breeding season, we were able to control the production of these sounds by a trainer's gestural and vocal cues via food reinforcement. Once the sounds had been conditioned to the cues, they could be reliably produced at any time during the animal's annual cycle. Further, Figure 3 shows vocalizations produced by several adolescent walrus in captivity. These observations lead us to believe that the vocal behavior of pinnipeds is somewhat malleable, and can be controlled by a variety of environmental conditions including social situations and conditioning contexts.

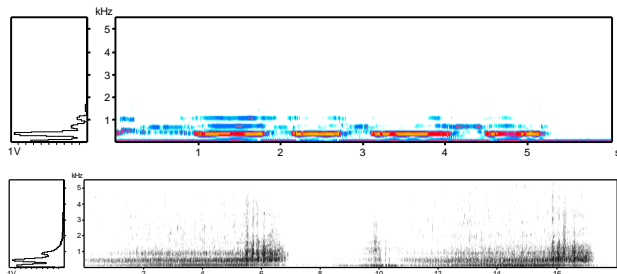


FIGURE 2. Energy spectra and spectrograms of an aerial “bellow” of an adult female northern elephant seal (upper) and an underwater “roar” of an adult male harbor seal (lower).

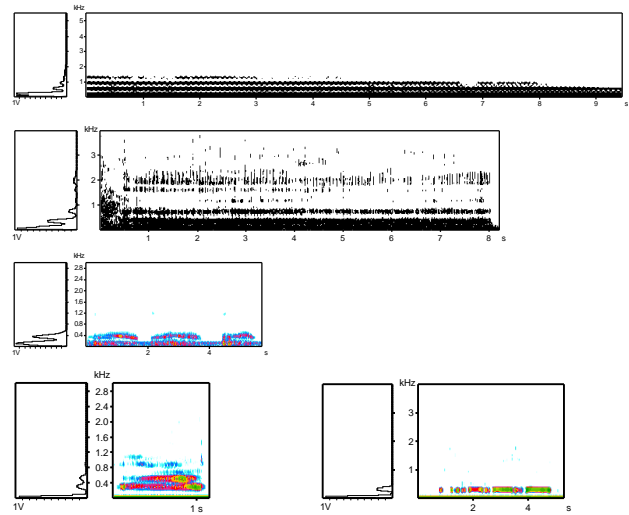


FIGURE 3. The top three rows show a sample of aerial sounds produced by captive walrus. These vocal emissions were shaped and conditioned using food reinforcement; the bottom row shows a sample of their spontaneous underwater vocalizations.

Conclusions

By concentrating on the attention getting characteristics of pinniped signals, the ability of the signaler to control its vocal output, and the degree to which these signals influence the behavior of recipients, new insights into the form and function of pinniped vocal communication emerge. For example, pairing vocal signals with emotion inducing behaviors, such as touching, nursing, posturing, pushing, biting, locomoting, and chasing, places signalers in an advantageous position within a variety of social contexts including mother-pup reunions, male-male competition, and sexual displays.

ACKNOWLEDGEMENTS

We thank Shannon Spillman and Marla Holt at Long Marine Lab for seal vocal conditioning and data collection, and Sue Negrini and Debbie Quihuis at Marine World/Africa USA for walrus vocal conditioning and recording.

REFERENCES

1. M.J. Owren and D. Rendell, *Evol. Anthro.*, **10**, 58-71 (2001).
2. T. Guilford and M.S. Dawkins, *Animal Behav.*, **42**, 1-14 (1991).
3. R.J. Schusterman, “Vocal communication in pinnipeds”, in *Behavior of Captive Wild Animals*, Edited by H. Markowitz and V.J. Stevens, Nelson-Hall, Chicago, 1978, pp. 247-285.