

## Pinniped vocal communication: an introduction

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*Communication forms the fabric of animal social life . . . in fact, looking at the way in which animals spend their time, it is striking how much of it they spend either influencing, or being influenced by, the behavior of other animals—in other words, in some form of communication.*

—Dawkins, *Unraveling Animal Behavior*, p. 71

The pinnipeds evolved and diverged tens of millions of years ago and spread throughout the oceans of the world, colonizing isolated shores and feeding in nearby productive waters. While the thirty-three living species of seals, sea lions, and walrus inhabit unique behavioural and ecological niches, one significant commonality amongst these animals is the apparent structural complexity of their vocalizations and the degree to which they use these vocalizations in communicative contexts. Some species, including the sea lions and some land-breeding seals, congregate seasonally on crowded rookeries where the repetitive calls of thousands of individuals swell into an incessant din. Other species, including most of the aquatically breeding seals, appear more reserved on their haul-outs, rarely producing audible sounds except for the occasional guttural threats of adults and the bleats of dependent pups. Many of these aquatic breeders were once thought to be relatively silent, but accumulating observations have shown them to have unusual and complex underwater vocal repertoires. Among the pinnipeds, the walrus are the most amphibious callers of all, producing frequent and assorted aerial and underwater sounds. Intriguingly, all pinnipeds appear capable of sound production on land and in water, and some even emit calls simultaneously above and below the water's surface.

In addition to the quantity of vocalizations emitted by pinnipeds is the surprising diversity of the sounds themselves, which have been categorized by listeners as clicks, creaks, bleats, growls, barks, whinnies, buzzes, grunts, snorts, songs, pulses, trills, thumps, blasts, groans, sirens, sweeps, yelps, roars, hums, chirps, belches, squeals, bells, whistles, knocks, mews, chucks, glugs, coos, gongs, clacks, claps, drones, trumpets, whimpers, puffs, burps, snarls, hisses, warbles, moans, and bellows, among

other descriptors. The variability in pinniped vocal signalling can be assessed at the level of the individual, as well as by age and gender class, emotive state, geographic location, and species, and the differences documented thus far reflect a degree of adaptation in vocal signalling that is rare among mammals. The acoustic characteristics of the signals produced by pinnipeds are well-designed to gain the attention of conspecifics—incidentally, these sounds have also captured the interest and imagination of human listeners.

For centuries, seals have been significant in the cultures of people living in close proximity to them. Not surprisingly, many of the legends and stories featuring these animals are concerned with their vocal communication. In these stories, seals may take on human form, talk and sing with people and with one another, and give warning of impending disaster (Maxwell, 1967; Thomson, 1914/1965). Many of these observations have been published as factual accounts. For example, Maxwell (1967) refers to a 1920's newspaper article which states that '*. . . there is undoubted testimony that the great grey seals of the Atlantic who visit the islands have been heard singing—for no other word applies to their very human voices.*' Many years later, a 'talking' harbour seal named Hoover at the New England Aquarium rekindled the notion that seals could learn to speak (Ralls, *et al.*, 1985).

In the 1960's, scientific exploration of pinniped vocal communication began in earnest, led by a handful of dedicated American investigators, including Thomas Poulter, Bill Scheville, Carlton Ray, Burney Le Bouef, Dick Peterson, Nicholas Collias, George Bartholomew, Ian Stirling, and one of the editors of this issue [RJS]. This early research tended to emphasize structural descriptions of aerial and underwater sounds emitted by readily accessible sea lions, fur seals, and elephant seals. In

addition to recording and describing vocalizations, these scientists attempted to establish hypotheses regarding the use of these sounds in socially communicative contexts, as well as in auto-communicative contexts, namely foraging and navigation via echolocation. Over the next 40 years, the possibility of pinniped echolocation diminished as observations and experiments on their sensory systems and their underwater-emitted sounds revealed that specialized echolocation abilities were lacking in most if not all species (Schusterman *et al.* 2000). However, ideas about the social functions of their vocalizations were transformed into field and lab investigations as more information about the vocal behaviour of various species began to accumulate. These efforts were later elevated and expanded by the advent of new recording technologies and improved geographic accessibility, which facilitated the acoustic monitoring of animals diving, foraging, and socializing at sea.

Presently, we know something about the vocal repertoires of over three-quarters of pinniped species, including terrestrial and aquatic breeders, and polar, temperate, and tropical species. Early researchers have trained and stimulated new generations of scientists, and these investigators continue to refine, increase, and synthesize our understanding of the relationship between sound production and behavioural ecology in pinnipeds. At the start of the new millennium, researchers representing several generations met at the 2001 meeting of the Society for Marine Mammalogy, in Vancouver, Canada, to participate in a special symposium organized by the guest editors of this issue [SVP and RJS]. This issue of *Aquatic Mammals* is the result of that symposium, with contributors including the speakers at that meeting and others working on original research in the field.

Following the Vancouver symposium in 2001, and our decision to co-edit this volume, we had a variety of discussions with one another, the contributors, reviewers, and our colleagues about pinniped vocal communication. The topics of these interactions ranged from editorial issues to technology gaps to philosophical points of view. Between us, one issue about animal communication emerged as particularly controversial and significant, and we would like to briefly outline it in this introduction.

The quote underscoring the importance of communication that appears at the start of this introduction appears in a textbook on animal behaviour by Marian Stamp Dawkins (1995). In this text, Dawkins points out that, despite intensive study and thoughtful theory, the whole subject of animal communication is nevertheless extremely confused,

largely because of the bringing together of conflicting terms along with conflicting definitions and unworkable metaphors. These definitions and metaphors are largely unworkable because of conflicts between group selectionist and selfish-gene theory views of communication. While ethologists and psychologists generally consider communication, along with other aspects of social behaviour, in a Darwinian evolutionary framework, many investigators still opt to describe communication among animals as involving the cooperative sharing of information.

This notion, as described by W. J. Smith (1977), has had strong support among workers in the field of marine mammalogy (Miller, 1991; Tyack & Miller, 2002; Dudzinski *et al.*, 2002). From our point of view, the greatest difficulty that such an information-transfer model has is the confusing of the separable roles and fitness interests of signallers and perceivers. For example, in a recent encyclopaedic review of communication in marine mammals, Dudzinski *et al.* 2002 state that during an exchange of information, both sender and receiver depend on the 'accurate interpretation of signals to meet common group challenges such as reproduction, predator defense, foraging, and parental care' (p. 249). The authors also go on to say that communication among marine mammals promotes group cohesiveness. It is difficult to reconcile such a view of communication with an evolutionary approach. According to Darwinian evolution, a communicative act should be beneficial to the sender, but not necessarily the receiver (this is particularly true of conflict situations or contests over resources where there is often a cost incurred by the receiver). In addition, a Darwinian approach suggests that communicative acts provide indirect benefits to receivers only when signals function to contribute to the welfare of kin, or as part of reciprocated altruism occurring among non-kin (Trivers, 1985).

Approaching animal communication, particularly vocal communication, without using constructs gleaned from information transfer theory, Owings & Morton (1998) and Owren & Rendall (1997) have taken a similar approach to disentangling the roles of sender and receiver in evolutionary-based models of communication. Basically, these theoreticians suggest that vocal communication is a reflection of the fundamental process of signallers regulating the behaviour of receivers, and receivers assessing the characteristics of signallers. From this selfish-gene perspective, signallers control the behaviour of receivers to their own benefit, and not necessarily to the benefit of listeners. Perceivers, on the other hand, receive the signal and respond or not depending on whether or not they receive a benefit for doing so. Thus,

signalling and perceiving can be viewed as serving independent self interests.

In a complementary evolutionary analysis of vocal communication, Morton's motivation-structural principles of vocal communication (1977), which have been previously applied to terrestrial mammals and birds, can readily be applied to pinnipeds. For example, the raucous sounds coming from terrestrial breeding grounds are generally loud, directional, often broadband, and are always highly repetitive. These signals are well-designed to attract a listener's attention. Morton's ideas about how affect relates to the structural components of acoustic signals can be seen in the low frequency, broadband, sharp-onset calls emitted by pinnipeds in aggressive contexts and their higher-frequency whine and bleat-like calls that are emitted in affiliative contexts. Thus, for example, in the context of sexual selection, because larger individuals win aggressive physical contests among males wanting access to females, selection favours harsh roar- and growl-like qualities that reflect body size. In this manner, vocal communication may serve to replace fighting because such acoustic signals can substitute for body size as an indicator of resource holding potential (Owings and Morton, 1998). This type of communication has been termed 'expressive size symbolism', or ESS, because, according to evolutionary game theory, it is an 'evolutionary stable strategy'.

In this brief introduction, we have attempted to highlight what we consider to be one of the major problem areas in the study of animal vocal communication in general and pinniped vocal communication in particular, namely, the importance of using an inclusive definition of communication, which places equal emphasis on regulation of the signal on the part of the sender and assessment of the signal on the part of the receiver. Our current understanding of pinniped vocal communication, that is, the relationship between sound production and behaviour, has been bolstered by an increasing number of studies and internationally published literature (see recent reviews in Tyack, 1999, and Tyack & Miller, 2002). In order to build on this foundation, Tyack & Miller (2002) have suggested that the areas presenting the greatest opportunities for future research on the proximate and ultimate causes of pinniped acoustic communication include acoustic perception and categorization, functional analyses of vocal behaviour, the behavioural significance of the variation in acoustic displays, and vocal development and vocal learning. It appears to us that all of these areas can be approached from the standpoint of the signallers and receivers, and their sometimes conflicting and sometimes coinciding interests.

The collection of papers included in this volume represents a significant step forward in the research area of pinniped vocal communication. The contributed articles are either reviews of specific sub-topics in the field or empirical studies of vocal communication in individual pinniped species. They draw from a fairly diverse group of scholars, all of whom have placed their work within an ecological/evolutionary context, sometimes with a heavy emphasis on how pinniped life-history patterns, such as the movement and distribution of individuals, maternal strategies, reproductive physiology and behaviour, breeding habitat, foraging, and predation—as well as ontogenetic factors—influence the form and function of vocal communication. Sexual selection is also a major theme in several of the papers. These papers deal with the structure and function of the vocal displays produced by males of aquatically mating pinniped species in the context of examining how acoustic-display behaviour may function in lek breeding situations, where individuals are likely to be evaluating the fitness of others on the basis of vocal signals. Perhaps the most exciting aspect of the reviews contributed on the role of acoustic signalling in individual recognition and social systems is the fresh comparative approach taken by the investigators. The new synthetic ideas and viewpoints contained in these articles arise from the accumulating body of descriptive acoustic and behavioural data that is now available for a considerable number of pinniped species.

As the papers in this volume illustrate, we have clearly moved beyond the anthropomorphic, anecdotal approach to the study of vocal communication in pinnipeds, and collectively, we are making steady progress towards achieving a high level of accurate, objective, cogent, and comparative descriptions of pinniped vocal behaviour. Future studies, which aim to encompass well-defined ethological, ecological, and evolutionary concepts dealing with communication in these animals, await us.

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