Vertebrate social communication: Ecological and evolutionary insights from social signals

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1 Communication and Social Signals

Wilson (1975) defines communication as "the action on the part of one organism (or cell) that alters the probability pattern of behavior in another organism (or cell) in a fashion adaptive to either one or both the participants". Only a definition this broad can capture all the term "communication" encompasses; eavesdropping - where only the receiver benefits from detection of the signal or cue, manipulation - where the signaler benefits at the expense of the receiver, and what Peter Marler (1977) described as "true communication", where both the signaler and receiver derive benefit from the information conveyed between the participants.

It is not an exaggeration to say that communication is the glue that binds societies together: just as cells within each living organism must be in constant communication to coordinate their activities, the individuals and their relationships that collectively define a society require ongoing, and often highly intricate forms of communication. Social signals then, are the various contact, recognition, recruitment, territorial, alarm, distress, arousal, intent, reproductive, and mobbing signals that serve to modulate social interactions among organisms. While the methods employed in studying communication have changed dramatically with advances in technology (Terhune, 2011), understanding the information content of signals remains the most valuable method of determining what is important to the organism from the organism's own perspective (Marler, 1961; but see Owren et al. 2010). As such, deciphering the information conveyed by social signals provides valuable insight into both the proximate and ultimate factors shaping organismal life-history and behavior, including both perceptual and underlying cognitive abilities (e.g., Cheney and Seyfarth, 1990; Zahavi and Zahavi, 1997; Pepperberg, 1999; Reby et al., 2005; Stevens 2010).

While this special issue focuses on vertebrate social signals, and within that circumscribed domain, almost exclusively on acoustic signals, it is critical to recognize that communication-related research as a whole involves a much wider range of taxa, deals with all possible sensory channels, and also provides information of applied value, including that used in censusing populations (e.g., Peake and McGregor, 2001), in promoting reproductive success among captive animals (e.g., Swaisgood et al., 2003), in controlling "pests" (e.g., Foster and Harris, 1997), or in other aspects of conservation, including the mitigation of potential affects of anthropogenic noise (e.g., Slabbekoorn et al., 2010; Pijanowski et al., 2011). Readers with a more general interest in communication are encouraged to consult more comprehensive resources, such as the most recent edition of Jack Bradbury and Sandra Vehrencamp's Principles of Animal Communication (Bradbury and Vehrencamp, 2011).

2 Contributions to the Special Issue

Within this special issue, the broader implications of research exploring communication are readily evident in two review contributions. Cäsar and Zuberbühler's review (2012) explores referentiality in the alarm calling systems of new world primates, revealing both productional and perceptual specificity paralleling the avian/terrestrial threat distinction described for several old world primates. Beyond categorical differences, however, their review also considers graded and combinatorial signals, documenting where syntax-like patterns arise through combinations of different vocalizations, thereby conveying meaningful information to receivers. Cäsar and Zuberbühler's novel empirical data on predator-related calls in black-fronted titi monkeys, demonstrate not only aspects of categorical referentiality, but combinations of signals that appear to encode information regarding predator type and location. Based on these findings, Cäsar and Zuberbühler conclude that combinatorial signals communicating referential information appeared prior to the evolution of language proper.

Lingle et al. (2012) also forge new ground in re-
viewing literature pertaining to vertebrate distress calls. Their review reveals that both isolation and capture calls universally serve to attract caregivers, often with their fundamental frequency acting as the critical stimulus parameter, and communicating the state of arousal of the signaler via shifts in amplitude, maximum frequency or the overall spectral envelope of the signal. Such commonalities in structure and function across taxa suggest not only that distress vocalizations exploit the same highly conserved productional and perceptual mechanisms, but that systems of this nature can provide the evolutionary substrate for signals that attract conspecifics in other contexts.

Other empirical studies focusing on signal production within this issue reveal the varied, sometimes detailed, and highly adaptive information encoded within signals. Schwing, Parsons and Nelson's categorization of kea parrot contact calls (2012) exemplifies principles put forth in the Lingle et al. review (e.g., the relationship of productional attributes to the presumptive function of the screech call), and provides a novel description of the vocal repertoire of kea parrots, broadening our comparative knowledge of Psittaciforme parrot vocal communication. Beyond providing a catalogue objectively defining call types, Schwing et al. address whether those call types are differentially produced by members of certain age/sex cohorts, sequencing of call types within individuals, and preliminarily document conspecific vocal responses to those calls, thereby providing tantalizing trends combined with a sound foundation for future research.

Retaining the focus on signal production, Slobodchikoff et al. (2012) report results of an experimental study documenting variation in Gunnison's prairie dog alarm call structure relative to manipulation of the shape and size of novel stimulus objects. Their findings reveal that these alarm vocalizations encode information about the shape and size of moving objects, indicating not only that the prairie dogs perceive such structural attributes, but that information on both shape and size is broadcast to receivers, potentially providing fine-grained information about the identity or morphological attributes of the presumptive predator eliciting the call.

Like Slobodchikoff et al., Schneiderova (2012) employs discriminant function analysis to explore how variation in the acoustic structure of European, Taurus and Anatolian ground squirrel alarm calls can provide information to receivers regarding the identity of individual alarm signalers. Her findings provide the first published evidence that Anatolian ground squirrels produce individually-distinctive alarm calls, adding this squirrel species to the seemingly ever-expanding list of species that produce individually-distinguishable alarm signals (Pollard and Blumstein, 2011), and thus potentially associate signaler identity with past signaler reliability (Cheney and Seyfarth, 1988; Hare and Atkins, 2001), assess the veracity of the assertion of threat by enumerating signalers (Sloan and Hare, 2008; Matrosova et al., 2009), or assess predator movement by integrating information from those multiple signalers (Thompson and Hare, 2010). Somewhat surprisingly, however, Schneiderova's analysis reveals that the incorporation of a second frequency-modulated signal element to form two-element calls did not improve the confidence with which calls could be assigned to individual signalers, despite each of those elements independently allowing calls to be assigned reliably to individuals.

That same focus on individuality and analytical approach are applied by Digweed et al. (2012) whose detailed acoustic analysis and subsequent discriminant function analyses reveal that territorial rattle calls of red squirrels are individually-distinct, particularly among neighboring squirrels within a territorial cluster. The authors conclude that these individually distinct territorial calls would prove adaptive in reducing costs implicit in escalating responses to known territorial neighbors (i.e. "dear enemies"; Fisher, 1954).

Despite the apparent importance of individually-distinct signals, contributions to this issue testing for a relationship between local population density of breeding birds and the degree of individuality of their territorial calls (Blumstein et al., 2012) or for differential response to individual-specific alarm calls of adult female Richardson's ground squirrels (Hare and Warkentin, 2012) fail to detect predicted effects. While there is little doubt that sociality is a potent factor selecting for individually-specific signals (Pollard and Blumstein, 2011), population density alone is apparently insufficient to account for the extent of individuality in avian territorial calls. Similarly, although individual discrimination of alarm calls can prove adaptive (see above), vulnerable young squirrels appear not to attend selectively to their own dam's call, responding equivalently to any adult female issued alarm signal.

The final research paper in this special issue (Sandoval and Wilson, 2012) cleverly uses playbacks of predator calls or mobbing calls of three of that predator's avian prey species across areas that vary in predator incidence to test whether mobbing responses of tropical bird species are related to predation pressure. The authors report a direct relationship between the strength of the mobbing responses elicited by playbacks and local predator abundance, supporting the notion that
cooperation is more likely to be expressed under adverse environmental conditions. Sandoval and Wilson's contribution thus effectively uses communication as a tool to understand the factors contributing to the evolution and variable expression of social cooperation. In so doing, they also provide valuable insights into the perception of mobbing signals by birds.

3 Conclusion

Fostering a more complete understanding of communication is critical for our own future, not only in terms of the function of human society and cooperation therein, but in promoting an understanding and appreciation of those species we will hopefully share a long future with! I trust that like the contributors, readers will find the information communicated in this special issue on Vertebrate Social Communication of use to that end.

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References