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INTRODUCTION

Acoustic Interaction in Animal Groups: Signaling in Noisy and Social Contexts

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It has long been known that individuals of many species vocally communicate with one another in noisy environments and in rich contexts of social interaction. It has recently become clear that researchers interested in understanding acoustic communication in animal groups must study vocal signaling in these noisy and socially complex settings. Furthermore, recent methodological advances have made it increasingly clear that the authors can tackle these more complex questions effectively. The articles in this Special Issue stem from a Symposium held at the June 2006 meeting of the Acoustical Society of America, and illustrate some of the taxonomic and methodological diversity in studies aimed at understanding how acoustic communication functions in social grouping. This introduction to the Special Issue provides a brief overview of the articles and key ideas in this field of inquiry, and suggests some future directions to take the field to help us understand how social pressures in animal groups may influence, and be influenced by, acoustic signals.

Keywords: acoustic signals, vocal communication, eavesdropping, social interactions

Over the past few decades, research has dramatically expanded our knowledge of acoustic communication in animal groups as data have been gathered to address long-standing questions, as well as more recently articulated ones. Moreover, technical advances have improved our ability to address hypotheses that formerly would have proven extremely difficult, if not impossible, to tackle. To provide an opportunity to discuss such developments, a symposium was held at the June 2006 meeting of the Acoustical Society of America. It was impossible to include all the researchers whose work spans the huge array of topics encompassed by the purposefully broad title of our symposium. However, the symposium attracted people doing excellent science that often incorporated new perspectives and methodological approaches. The taxa discussed included insects, fish, amphibians, birds, and mammals. Most of the speakers are contributors to this special issue of the *Journal of Comparative Psychology*.

Our own fascination with the subject of this issue goes back to the beginning of our research careers. For Schwartz, this occurred about 28 years ago when he began his doctoral research on communication in treefrogs in a flooded meadow in Panama. In addition to being impressed by the painfully loud chorus produced each evening by males in the multispecies assemblage, he and Kent Wells were immediately struck by the temporal structure of chorusing of two of the species. Males of *Hyla microcephala*, the more abundant and louder species, structured their calling into bouts lasting approximately 5 to 25 seconds. During the relatively quiescent interbout intervals, males of the second species, *H. ebraccata*, concentrated their calling (Schwartz & Wells, 1983a). Similar behavior had been reported by Littlejohn and Martin (1969) in unrelated anurans halfway around the world, and seemed to be an adaptation that enabled males of one species to reduce acoustic interference with the other species and thus improve their ability to attract potential mates. In a set of fairly straightforward experiments with both males and females, Schwartz and Wells (1983a, 1983b) obtained data consistent with this hypothesis. In response to broadcasts of recordings of heterospecific choruses and appropriately filtered noise, males of *H. ebraccata* reduced their calling rate as well as their proportion of multinote and aggressive calls. The last two changes suggested that the calls of the neighbors of test subjects were masked during chorus playbacks. Females of *H. ebraccata*, in turn, discriminated against conspecific calls that were overlapped by broadcasts of *H. microcephala* chorus recordings. Subsequent research addressed aspects of call- and note-timing in these two species on a much finer scale, as well as hypotheses that could explain the organization of *H. microcephala* choruses into bouts (reviewed in Schwartz, 2001). Addressing many of these questions required the creation of both hardware and software to monitor the calling dynamics in choruses

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of calling males accurately. Of course, call-timing interactions represent just one category of the fascinating smorgasbord of acoustic interactions that occur in groups of animals. The bottom line was that Schwartz was hooked not only on studying anuran communication at the level of dyads, but especially on the challenges to frogs posed by communication in aggregations.

For Freeberg, the interest in vocal communication in social groups began with his graduate training at Indiana University in the laboratory of Meredith West and Andrew King, studying different populations of brown-headed cowbirds, *Molothrus ater*. Early studies tested the influence of social experience on the development of songs and of singing in male cowbirds, employing the traditional approach of housing young males in sound isolation chambers to control the males' social and acoustic experiences. Quite unsurprisingly, young males housed with heterospecifics developed deficient songs as assayed by female copulatory responses to song playbacks, compared to young males housed with female conspecifics (Freeberg, King, & West, 1995; West, King, & Freeberg, 1996). Thanks in part to a timely visit and methodological suggestion by the late Gilbert Gottlieb, the research moved beyond the traditional approach, however, and tested the actual courtship behavior of those young males. Quite surprisingly, the effectiveness of their songs did not necessarily predict the effectiveness of those males at courting and copulating with females. Further manipulations of the social environments of those males for an additional year pointed to the importance of social interaction with adult males to the development of courtship effectiveness (Freeberg et al., 1995; West et al., 1996). The importance of the social group to the development of vocal signals—and, perhaps more importantly, of vocal signaling—was tested in a series of studies of the social transmission of population-level variation in courtship behavior and mating preferences (reviewed in Freeberg, 2004). Furthermore, the importance of research methodologies different enough (and apparatus and housing facilities large enough) to provide for the complexity of social interactions among group members was made clear to Freeberg by this work.

In the remainder of this introduction to the Special Issue, we would like to touch on some directions for future investigation (focusing on work in anurans and in birds), and will briefly describe the articles that follow. Although some of the questions we mention have received a fair amount of attention, we suggest some novel research strategies as well as some additional questions to consider. The questions we address are relevant to taxa other than anurans and birds and, in fact, some of these are discussed in the papers that follow, as well as in contributions to the recent volume, *Animal Communication Networks* (McGregor, 2005).

In frogs, an area ripe for study is the significance, if any, of eavesdropping (sensu Peake, 2005). It is easy to imagine how eavesdropping could be significant during male-male interactions and female mate choice (see Grafe, 2005 for a detailed treatment). Males of many species attend to the calls of neighboring advertizing males and may not only modify their call timing, as mentioned earlier, but also adjust the attractiveness to conspecific females of their vocal output (e.g., through elevations in call rate, call duration, or call complexity; Gerhardt & Huber, 2002; Wells, 2007). We need to know not only what are the domains in the chorus over which males are responsive in the latter manner but also whether they modify their calling in response to cues obtained by eavesdropping on males during the final stages of female approach. At this time, a male who has detected an approaching female may, evidently to improve his chance of success, dramatically increase his calling effort to a degree that is probably only briefly sustainable. For example, in *H. versicolor*, call duration can jump to 70 pulses (about 4 times the typical average) and calling effort more than double (Schwartz, personal observations). How good are nearby males at detecting this brief change and do they quickly ratchet up their own calling effort? If so, how often are these efforts rewarded? Males also may interact agonistically by exchanging aggressive vocalizations and even by using physical combat. Do other males attend to these contests and respond differently to winners and losers? For example, might males be more likely to intrude on the territories or calling space of losers? Do females listen in as well? How might the outcome of aggressive encounters impact on their choices?

As articulated by Bee and Micheyl in this issue, we also need to know more about how both males and females acquire information from the often extremely complex acoustic scene present in the chorus (also see Gerhardt & Huber, 2002, for a review of current knowledge). What is the relative importance of spectral and temporal attributes in calls to this process? How does the spatial distribution of individuals in 3-dimensions contribute to scene analysis? Additional data are needed on the extent to which capabilities of (or constraints imposed by) the peripheral and central auditory system of males and females influence how males distribute themselves and time their calls. How might the spatial and temporal structure of the chorus influence the behavior of receptive females within it?

Without a sufficient population of males at a particular breeding area, chorusing activity may not arise (Brooke, Alford, & Schwarzkopf, 2000). Are there additional transitions in the behavior of the chorus that occur with increases in male number or density? How might acoustic phenomena that emerge from signaling in a chorus setting feedback on the individuals within these aggregations? What mechanisms are most important? For example, the bout structure of *H. microcephala* choruses may be in part linked not only to energetic limitations of males (Schwartz, Ressel, & Bevier, 1995) but also to neural processes controlling fine-scale aspects of call-timing of individual males. Indeed, patterns of both call synchrony and call alternation may be epiphenomena of such mechanisms (Greenfield, 2005), and we need to test this hypothesis in more species of chorusing organisms.

Studies of chorusing in anurans (and insects) pointed to the powerful role of the social context in influencing acoustic signaling decades before the importance of the social context was formally addressed by current interests in communication networks in birds and mammals (see McGregor, 2005). Much of the current focus of communication networks is on the functional implications of individuals attending to information in their social contexts. For example, using song playbacks, Mennill, Ratcliffe, and Boag (2002) demonstrated that female black-capped chickadees, *Poecile atricapillus*, eavesdrop on acoustic interactions between their mates and other males in the local population, and gain extrapair fertilizations based in part on how they perceive their mates to have fared in "winning" or "losing" status in those acoustic interactions (see also Otter et al., 1999 for evidence of eavesdropping in possible female assessment of males in great tits, *Parus major*; and Peake, 2005 for a review). How do the experiences of individuals and the particular nature of the immediate communication network impact the way individuals respond to information they gain through eavesdropping? How do these factors impact the behavior of the individuals producing acoustic signals in these environments? Can signalers be strategic and more directional in signal production to minimize possible eavesdropping in certain contexts (e.g., McGregor, Otter, & Peake, 2000)?

Researchers have long been interested in bird song, and there is a general view that social experience must play an important role in how young birds develop their songs. However, only recently have researchers really begun to work at manipulating social contextual variables in experimental studies of song development (Beecher & Brenowitz, 2005; Marler & Slabbekoorn, 2004). Furthermore, how do the earliest vocal signaling interactions between young birds (or young animals in general) and their parents influence the vocal and nonvocal social behavioral development of those young individuals? Recent evidence in brown-headed cowbirds indicates that the social structure of cowbird groups influences the types of interaction that are possible between young and adult individuals of both sexes, and plays a role in the social preferences of young females and the song (and singing) development of young males (Freed-Brown, King, Miller, & West, 2006; Miller, Freed-Brown, White, King, & West 2006). The role that group structure plays in vocal signaling development in other avian and nonavian species is largely an open question—perhaps manipulation of social contexts may reveal more plasticity in the development of such signals than has been documented to date (for examples of the influence of social experience on primate vocal behavior and sexual behavior, see Snowdon & de la Torre, 2002, and Mason, 1960, respectively). Finally, the role that vocal signaling might play in the development and maintenance of group structures is an exciting direction to take our research. For example, recent work in baboons (*Papio cynocephalus*) beautifully demonstrates how a grunt vocalization by an individual that has just acted aggressively toward another (or by the kin of such an aggressor) serves to help reconcile the social relationship between the aggressor and victim (Cheney & Seyfarth, 1997; Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007).

We are beginning to tackle many of the questions raised above, and many of the articles in this Special Issue are beginning to provide some answers. Bee and Micheyl discuss a topic of particular relevance to communication by frogs and other organisms that call in dense assemblages: the cocktail party problem. They provide a necessarily succinct yet informative historical review of the literature and cogently argue for more research by students of animal communication. Their paper also provides a lucid primer on auditory scene analysis as well as illustrative examples from work on anurans. Mechanistically, the responses of neurons at both the individual and population level will ultimately determine whether, for example, signals can be recognized and discriminated. Ronacher et al. examined the spiking patterns of auditory neurons in grasshoppers and show how these can meet the response properties required for dependable differentiation of the calls of different individuals. Furthermore, in agreement with data on other species, their analysis suggests a shift at different levels of the auditory system in the relative importance of neural coding of modulated signals based on spike timing and spike rate.

A female anuran entering a chorus to select a mate can face the problems of discriminating conspecific males from heterospecific males and of choosing among an array of males of her own species. Often different attributes of calls facilitate these two tasks, and discerning these important acoustic cues under conditions of high ambient noise and acoustic clutter can be a challenge. Acoustic cues must also be used by females to estimate the location of males, and this information may affect their mate choice decisions. In barking treefrogs, *H. gratiosa*, a male's distance from a female is influential, but it has not been clear which of the potential acoustic sources of distance information were most important. Murphy used a series of ingenious multispeaker phonotaxis tests to evaluate reasonable hypotheses. His results refute some of the more obvious of these and implicate a more complex mechanism. Simmons et al. have employed a technically sophisticated system (that has also been used to track echolocating bats) to study vocal interactions in choruses of the bullfrog, *Rana catesbeiana*. Two 'cubes', each housing multiple microphones, were used to record the calls of males; thus data acquisition does not depend on running microphone cables through the habitat. Signal processing, mimicking aspects of the mammalian auditory system, was used to pinpoint the location of callers and segregate vocalizations of individuals. The data reveal intriguing patterns of call timing and suggest substructuring of the chorus based on male proximity.

The ability of signalers and receivers to communicate using sound is, of course, not only a function of the ambient acoustic environment but also of the capacity of the sensory system to acquire and appropriately encode necessary information. Signal detection theory (SDT) provides an extremely powerful framework within which to examine constraints on effective communication (Wollerman & Wiley, 2002). A prediction of SDT is that under the noisy conditions of anuran and insect choruses, the task of the sensory system can be made easier by behavioral adjustments of the animals themselves, including the use of more exaggerated signals.

Males of the gray treefrog, *Hyla versicolor*, increase call duration while simultaneously reducing call rate in response to the calls of other males. Schwartz et al. present the results of experiments designed to test one explanation dealing with the selective advantage of this behavior. This 'interference risk hypothesis' is related to the problem of transmitting attractive signals to potential mates in an environment replete with calling males. However, the problem addressed is not masking per se but rather that of perceived alteration of call elements critical to call recognition by females. Greenfield and Schul discuss how receiver perceptual biases and signal production mechanisms in choruses of insects can lead to the emergence of calling alternation or calling synchrony among neighbors in a group. In some cases, the adaptive significance of these temporal patterns of calling are known and competition or cooperation between signalers may contribute to the temporal pattern that emerges. Greenfield and Schul illustrate these points using data from two species of katydids while describing models of signaling based on insect psychoacoustic parameters that can lead to such synchrony or alternation of calls.

Much of the work on choruses, and the theory that has emerged from such work, has focused on acoustically interacting individuals separated in space. Horn approaches the chorus question from the standpoint of the confines of a nest of begging nestling songbirds, and provides an overview of his experimental work on the begging interactions of nestling tree swallows, *Tachycineta bicolor*. This work has found that nestlings can alter their calling rates and calling amplitude when begging, depending on the kind of acoustic interference they face in the nest. This work points to some of the developmental implications of this signaling, addressing the ways in which information in begging calls can influence the behavior of other nestlings and of parents. How acoustic signals can impact the movement behavior of group members is addressed in a very different context by Janik and Quick. Tracking wild bottlenose dolphins, *Tursiops truncatus*, with an array of microphones to allow for the identification of individual callers, the authors provide evidence that whistled vocal exchanges among individuals can coordinate the joining of one dolphin subgroup with another.

The vocal behavior of individuals obviously impacts the social behavior of other individuals in a group of animals. It is also becoming clear that the social behavior occurring within groups—indeed, the social structure of the group—can impact the vocal behavior of individuals in the group. Freeberg and Harvey review work indicating that differences in the number of individuals in groups of Carolina chickadees, *Poecile carolinensis*, can influence the structural complexity of individuals' calls. The impact of social groups and social relationships on the vocal signals of individuals is also demonstrated by the phenomenon of vocal convergence, in which vocal signals of individuals within a group tend to become acoustically more similar to one another over time. Tyack reviews work on vocal convergence and the social bonds that may give rise to it, and discusses some of the possible functions, and evolutionary implications, of the sharing of vocalizations.

To conclude, the articles in this Special Issue review extensive bodies of work in diverse taxa illustrating links between social groups of animals and their acoustic signals. This work is helping us to understand how acoustic signals influence behavior of members of a group and how the structures of interaction between members of a group can influence acoustic signals of individuals. Each article furthermore raises important issues that future work will need to address if we truly wish to get at the heart of how acoustic interactions socially function in animal groups.

References

Beecher, M. D., & Brenowitz, E. A. (2005). Functional aspects of song learning in songbirds. *Trends in Ecology and Evolution, 20,* 143–149.

Brooke, P. N., Alford, R. A., & Schwarzkopf, L. (2000). Environmental and social factors influence chorusing behaviour in a tropical frog: Examining various temporal and spatial scales. *Behavioral Ecology and Sociobiology, 49,* 79–87.

Cheney, D. L., & Seyfarth, R. M. (1997). Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour, 54,* 409–418.

Freeberg, T. M. (2004). Social transmission of courtship behavior and mating preferences in brown-headed cowbirds, *Molothrus ater. Learning and Behavior, 32,* 122–130.

Freeberg, T. M., King, A. P., & West, M. J. (1995). Social malleability in cowbirds: Species and mate recognition in the first two years of life. *Journal of Comparative Psychology, 109,* 357–367.

Freed-Brown, S. G., King, A. P., Miller, J. L., & West, M. J. (2006). Uncovering sources of variation in female sociality: Implications for the development of social preferences in female cowbirds (*Molothrus ater*). *Behaviour, 143,* 1293–1315.

Gerhardt, H. C., & Huber, F. (2002). *Acoustic communication in insects and frogs: Common problems and diverse solutions.* Chicago: University of Chicago Press.

Grafe, T. U. (2005). Anuran choruses as communication networks. In P. K. McGregor (Ed.), *Animal communication networks* (pp. 277–299). Cambridge, United Kingdom: Cambridge University Press.

Greenfield, M. D. (2005). Mechanisms and evolution of communal sexual displays in arthropods and anurans. *Advances in the Study of Behavior, 35,* 1–62.

Littlejohn, M. J., & Martin, A. A. (1969). Acoustic interaction between two species of leptodactylid frogs. *Animal Behaviour, 17,* 785–791.

Marler, P., & Slabbekoorn, H. (2004). *Nature's music: The science of birdsong.* Amsterdam: Elsevier.

Mason, W. A. (1960). The effects of social restriction on the behavior of rhesus monkeys: I. Free social behavior. *Journal of Comparative and Physiological Psychology, 53,* 582–589.

McGregor, P. K. (2005). *Animal communication networks.* Cambridge, United Kingdom: Cambridge University Press.

McGregor, P. K., Otter, K., & Peake, T. M. (2000). In Y. Espmark, T. Amundsen, & G. Rosenqvist (Eds.), *Animal signals: Signalling and signal design in animal communication* (pp. 329–340). Trondheim, Norway: Tapir Academic Press.

Mennill, D. J., Ratcliffe, L. M., & Boag, P. T. (2002). Female eavesdropping on male song contests in songbirds. *Science, 296,* 873–873.

Miller, J. M., Freed-Brown, S. G., White, D. J., King, A. P., & West, M. J. (2006). Developmental origins of sociality in brown-headed cowbirds (*Molothrus ater*). *Journal of Comparative Psychology, 120,* 229–238.

Otter, K., McGregor, P. K., Terry, A. M., Burford, F. R. L., Peake, T. M., & Dabelsteen, T. (1999). Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. *Proceedings of the Royal Society, B, 266,* 1305–1310.

Peake, T. M. (2005). Eavesdropping in communication networks. In P. K. McGregor (Ed.), *Animal communication networks* (pp. 13–37). Cambridge, United Kingdom: Cambridge University Press.

Schwartz, J. J. (2001). Call monitoring and interactive playback systems in the study of acoustic interactions among male anurans. In M. J. Ryan (Ed.), *Anuran communication.* (pp. 183–204). Washington, DC: Smithsonian Institution Press.

Schwartz, J. J., Ressel, S., & Bevier, C. R. (1995). Carbohydrate and calling: Depletion of muscle glycogen and the chorusing dynamics of the neotropical treefrog *Hyla microcephala. Behavioral Ecology and Sociobiology, 37,* 125–135.

Schwartz, J. J., & Wells, K. D. (1983a). An experimental study of acoustic interference between two species of neotropical treefrogs. *Animal Behaviour, 31,* 181–190.

Schwartz, J. J., & Wells, K. D. (1983b). The influence of background noise on the behavior of a neotropical treefrog, *Hyla ebraccata. Herpetologica, 39,* 121–129.

Snowdon, C. T., & de la Torre, S. (2002). Multiple environmental contexts and communication in pygmy marmosets (*Cebuella pygmaea*). *Journal of Comparative Psychology, 116,* 182–188.

Wells, K. D. (2007). *The ecology and behavior of amphibians.* Chicago: University of Chicago Press.

West, M. J., King, A. P., & Freeberg, T. M. (1996). Social malleability in cowbirds: New measures reveal new evidence of plasticity in the eastern subspecies (*Molothrus ater ater*). *Journal of Comparative Psychology, 110,* 15–26.

Wittig, R. M., Crockford, C., Wikberg, E., Seyfarth, R. M., & Cheney, D. L. (2007). Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proceedings of the Royal Society, B,* 1109–1115.

Wollerman, L., & Wiley, R. H. (2002). Background noise from a natural chorus alters female discrimination of male calls in a Neotropical frog. *Animal Behaviour, 63,* 15–22.

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