SYNOPSIS III

Complexities in vocal communication

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Overview

The vocal systems of Parids are among the most complex communicative systems documented in the avian world. Part of this complexity stems from the large number of acoustically and functionally distinct vocal signals, each of which has its own acoustic and functional diversity (Ficken *et al*. 1978; Hailman and Ficken 1996; Chapter 13). Because of the vocal complexity of most, if not all Parids, this group could be a model system for understanding how social and physical environmental pressures might drive variation in signaling systems. In this synopsis, we briefly review some of the major advances that have been made in understanding the vocal systems of chickadees and related species and then draw comparisons to vocal systems in Parids outside North America. Our primary focus, however, is to delineate questions that need to be addressed if we hope to answer perhaps the most fundamental question about this vocal complexity; namely, why does it exist in this group?

Vocal complexity of chickadees and titmice

Beginning with the seminal work of Ficken *et al*. (1978) on the vocalizations of black-capped chickadees, we have made significant advances in understanding vocal communication in a number of chickadee species. Much of this work is described in the chapters in this section of the book. Research on *fee-bee* vocalizations shows the extent of species-level information (Chapter 12), elucidates the causes and functions of absolute and relative pitch changes (Chapters 10 and 14), and demonstrates significant geographic variation (Chapter 12). We are starting to understand the “syntax” of gargles and the nature and functions of local sharing and social transmission of *gargle* types (Chapter 11). We continue to decode the information conveyed in *chick-a-dee* calls, from messages and meanings of different note types to different markers of identity that reside in acoustic parameters—individual, population, and species (Chapters 10 and 13).

As the chapters in this section attest, the vocalizations of chickadees and titmice offer an exciting and rich comparative system with which to address questions of mechanisms, development, function, and phylogeny of vocal behavior (e.g. Tinbergen 1963). Of these four “why” questions for behavior, we know much more about the function question than the other three, so clearly one of our general aims should be to gain greater understanding of mechanistic, ontogenetic, and phylogenetic influences on Parid vocal communication.

The "song versus call" distinction and social complexity

One intriguing feature of the vocal systems of North American Parids is the seemingly reversed structure–function relationship of their songs and calls (also intriguing is the fact that the major vocalizations of many European Parids do seem to fit into the typical "song/call" distinctions). As described recently by Marler (2004, p. 132): "songs are usually longer and more complex acoustically, involving a variety of different notes and syllables, ordered in statistically reliable sequences; calls are often short, monosyllabic, with simple frequency patterning, often delivered in what often appears to be a disorderly fashion. Functionally, whereas songs play a somewhat restricted role, in territory establishment and maintenance, and mate attraction, the functions of calls include not only reproduction, but also predator alarm, the announcement and exchange of food, and the maintenance of social proximity and group composition and integration."

Whereas the *fee-bee* song and *chick-a-dee* call obey the functional criteria outlined in the quote above, the structural characteristics of these two vocal signals are quite reversed, with *fee-bees* being, acoustically, relatively simple and *chick-a-dee* calls variable and diverse (but its combinatorial nature is by no means disorderly). The *gargle* is similarly difficult to fit into this traditional song–call framework, as it is structurally complex like the *chick-a-dee* call (though more stereotyped and not as combinatorial), but appears to be used in fewer social contexts than the *chick-a-dee* call. The *gargle* shares a functional characteristic with the *chick-a-dee* call that makes them different from *fee-bees*—*gargles* and *chick-a-dees* are used year-round (feature of calls), whereas *fee-bees* are used almost exclusively in pairing and breeding (feature of songs). Furthermore, songs in oscine passerines are usually characterized as being learned, and calls as being unlearned (e.g. Catchpole and Slater 1999). Research has found evidence of vocal learning for all three vocal signals: *fee-bees* (Shackleton and Ratcliffe 1993; Kroodsma *et al*. 1995), *gargles* (Ficken and Popp 1995), and *chick-a-dees* (Hughes *et al*. 1998).

Why do these species seem to defy the more typical song–call structure–function characteristics followed by most passerines? We do not know, but we suggest the following possibilities. First, *gargle* and *chick-a-dee* calls can convey individual, population, and species identity (e.g. Ficken and Popp 1995; Chapter 10), so perhaps this has taken pressure off *fee-bees* to solely encode this information, resulting in structurally simpler signals. Alternatively, perhaps "song" is more complex than we have realized. For example, complexity in the *fee-bee* vocalization may occur in different dimensions than is typical of other passerines (e.g. frequency shifting—Chapter 14). The complexity of the *fee-bee* vocalization could also be augmented by the addition of other vocal signals, particularly *gargles*, to song displays. Another possibility is that the complex social structure of many chickadee species (Chapter 9) may have generated selection pressure for greater complexity in their year-round social signals (*chick-a-dees* and *gargles*) than would otherwise be the case.

The complexity in the vocal repertoire of chickadees and titmice seems to exist for the purpose of conveying different kinds of information, and not as a result of selection for diversity *per se*, as in the case of sexual selection for larger song repertoires in male northern mockingbirds, *Mimus polyglottos* (Howard 1974). Might the vocal complexity be driven by social complexity? Recent findings indicate that chickadees in larger (and presumably therefore more complex) social groups produce *chick-a-dee* calls that contain greater information than chickadees in smaller social groups (Freeberg 2006). Further support for this hypothesis is the fact that other groups with complex social structures, such as the Corvidae (jays, crows, and magpies) and Psittaciforms (parrots), often seem to show considerable complexity in their vocal repertoires (e.g. Brown and Farabaugh 1997; Bradbury 2003).

One major unanswered question circles back to the title of this book and how little we actually know about titmouse vocal behavior. Titmouse vocal repertoires seem to be comparable to chickadee vocal repertoires in terms of the diversity of vocal types that occur and the functions they likely serve (Gaddis 1979; Hailman 1989). However, titmice have been severely understudied relative to chickadees for virtually all aspects of their vocal behavior. Of the small number of studies on titmouse vocal behavior, most have addressed the song and what social contexts promote singing behavior (Gaddis 1983; Johnson 1987; Schroeder and Wiley 1983; Duguay and Ritchison 1998). Do titmouse signals, like those of the chickadees that have been studied, fall with difficulty into the traditional song–call distinctions? Finally, vocal behavior of the true tits (Paridae) has been studied much more extensively than that of the penduline tits (Remizidae). One of our major aims should therefore be to increase our understanding of the vocal systems of these under-studied groups, a point to which we return later.

Methodological advances

We know much more about the vocal systems of chickadees and titmice, and of songbirds in general, than we do about their visual (or other) display systems. The primary reason is that it has been far easier to record, analyze, and manipulate sounds produced by birds in the laboratory and field than it has been to conduct studies of other signaling systems, largely due to the availability of portable recording and playback equipment (e.g. Baptista and Gaunt 1994). Video and other methods of visual analysis (e.g. measuring UV) are becoming more accessible and providing some exciting avenues of research (see Chapter 2) , but have yet to catch up to the decades of research on vocal behavior in tits. Playbacks of vocal signals have a long history in studies of birds in field and laboratory settings (McGregor 1992). Various methodological advances are aiding our ability to understand the behavior of receivers and signalers with respect to vocal communication. For example, the recent development of interactive playback designs has revealed behavioral outcomes that might not otherwise have been obtainable. These developments include work on black-capped chickadees and great tits (reviewed in Chapter 14). Other methodological advances, such as multi-channel real-time spectrogram capabilities and multimicrophone recording arrays are allowing for very detailed information about multiple signalers interacting over time and space (Bower and Clark 2005; Burt and Vehrencamp 2005). As our thinking about communication extends from a sender → signal → receiver framework to that of senders and receivers interacting in complex communication networks, our understanding of the real-world causes and consequences of vocal signaling in these species will continue to grow (McGregor 2005).

Within chickadees, there has perhaps also been a bias against investigations of visual signals by the apparent lack of sexual dimorphism in coloration patterns. However, increased understanding of UV perception in birds and techniques for measuring these cues has resulted in recent work showing previously unsuspected variation in plumage brightness in chickadees (Mennill *et al*. 2003). Not only does variation in plumage brightness appear to convey information about male rank and reproductive success (Doucet *et al*. 2005), but females appear to be able to assess male social standing on these visual cues in the absence of witnessing dominance interactions, and apparently in the absence of other vocal signals (Woodcock *et al*. 2005). Clearly, visual signaling in chickadees is an avenue for future research.

What is to be done?

We end this synopsis by raising some additional questions we need to pursue in vocal communication in Parids. We also try to link our understanding of North American Parids to some of the work that has been conducted with species outside North America.

Previous research in Parids has demonstrated a severe geographic and taxonomic bias. Phylogenetic relationships of Parids are being clarified, but in terms of gaining understanding of vocal system evolution, we have a long way to go because vocal repertoires of so few of the species have been adequately documented (see also Hailman and Ficken 1996). We have minimal information on dawn chorus behavior, on types of vocalizations and their contexts of use, and on the relationship between vocal signaling and mating behavior in most of the Paridae—for example, much of the “Voice” descriptions for Paridae species provided in Harrap and Quinn (1995) are taken from field guides and not from primary science articles devoted to addressing vocalizations for a given species. To cite a couple of examples, we know almost nothing about the vocal behavior of the penduline, black, and grey tits in Africa. The one example documented thus far of commonly occurring syntactic permutation in the *chick-a-dee* call (thus perhaps approaching more closely the human language notion of syntax) exists in the call of the black-lored tit, *Parus xanthogenys*, of India (Hailman 1994). However, very little is known about the vocal behavior of the other *Parus* genus members in India and east Asia (though much more is known about the European member of this genus, the great tit). In North America, we know relatively little about the vocal behavior of the brown-capped chickadee group—the Siberian tit and the chestnut-backed and boreal chickadees.

From recent work with interactive playbacks, it is clear that how a chickadee's signals are perceived is not just dependent upon what it signals but also how and when it signals. This raises the need for us to study countersinging and countercalling in these species. How does assessment of senders occur in species such as chestnut-backed chickadees that seem to lack long-range signals, or in species that rely more on the shorter-range *gargles* in their dawn choruses? Recent work indicates that environmental noise impacts frequency characteristics of song in great tits (Slabbekoorn and Peet 2003); do background noises also impact the shorter-range *gargles* and *chick-a-dee* calls?

Within even the well-studied chickadee species, numerous questions remain to be answered. For example are pitch-shifted versions of *fee-bees* perceived as being distinct from one another by receivers? How are intermediate pitch shifts perceived? In the *chick-a-dee call*, the C and D notes seem to have been most studied—what roles do the A and B notes play in communication? In the *gargle*, do patterns of geographic variation and local sharing occur in species other than black-capped chickadees, and do these other species follow the same "rules" for constructing gargles?

Earlier we raised the difficulty of placing the *fee-bee*, *gargle*, and *chick-a-dee* neatly into "song" or "call" bins. An exciting prospect that stems from these different vocal signals is to understand the neural underpinnings of the behaviors. For example, are the neural circuits for vocal development and production the same for the three signals? Decades of work have clarified the neural substrates for bird song (Nottebohm 1999), but only recently have neural influences on calls in songbirds been addressed (Vicario *et al*. 2002). Neural regions underlying signals used seasonally would likely themselves show seasonal changes (for example brain regions underlying spatial memory change seasonally with respect to the time periods of reliance on cached food items in these species; Chapters 2, 3, and 4). Very interestingly, recent work with black-capped chickadees found no seasonal changes in nuclei of the song system despite seasonal changes in song structure (Smulders *et al*. 2006). Seasonal influences in song system nuclei have been documented in blue tits (Caro *et al*. 2005), but the extent to which these neural changes may differentially influence singing and calling behavior is not known. Gene expression patterns in the brain may help our understanding of vocal variation in these species, particularly if calls induce such patterns in different ways in the brain relative to songs (e.g. Mello 2002). Chickadees, tits, and titmice would thus seem to offer a powerful experimental system with which to address neurophysiological questions related to vocal signaling, learning, and seasonal changes.

We have learned an enormous amount of information about the vocal complexity of chickadees in the past three decades. The richness and variation in the vocal and social behavior of these species is such that they likely represent an ideal system for tackling important questions about ecological and evolutionary influences on vocal communication. Still, it is important to take a cautious view about how much we really do understand about Parid vocal complexity—we will likely need all the conceptual and methodological advances at our disposal to gain a firm hold of this daunting system. We have learned enough at this point, however, to feel confident in arguing that the payoffs of continued efforts to integrate proximate and ultimate approaches to understanding this complex system of vocal behavior could be quite large indeed.

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