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Group Size and Social Interactions Are Associated With Calling Behavior in Carolina Chickadees (*Poecile carolinensis*)

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The complexity of a social group may influence the vocal behavior of group members. Recent evidence in Carolina chickadees, *Poecile carolinensis*, indicated that one component of social complexity, group size, influenced the complexity of the "chick-a-dee" call, a vocalization functioning in social cohesion. Individuals in larger social groups used calls with greater information than did individuals in smaller social groups. Here, the authors review this earlier work, and describe a recent study indicating that social interactions between females and males within female-male pairs of chickadees were associated with rates of chick-a-dee call production in the males. Together, these studies suggest that the nature and complexity of social interactions among members of chickadee social groups influence chick-a-dee calling behavior.

Keywords: social complexity, social interaction, chick-a-dee call, information, Carolina chickadee

Variation in the vocal signals of avian species can be influenced by sexual selection and by characteristics of the physical habitat (reviews in Catchpole & Slater, 1995; Kroodsma & Miller, 1982, 1996). It has become apparent that characteristics of the social group of which an individual is part can influence the vocal signals it uses (Catchpole & Slater, 1995; McGregor, 2005). This "social selection" pressure is an exciting hypothesis on which to frame tests of variation in vocal communication systems for at least two main reasons. First, within avian genera (or within species), different species (or populations) can vary substantially in patterns of social organization, thus providing for strong comparative tests. Second, recent hypotheses argue that, as the social complexity of a group increases, there is a need for individuals to have increased cognitive processing abilities (e.g., the Machiavellian Intelligence Hypothesis: Byrne & Whiten, 1988; Shettleworth, 1998). One extension of the Machiavellian Intelligence Hypothesis is that increased social complexity within animal groups demands greater communicative complexity—individuals in larger and more complex groups need to be able to produce a greater diversity of messages. Several studies have obtained comparative evidence indicating that more complex social groups tend to have greater vocal complexity (e.g., Blumstein & Armitage, 1997; McComb & Semple, 2005). Recent experimental support for this idea has emerged in Carolina chickadees, *Poecile carolinensis* (Freeberg, 2006; described in more detail below), an avian species with a large vocal repertoire and complex social organization (Ekman, 1989; Mostrom, Curry, & Lohr, 2002).

One of the most commonly used vocalizations in the repertoire of chickadees is the "chick-a-dee" call. The chick-a-dee call of the avian genus *Poecile* is produced in a variety of social contexts related to group cohesion, as individuals move through their territories and may be out of visual contact with one another for periods of time (Ficken, Ficken, & Witkin, 1978; Hailman, 1989; Smith, 1991; Smith, 1972). The most extensive work on chick-a-dee call structure has been conducted with black-capped chickadees, *P. atricapillus*. The call in this species comprises four distinct note types (arbitrarily defined as A, B, C, and D notes) that may be produced a varied number of times within any given call and that follow a general A-B-C-D rule of note ordering (Charrier, Bloomfield, & Sturdy, 2004; Hailman, Ficken, & Ficken, 1985, 1987). The chick-a-dee call in Carolina chickadees, *P. carolinensis*, the focal species of the current studies, is structurally similar to that of black-capped chickadees, but appears to have a greater number of distinct note types (Bloomfield, Phillmore, Weisman, & Sturdy, 2005). The different note types can be present or absent in any given call and, if present, can occur more than once, following general rules of note ordering (Figure 1; Bloomfield et al., 2005; Lucas & Freeberg, 2007).

It has been suggested that chick-a-dee calls differing in note composition could convey different messages to receivers (Hailman & Ficken, 1986; Hailman et al., 1985). Studies are providing increasing evidence to support this suggestion. For example, in a study of captive black-capped chickadees, Templeton, Greene, and Davis (2005) found that when individuals detected smaller, quicker, and therefore more threatening avian predators, they called more and their calls had a greater number of D notes,

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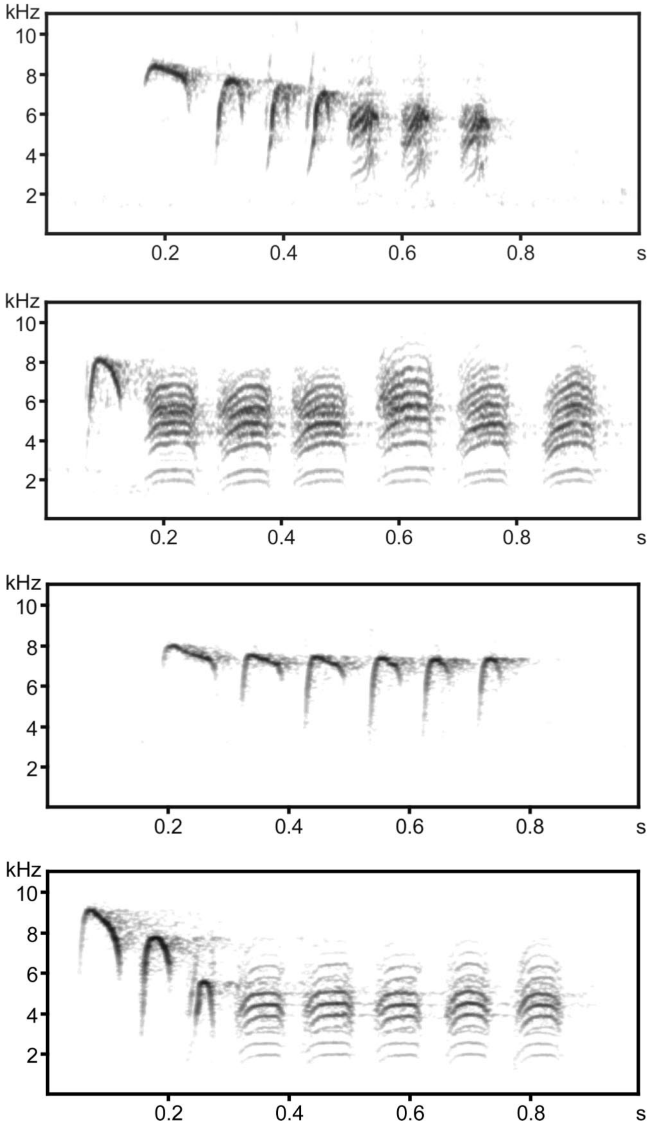

Figure 1. Sound spectrograms of chick-a-dee calls of Carolina chickadees, illustrating some of the diversity in note composition. In each panel, the Y-axis measures frequency (0 – 11 kHz) and the X-axis measures time (0 – roughly 1 sec). Sound spectrograms were generated using Avisoft SASLab Pro with an FFT length of 512, frame 75%, and Blackman window.

compared to when individuals detected larger, less agile, and therefore less threatening avian predators. In addition, playbacks of chick-a-dee calls differing in numbers of D notes produced mobbing-like behavior in receivers that was predictive of predator size. Thus, calls differing in note composition may provide information about urgency or immediacy of threat (see also Baker & Becker, 2002). Further support for the notion that calls with different note composition may convey different messages has been obtained in Mexican chickadees, *P. sclateri* (Ficken, Hailman, & Hailman, 1994) and in Carolina chickadees, *P. carolinensis* (Freeberg & Lucas, 2002). These findings increasingly support the arguments of Hailman et al. (1985), that the structural rules governing the way chick-a-dee calls are produced result in a call system that can transmit a very large amount of information (see also Lucas & Freeberg, 2007; Sturdy, Bloomfield, Charrier, & Lee, 2007).

Is this large amount of information in the chick-a-dee call somehow related to the fact that chickadees (and related species) have a complex social organization? Many of these species form overwintering flocks, often of unrelated individuals, that are fairly stable (Ekman, 1989). Flocks persist for months, and flock members jointly defend their territory from other flocks. Perhaps this social complexity has generated a need for greater vocal complexity, and part of that vocal complexity is packaged into the chick-a-dee call. Here, we provide two lines of evidence to suggest this may be the case.

The remainder of this article is broken into three parts. First, we briefly review the Freeberg (2006) study mentioned above. That study indicated that individuals in larger groups used more diverse calling behavior than individuals in smaller groups. However, the Freeberg study did not provide information on the nature of social interactions in the groups that were tested. We next describe a recent study conducted with 14 female-male pairs in captive laboratory settings that began to address social interactions. In this study, we asked whether close spatial associations between the female and male of a pair, which provide a context for close-proximity interactions between those two individuals, were associated with rates of calling in the males of these pairs. If so, it would suggest that not only call structure, but also call use, may be influenced by the nature of interactions among chickadees in stable social groups. The final part of the article briefly raises some questions that we need to answer in chickadees, as well as in other species, to determine the ways in which social interactions within stable social groups may developmentally and evolutionarily constrain the structure and complexity of vocal signals of group members.

Group Size Influences Vocal Complexity: A Review

Freeberg (2006) addressed the question of a relationship between group size and chick-a-dee call complexity in two studies. The first study was conducted with nonmanipulated groups of chickadees in field settings in the winter and early spring of 2003. The second study took an experimental approach, in which a number of individuals were manipulated in captive groups of chickadees tested from Fall 2004 through Spring 2005. Both studies are described briefly here; see Freeberg (2006) for more detail.

In the first study, chickadees (*Poecile carolinensis*) were recorded at 30 different sites. Each recording site was at least 400 m from the next closest site. This distance helped ensure that birds from different sites were from different flocks. Recording involved approaching a group of chickadees to roughly 10–20 m to obtain high-quality calls, but also to avoid disrupting normal behavior patterns. At the time of recording, Freeberg noted the total number of individuals observable within a 10 m × 10 m recording space. Sites were classified into “small groups” (19 sites) if most of the calls from the site were recorded when only one or two birds were in that recording space; and “large groups” (11 sites) if most of the calls from the site were recorded when three or more birds were in that recording space.

Over 4100 calls were obtained ($M = 138.4$ calls/site; range = 58 – 272). Notes of calls were classified according to the nine note categories published for the species by Bloomfield et al. (2005). Freeberg analyzed the note compositions of all the calls for each site using the UNCERT program (written by E.D. Hailman and J. P. Hailman; Hailman et al., 1985). UNCERT generated uncertainty measures (bits of information) for the set of calls for each site. Here we report data on first-order uncertainty (U_1), which is calculated as $U_1 = -\Sigma\ [P_{ij} \log_2 (P_{j|i})]$, where P_{ij} is the probability of the i and j note occurring in the ij sequence, and $P_{j|i}$ is the conditional probability of the j unit occurring given that the i unit has occurred. U_1 therefore assesses the uncertainty in these calls due to the transitional probabilities between ordered pairs of notes. Maximum first-order uncertainty would occur in a call system in which all note types were equally likely to follow one another. (In the case of a call system with eight units, such as the chick-a-dee call of Carolina chickadees, maximum uncertainty would be 3.0 bits of information. Typically U_1 in nonhuman animal vocal signals is much lower than the maximum possible uncertainty, as the presence of one unit is often highly predictive of the next unit in a signal.) Greater uncertainty represents greater diversity of note compositions and of *potential* messages in calls being produced by the birds.

Calls obtained from birds at the "large group" sites had greater uncertainty (greater complexity) than calls obtained from birds at the "small group" sites. See Figure 2a; mean ± *SD* of 0.81 ± 0.20 bits for "large group" calls and 0.62 ± 0.17 bits for "small group" calls; $F(1, 28) = 7.15$, $p = .012$. These uncertainty measures were not correlated with the number of calls obtained at each site (Spearman rank-order correlation, $N = 30$, $r_s = .121$, $p = .526$). Calls recorded in "large groups" did not differ from calls recorded in "small groups" in terms of the number of calls recorded, $F(1, 28) = 0.252$, $p = .620$, or the average number of notes per call, $F(1, 28) = 0.088$, $p = .769$.

The first study suggested that when birds interact in larger groups, they tend to use chick-a-dee calls with greater diversity of note compositions, compared to birds producing calls by themselves or when they are interacting closely with only one other individual. The findings of this first study suggest a potential relationship between group size and call complexity, but no causal inference could be made. In the second study, conducted in outdoor aviaries, Freeberg (2006) manipulated group size to determine its effect on the complexity of calls used by individuals interacting in these groups.

Typical Carolina chickadee flock sizes are roughly 3 – 5 birds (range 2 – 8; reviewed in Mostrom et al., 2002). Freeberg established groups that spanned these flock sizes in two large aviaries (6 m × 9 m × 3.5 m). Groups of size 2, 4, and 6 were generated at different times from late fall of 2004 though early spring of 2005. Each group was made up of chickadees captured from the same site and closely in time on the same day. Due to the stability and territoriality of chickadee flocks, this capture method helps ensure that each group comprised individuals from the same flock (Mostrom et al., 2002). Sex of individuals was balanced as much as possible within each group, to mimic the 1:1 ratio of females and males in natural flocks (Mostrom et al., 2002). Sex was determined based on wing chord measurements: birds with wing chords ≤ 60 mm were classified as females, and birds with wing chords ≥ 62 mm were classified as males (based on Thirakhupt, 1985). Birds were uniquely color-banded to permit individual identification in the aviaries. After being placed into the aviaries, birds in the different groups were given roughly 3 weeks to acclimate to their new setting and social context, and then were recorded.

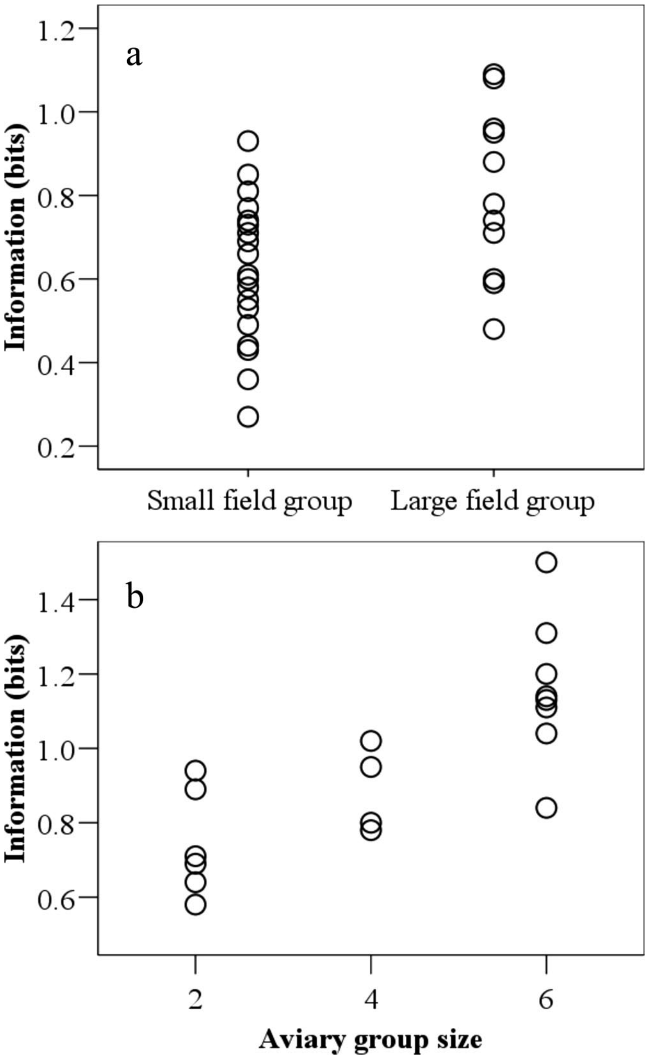

Figure 2. Information in chick-a-dee calls of birds of different group sizes; redrawn from Freeberg (2006). A. Each circle represents the uncertainty value of calls produced at a single site, with sites classified as either "small groups" or "large groups." B. Each circle represents the uncertainty value for the calls of each individual in the three different group sizes. The measure of complexity here is First-Order Uncertainty, which represents the uncertainty associated with transition probabilities between consecutive pairs of notes in a call. As this measure of uncertainty increases, calls have greater diversity of note pairings. Some birds in the aviary study did not produce enough calls to be included in the analysis, thus were not plotted.

Over 1300 calls were obtained ($M = 73.4$ calls/individual; range = 10 – 248). As described above, notes of calls of each individual were classified according to the note categories of Bloomfield et al. (2005). The note compositions of the call set for each individual were analyzed using UNCERT, such that each individual had its own uncertainty measure that went into the statistical analyses. As in the field study reviewed above, group size had a significant effect on call complexity. In the aviaries, individuals placed into larger groups were using calls with greater uncertainty than birds placed into smaller groups. See Figure 2b; mean ± *SD* of 1.16 ± 0.19 bits for calls of birds of group size 6, 0.89 ± 0.12 bits for calls of birds of group size 4, and 0.74 ± 0.14 bits for calls of birds of group size 2; $F(2, 15) = 11.61$, $p = .001$. These uncertainty measures were not correlated with the number of calls obtained from each bird (Spearman rank-order correlation, $N = 18$, $r_s = -.027$, $p = .916$).

Findings from Freeberg (2006) indicated that birds in larger groups were using calls with more complexity than birds in smaller groups, in both nonmanipulated field settings and in experimental captive settings. Group size is one of the major components of social complexity (though there are other important considerations, as described further below). Larger groups, simply by having greater numbers of individuals, provide for the possibility of more diversity and complexity of social interactions among their members, relative to smaller groups. The Freeberg study did not collect information on actual interactions among members of a group; therefore, the relationship between social interactions and calling behavior could not be determined. We began to address this question with a study of the most basic social group in chickadees: a female-male pair.

Social Associations Correlate With Chick-a-dee Call Production

For this next study, 28 wild-caught adult male ($N = 14$) and female ($N = 14$) Carolina chickadees (*Poecile carolinensis*) were captured from one of two locations in eastern Tennessee. The study was conducted over a 2-year period, during the overwintering months when chickadees normally reside in flocks (six pairs tested between fall of 2004 and spring of 2005 and eight pairs tested between winter of 2005 and spring of 2006). One female and one male chickadee from a particular site were captured together at one of these locations. Just as in the Freeberg (2006) study reviewed above, female-male pairs were captured from the same site and closely in time on the same day, and so very likely were members of the same flock, if not actual mating pairs. In total, we had 14 female-male pairs. At time of capture, we uniquely color-banded birds for individual identification and measured their wing chords (mm) to determine sex.

In the laboratory, female-male pairs were housed in MED-Associates Large Monkey Cubicles; different pairs were isolated from one another. Cages (0.5 m × 0.5 m × 1 m) within these cubicles were supplied with three natural perches (two near the top of the cage and one near the floor of the cage). Daily maintenance included providing the chickadees with ad libitum food (an equal mixture of black oil sunflower and safflower seeds, crumbled suet, and grit with crushed oyster shell). Fresh Bronx Zoo diet for omnivorous birds mixed with sprouted seed, chopped fresh fruit and vegetables, and 3–4 mealworms were supplied daily. Fresh vitaminized water was also given to the pairs on a daily basis. The lights were maintained on a light:dark cycle that was changed weekly to match sunrise/sunset times of the local environment.

After capture and transport to the laboratory, all pairs were provided with a 3-week acclimation period, allowing the birds to adjust to the new surroundings. After this acclimation period, we observed the birds for two weeks. During this 2-week period, we focal sampled each male with its cage mate for eight 15-min observation sessions. During observations, the researcher sat in front of the chamber with the door closed in a darkened laboratory room. Observations began at least 30 min after the chamber lights automatically turned on in the morning and were completed by 1400 hours. The primary measures collected for the purposes of this study were instances of perching close (female and male situated within 15 cm of one another for at least 2 sec), supplants (an agonistic behavior between two individuals in which one bird, usually arriving via flight, takes the spot on a perch occupied by the other bird, causing the other bird to leave), and numbers of chick-a-dee calls produced (for more detail see Harvey & Freeberg, 2007).

We found that males who displayed greater rates of perching close to their female flockmates also produced higher rates of chick-a-dee calling (Figure 3; Spearman rank-order correlation, $N = 14$, $r_s = .641$, $p = .014$). Calling behavior did not occur systematically with close perching behavior during the sampling (perching close to a female did not automatically result in directing a chick-a-dee call to a female, or vice versa), however. Supplants were negatively correlated with rates of chick-a-dee calling, though the correlation was not statistically significant (Spearman rank-order correlation, $N = 14$, $r_s = -.336$, $p = .241$). These results indicate a relationship between extent of perching close with a female flockmate (which likely provides an important context for close-proximity social interaction) and extent of vocal signaling by these males. Although we must be cautious in extrapolating from the dyadic interactions here to the more complex social relationships in flocks, the results suggest that production of chick-a-dee calls, an important mechanism of social cohesion in flocks (Ficken et al., 1978), may be linked to the nature of the signaler's social relationships.

General Discussion

The two sets of studies point to the important role the chickadee social group can play on the vocal signals used by group members.

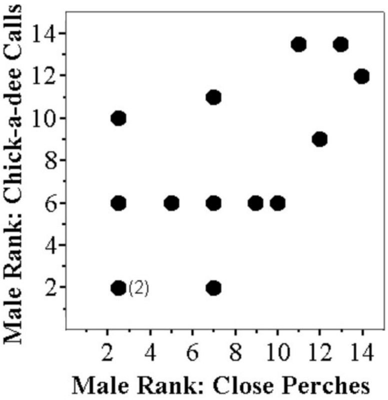

Figure 3. Association between ranks for close perching and ranks for chick-a-dee call production for the 14 males housed individually with females from their social flock. Each point represents an individual male. The (2) near the lower left hand point in the graph refers to two males who had scores of 0.0 times perched close to their respective female social companion and 0.0 chick-a-dee calls produced.

First, the Freeberg (2006) study we reviewed indicated that group size can influence the complexity (diversity of note compositions, and potentially of messages) of chick-a-dee calls produced by Carolina chickadees. Birds in larger groups produced calls with greater complexity. One potential explanation for this is that the manipulation of group size affected the frequency of social interactions and the overall group behavior, and as group size increased individuals needed to be able to produce a greater number of different messages with their chick-a-dee calls. Second, the study focusing on female-male pairs of chickadees found a positive correlation between rates of close associations between the female and male of a pair and rates of chick-a-dee call production by the male of the pair. Although not entirely surprising, given the general social function of the chick-a-dee call, this latter finding is important in that it is our first evidence in this species to suggest that social interactions are associated with the chick-a-dee call. Ongoing work in our laboratory is testing this association in larger social groups.

Understanding how the nature of social groups may influence the complexity of vocal signals used by group members has been an aim of recent comparative research efforts. For example, Wilkinson (2003) compared eight bat species and found that information in the isolation calls of infant bats was greater for species occurring in larger rather than smaller colonies. Presumably these species differences stem from an increased need for individual distinctiveness in infant isolation calls for species residing in larger colonies—greater information in these calls stems from greater variation in acoustic features across infant bats. McComb and Semple (2005) found that vocal repertoire size was strongly associated with group size in a large comparative study of nonhuman primates: species having groups with greater numbers of individuals had larger vocal repertoires than did species in which group sizes were smaller. In the first explicit test of a relationship between social complexity and vocal complexity, Blumstein and Armitage (1997) found evidence for such a relationship in ground-dwelling sciurid species: groups of marmot and squirrel species utilizing more unique social roles had a greater number of distinct alarm calls in their vocal repertoires, relative to species with groups having fewer social roles. The studies done to date have provided strong comparative evidence in support of the hypothesis of social complexity driving vocal complexity.

The studies described in the previous paragraph took evolutionary approaches to address the relationship between social and vocal complexity. The Freeberg (2006) study reviewed above took a developmental approach and provided experimental evidence for social complexity playing a causal role in vocal complexity in chickadees. The social organization of chickadees and related species offers a strong system to test questions of both proximate and ultimate causation in vocal complexity-similar arguments could be made for other avian groups with complex social structures, such as the corvids (Marzluff & Angell, 2005), jays (Dahlin, Balda, & Slobodchikoff, 2005; Hopp, Jablonski, & Brown, 2001), and parrots (Farabaugh & Dooling, 1996; Wright & Wilkinson, 2001). Features of the social group in chickadees have an influence on fitness of group members (Ratcliffe, Mennill, & Schubert, 2007; Smith, 1991), and will also serve as an important learning environment for members of the group, perhaps particularly for young birds joining a flock for the first time. Increased focus on the dynamics of social interaction between members of stable groups would increase our ability to understand how social groups may constrain the vocal behavior of groups members (see King, West, & White, 2002; Miller, Freed-Brown, White, King, & West, 2006; see also Snowdon & Hausberger, 1997). Future work in our laboratory will aim to integrate proximate and ultimate approaches to understand the causal links between social and vocal complexity.

Much of the work that has been done to test the potential relationship between social and vocal complexity has relied on group size as the measure of social complexity. The Blumstein and Armitage (1997) study described above used a different measure of social complexity—the number of social roles in a group—raising an important point for future work on this question. Groups with a greater number of social roles (e.g., a species in which groups comprise reproductive females, reproductive males, adult nonreproductive males, adult nonreproductive females, juveniles, infants) are very likely to have a greater diversity of social relationships and social interactions than groups with a smaller number of social roles (e.g., a species in which groups comprise a reproductive female, a reproductive male, and their current set of offspring). Following from this approach, we believe increased effort should be devoted to assessing the nature and complexity of social interactions in groups to understand social pressures on vocal behavior better. We have taken the first step in this direction with chickadees, by demonstrating that a measure of social interaction—close spatial associations between two chickadees—correlates positively with rates of chick-a-dee call production.

In studying the complexity of social groups, we note that characteristics of specific individuals within a group have the potential to affect the dynamics of the larger group (Sih & Watters, 2005). For example, groups with a large proportion of "bold" individuals likely represent very different social structures than groups composed of a large proportion of "shy" individuals (Coleman & Wilson, 1998; Sih, Bell, Johnson, & Ziemba, 2004). We argue, then, that future research on social complexity and its possible link to communicative complexity should address the behavioral profiles of members within the groups of study. For example, Akert and Panter (1988) found that humans classified as extraverts (by standard psychological assessments of personality) were better able to interpret nonverbal communication of two people conversing than were humans classified as introverts. Akert and Panter argue that extraverts engage in a higher frequency of social interaction than introverts, and frequency of social interactions is directly related to an individual's ability to signal efficiently and respond effectively to signals from group members (see also Lieberman & Rosenthal, 2001; Mehrabian & Diamond, 1971; Patterson, 1995; Wiener, Devoe, Rubinow, & Geller, 1972). Lieberman and Rosenthal argue that extraverts do not hold a general advantage over introverts regarding signal decoding, but are better able to do so in contexts of multitasking, when many different kinds of information need to be processed simultaneously. This argument would seem of relevance to nonhuman animals engaged in communicative interactions while also needing to be able to detect key environmental stimuli (e.g., predators) and solve other problems facing them. In short, we believe greater focus on these "personality" influences in nonhuman animal groups would aid our understanding of how characteristics of groups may influence communication in group members.

Finally, we wish to begin to address the basic question of why the complexity of a social group might influence the complexity of vocal signals used by group members. Potential answers to this question will depend largely on the specific natural history of a given species. Here, we offer two potential explanations that are in good accordance with the natural social structures and problems faced by chickadees and related species. The first, a more individual-centered view, stems from the Assessment/Management approach to vocal communication put forward by Owings and Morton (1998). Put simply, to be successful, individuals need to regulate the behavior of others in their environments, and a primary way many species do this behavioral regulation is with vocal signals. Thus, a first potential answer to our question is that an individual in a larger group, that has to manage successfully and efficiently the behavior of members of its group, may need a greater variety of vocal signals in its repertoire to do so, compared to an individual in a smaller group with a smaller number of individuals to manage. The second, a more group-centered view, stems from the idea that larger groups often provide substantial benefits to group members (Krause & Ruxton, 2002; Wilson, 1975). To be successful, a larger group may need to solve more problems (maintaining group cohesion when finding food, defending food, detecting predators, deterring predators, exploiting other necessary resources, etc.), compared to smaller groups or to solitary individuals. Vocal communication provides one mechanism for this sort of problem solving faced by larger groups (Bradbury & Vehrencamp, 1998; Maynard Smith & Harper, 2003). To communicate effectively about more stimuli in the environment and about group responses to those stimuli, members of a larger group may require a greater diversity of vocal signals than members of a smaller group.

Much more work is needed to test these hypotheses, and clearly there are other hypotheses regarding the potential links between social and vocal complexity. For example, if individual distinctiveness in vocal behavior is important and groups are large, there should be strong selection pressure for substantial amounts of acoustic diversity across individuals, as seen in the Wilkinson (2003) study with bat species varying in colony size. We believe that testing these potential links is an important topic for future research, as it points to a potentially powerful explanation for vocal diversity across groups of related species, and how that diversity may also help explain other social behavior (e.g., McComb & Semple, 2005). Furthermore, the notion that greater social complexity may cause greater vocal complexity is at the heart of recent arguments about the origins of language in our own species (Dunbar, 1996, 2003; Pinker, 2003), so increased efforts at understanding these social—vocal complexity links may also help inform theories of language evolution.

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