Research Report

Social Complexity Can Drive Vocal Complexity

Group Size Influences Vocal Information in Carolina Chickadees

Todd M. Freeberg

University of Tennessee

ABSTRACT—*One hypothesis to explain variation in vocal communication in animal species is that the complexity of the social group influences the group's vocal complexity. This social-complexity hypothesis for communication is also central to recent arguments regarding the origins of human language, but experimental tests of the hypothesis are lacking. This study investigated whether group size, a fundamental component of social complexity, influences the complexity of a call functioning in the social organization of Carolina chickadees,* Poecile carolinensis. *In unmanipulated field settings, calls of individuals in larger groups had greater complexity (more information) than calls of individuals in smaller groups. In aviary settings manipulating group size, individuals in larger groups used calls with greater complexity than individuals in smaller groups. These results indicate that social complexity can influence communicative complexity in this species.*

Can the complexity of a social group drive the complexity of communicative signals used by members of the group? This social-complexity hypothesis is a major component in arguments regarding the origins of human language (Dunbar, 1998, 2003; Pinker, 2003) and may more generally explain variation in systems of vocal communication in animal species. Although some comparative and correlational evidence supports the hypothesis (Blumstein & Armitage, 1997; Maestripieri, 1999; McComb & Semple, 2005; Wilkinson, 2003), experimental tests are lacking. In the study reported here, I examined whether group size, a fundamental aspect of social complexity, affects the complexity of the chick-a-dee call, a major vocal signal of social cohesion in chickadee (*Poecile*) species (Freeberg & Lucas, 2002; Hailman & Ficken, 1996; Templeton, Greene, & Davis, 2005).

The social organization of chickadee species changes from a female and male pair defending its territory during the breeding season to two or more pairs of unrelated chickadees forming a flock and defending their territory from other such flocks in the fall and winter months (Ekman, 1989; Mostrom, Curry, & Lohr, 2002; Smith, 1991). Sociality brings a number of benefits to individuals (Krause & Ruxton, 2002), and social organization in many species is facilitated by vocal communication. In chickadees, the chick-a-dee call serves a number of social functions and is used year-round by both sexes. The chick-a-dee call comprises distinct note types that may be present and repeated in any given call (Fig. 1), and the rules for call construction generate an open-ended communication system with similarities to language (Hailman & Ficken, 1986; Hailman, Ficken, & Ficken, 1985). Unlike songs in most songbird species, in which individuals possess a relatively small number of distinct and stereotyped songs that remain largely unchanged once developed (Catchpole & Slater, 1995; Kroodsma, 2005; Marler & Slabbekoorn, 2004), the chick-a-dee calls of any given individual chickadee represent a flexible and inherently diverse communicative system. By varying the number of the different note types it produces in its calls, an individual chickadee could theoretically generate hundreds if not thousands of call types that are unique in their note composition (Hailman & Ficken, 1996; Hailman et al., 1985).

Call complexity in this study was measured in terms of uncertainty (bits of information), the diversity of potential messages conveyable by a signal system. Calculation of this measure was based on Shannon's mathematical theory of information (Garner, 1962; Hailman et al., 1985; Shannon & Weaver, 1949).

Address correspondence to Todd M. Freeberg, Department of Psychology, University of Tennessee, Knoxville, TN 37996, e-mail: tfreeber@utk.edu.
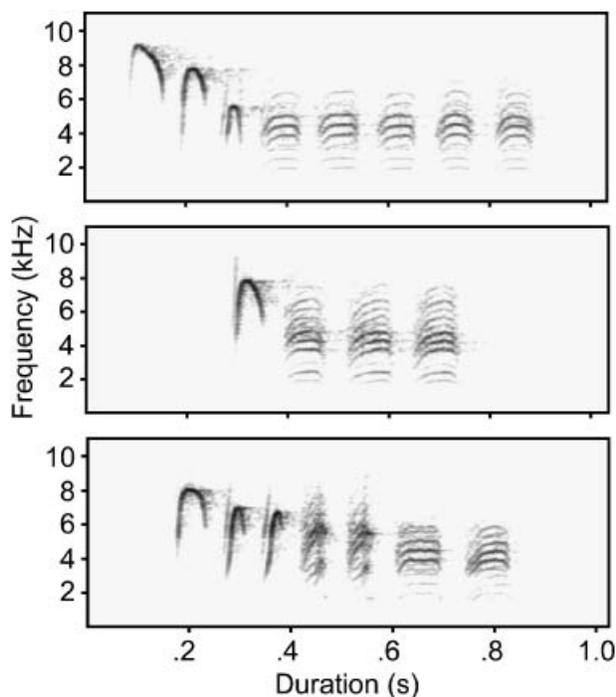
Volume 17—Number 7   557

Fig. 1. Sound spectrograms of chick-a-dee calls of Carolina chickadees illustrating some of the diversity in note types. The spectrograms were generated using Avisoft SASLab Pro (Specht, 2002), with a fast Fourier transform length of 512, a 75% frame, and a Blackman window. In all three spectrograms, the *y*-axis represents frequency (0–11 kHz), and the *x*-axis represents time.

I assessed two measures of chick-a-dee call complexity. One was based on the diversity and proportional frequency of different note types in calls, and the other was based on the diversity and proportional frequency of different pairs of consecutive note types in calls. I tested whether group size affected these complexity measures in chick-a-dee calls in both a field study and an experimental aviary study.

FIELD STUDY

Method

Chick-a-dee calls of Carolina chickadees were recorded at 30 sites at three locations in eastern Tennessee: Ijams Nature Center (3 sites); Norris Dam State Park (12 sites); and the University of Tennessee Forest Resources, Research, and Education Center (UTFRREC; 15 sites). Because birds were not uniquely color-banded or individually identifiable at these locations, I selected sites that were at least 400 m from each other, to help ensure independence of the sites. (Freeberg & Lucas, 2002, in an earlier study with a small number of uniquely color-banded birds, found a 250-m distance between adjacent recording sites to provide good independence.) Recordings at 10 additional sites were not analyzed for the present study as some calls at those sites were collected at feeding stations, and food contexts can affect note composition of calls and, potentially, call complexity (Freeberg & Lucas, 2002).

I recorded birds from January through March 2003, from 8:00 a.m. through 3:00 p.m. At the time of recording, I documented the maximum number of chickadees I could observe within a 10-m × 10-m recording space. For purposes of comparison, I categorized the sites by whether more than 50% of the calls were collected from chickadees when only 1 or 2 individuals were in that recording space (*small group*, 19 sites) or whether more than 50% of the calls were collected from chickadees when 3 or more different individuals were in that recording space (*large group*, 11 sites).

Calls were recorded with Sennheiser ME-66 microphones on Maxell XL-II tape with Marantz PMD-222 recorders. Recordings were digitized using Cool Edit Pro (Syntrillium Software, 2002) at a sample rate of 22,050 with 16-bit resolution. I classified call notes from the Spectral View (Blackman-Harris window, 256-band resolution) according to published note categories for the species (Bloomfield, Phillmore, Weisman, & Sturdy, 2005). A trained observer independently scored call notes for two randomly selected sites, and interobserver reliability was 88.1%.

The measures of uncertainty were obtained using the UNCERT program written by E.D. and J.P. Hailman (Hailman et al., 1985). Zero-order uncertainty is measured as $U_0 = -\Sigma[P_i \log_2(P_i)]$, where P_i is the probability of each of the i units occurring in the system. U_0 assesses the amount of information in a signaling system due to the number and proportional frequencies of units of that system. Maximum U_0 is achieved when all units in the signaling system are equally likely. First-order uncertainty is measured as $U_1 = -\Sigma[P_{ij} \log_2(P_{j|i})]$, where P_{ij} is the probability of the *i-j* sequence, and $P_{j|i}$ is the conditional probability of the j unit occurring given that the i unit has occurred. U_1 assesses the amount of information in a signaling system due to transition probabilities between units of the system. Maximum U_1 is achieved when all pairs of units in the signaling system are used with equal probability. In chick-a-dee calls, higher uncertainty indicates greater potential information (greater complexity) because of increased diversity of notes and note pairings.

U_0 and U_1 were measured for each of the 19 small-group and 11 large-group sites. I used general linear model analysis of variance (GLM ANOVA; SPSS Version 13.0) to determine whether field-group size had a significant effect on call uncertainties. Residuals were normally distributed. Neither site U_0 nor site U_1 was significantly correlated with the number of calls obtained per site.

Results and Discussion

I recorded 4,152 chick-a-dee calls from free-living Carolina chickadees at the 30 sites ($M = 138.4$ calls/site, $SD = 51.8$, range = 58–272). The calls obtained from birds interacting in large groups were more complex than the calls from birds in small groups (Fig. 2a), $F(1, 28) = 4.0$, $p_{rep} = .86$, $\eta^2 = .13$, for U_0; $F(1, 28) = 7.1$, $p_{rep} = .95$; $\eta^2 = .20$, for U_1.
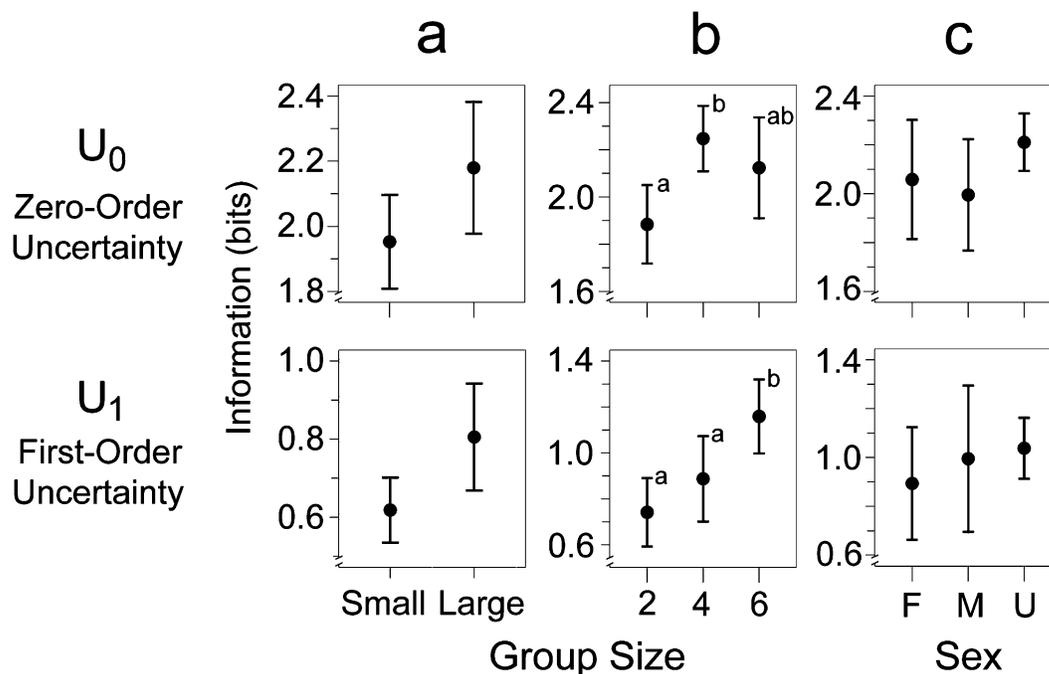
Fig. 2. Complexity (amount of information) of calls recorded in field and aviary settings. The graphs show means and 95% confidence intervals. In the field study (a), calls were recorded from free-living birds in flocks. In the small groups, more than 50% of the calls were recorded from chickadees when only 1 or 2 individuals were in the recording space, whereas in the large groups, more than 50% of the calls were recorded from chickadees when 3 or more individuals were in the recording space. In the aviary study (b, c), group size was manipulated. Results are plotted by group size (b) and sex of the individual (c). In (b), confidence intervals that do not share a letter are significantly different from one another. F = female; M = male; U = unknown.

The results from the field study indicate that when chickadees are in larger groups, their chick-a-dee calls contain greater complexity and presumably carry more information than when chickadees are in smaller groups. The next study addressed whether experimental manipulations of group size would influence the complexity of chick-a-dee calls.

AVIARY STUDY

Method

I created three sets of groups, each containing two different group sizes, in two outdoor aviaries (6.1 m × 9.1 m × 3.7 m) located at UTFRREC. The first set had one group of 2 birds and one group of 6 birds (November 2004), the second set had one group of 2 and one group of 4 birds (January 2005), and the third set had one group of 2 birds and one group of 6 birds (February 2005).

All birds within the same aviary group were captured from the same field site and presumably were from the same flock and had had considerable experience with one another. I attempted to balance the sexes within each group to mimic sex composition in natural flocks (Smith, 1991). Sex of birds was determined by wing chord measurements (Thirakhupt, 1985). Although chickadees are a highly monomorphic species, males tend to be slightly larger and tend to have longer wing chord measures

than females. Birds were banded with unique combinations of colored plastic leg rings for individual identification, were released into the aviary and given 3 weeks to adjust to captivity, and then were recorded. Aviary birds were provided with ad libitum sunflower seed, safflower seed, suet, grit, and crushed oyster shell; each bird was given one to two mealworms and fresh vitamin-treated water daily. Sennheiser ME-66 microphones were mounted atop microphone stands (2.5 m high) to record calls using Fostex FR-2 field memory recorders with sample rates of 22,050 and 16-bit resolution. The birds were released at their site of capture after all were recorded.

For each individual, I scored call notes on the basis of published note categories for the species (Bloomfield et al., 2005) and ran UNCERT on the calls. Each individual therefore had both a U_0 measure and a U_1 measure that went into the analysis. Birds from which I obtained fewer than five calls were not included (1 bird in the first group of size 6 and 3 birds in the second group of size 6). I used GLM ANOVA to determine whether aviary group size had a significant effect on call uncertainties and then conducted pair-wise comparisons of the three group sizes using a Bonferroni adjustment for multiple tests. I also tested whether the sex of the individual had an effect on its call complexity (the wing chord measure indicated there were 8 females, 6 males, and 4 birds of unknown sex in this analysis). Residuals were normally distributed. Neither

Social Complexity Can Drive Vocal Complexity

U_0 nor U_1 was correlated with the number of calls obtained from a bird.

Results and Discussion

I recorded and analyzed 1,322 calls ($M = 73.4$ calls/bird, $SD = 57.3$, range = 10–248). Group size had a significant effect on U_0 (Fig. 2b), $F(2, 15) = 4.43$, $p_{rep} = .91$, $\eta^2 = .37$. Specifically, birds in the group of size 4 had greater U_0 in their calls than did birds in groups of size 2. Group size also had a significant effect on U_1 (Fig. 2b), $F(2, 15) = 11.61$, $p_{rep} = .99$, $\eta^2 = .61$. Birds in groups of size 6 had greater U_1 in their calls than did birds in groups of sizes 2 and 4. Thus, birds in the larger groups produced chick-a-dee calls with greater information, and theoretically greater message diversity, than birds in the smaller groups.

I detected no effect of the sex of the bird on the complexity of its calls for either U_0 (Fig. 2c), $F(2, 15) = 1.01$, $p_{rep} = .57$, $\eta^2 = .12$, or U_1 (Fig. 2c; $F < 1$).

One way in which birds in the larger groups seem to have achieved greater uncertainties than birds in the smaller groups was by using proportionally fewer D notes (the concluding note type in the spectrograms of Fig. 1 and the most common note type in calls of many chickadee species), and therefore increasing slightly the proportional frequencies of rarer note types (median proportion of D notes was .499 for birds in groups of size 2, .300 for birds in groups of size 4, and .157 for birds in groups of size 6; Kruskal-Wallis ANOVA, $p_{rep} = .98$). For example, in the sound spectrograms of chick-a-dee calls in Figure 1, the bottom call, with its greater diversity of different note types and greater diversity of transitions between consecutive note types, would be most typical of calls produced by birds in the larger groups.

DISCUSSION

The current results provide the first experimental support for the social-complexity hypothesis for communication in animal species and may help inform hypotheses regarding language origins (e.g., Dunbar, 2003). Chickadees and related species have complex social structures in that they form overwintering flocks that are fairly stable in both space and time, and a key signal that functions to maintain flock cohesion is the chick-a-dee call (Ekman, 1989; Smith, 1991). Previous research has indicated that variation in the acoustical structure and composition of chick-a-dee calls can be associated with the signaler's species, population, flock, behavioral and motivational propensities, changes in physiology and arousal, and affective state, and may also be referential to external stimuli (Hailman & Ficken, 1996; Lucas & Freeberg, in press). The present work indicates that one basic component of chickadee social complexity, group size, affects the complexity of the chick-a-dee call. Birds in larger groups in field and laboratory settings used chick-a-dee calls with greater diversity of note types and note combinations, and thus were theoretically capable of transmitting a greater number of messages to receivers. The fact that the changes in call complexity in the aviary study occurred over the course of weeks indicates that call complexity in this species can be a facultative and fairly rapid response to the social context. Ongoing studies are testing the time course of changes in vocal complexity in individuals when their social context changes. More tests of relations between social dynamics and communication are now needed at the individual, population, and species levels to determine whether longer-term changes in social structure might serve as a selection pressure for vocal-system complexity.

REFERENCES

Bloomfield, L.L., Phillmore, L.S., Weisman, R.G., & Sturdy, C.B. (2005). Note types and coding in parid vocalizations: III. The chick-a-dee call of the Carolina chickadee (*Poecile carolinensis*). *Canadian Journal of Zoology, 83*, 820–833.

Blumstein, D.T., & Armitage, K.B. (1997). Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *American Naturalist, 150*, 179–200.

Catchpole, C.K., & Slater, P.J.B. (1995). *Bird song: Biological themes and variations*. Cambridge, England: Cambridge University Press.

Dunbar, R.I.M. (1998). Theory of mind and the evolution of language. In J.R. Hurford, M. Studdert-Kennedy, & C. Knight (Eds.), *Approaches to the evolution of language* (pp. 92–110). Cambridge, England: Cambridge University Press.

Dunbar, R.I.M. (2003). The social brain: Mind, language, and society in evolutionary perspective. *Annual Review of Anthropology, 32*, 163–181.

Ekman, J. (1989). Ecology of non-breeding social systems of *Parus*. *Wilson Bulletin, 101*, 263–288.

Freeberg, T.M., & Lucas, J.R. (2002). Receivers respond differently to chick-a-dee calls varying in note composition in Carolina chickadees, *Poecile carolinensis*. *Animal Behaviour, 63*, 837–845.

Garner, W.R. (1962). *Uncertainty and structure as psychological concepts*. New York: John Wiley & Sons.

Hailman, J.P., & Ficken, M.S. (1986). Combinatorial animal communication with computable syntax: Chick-a-dee calling qualifies as 'language' by structural linguistics. *Animal Behaviour, 34,* 1899–1901.

Hailman, J.P., & Ficken, M.S. (1996). Comparative analysis of vocal repertoires, with reference to chickadees. In D.E. Kroodsma & E.H. Miller (Eds.), *Ecology and evolution of acoustic communication in birds* (pp. 136–159). Ithaca, NY: Comstock Publishing Associates of Cornell University Press.

Hailman, J.P., Ficken, M.S., & Ficken, R.W. (1985). The 'chick-a-dee' calls of *Parus atricapillus*: A recombinant system of animal communication compared with written English. *Semiotica, 56,* 191–224.

Krause, J., & Ruxton, G.D. (2002). *Living in groups.* Oxford, England: Oxford University Press.

Kroodsma, D. (2005). *The singing life of birds: The art and science of listening to birdsong.* Boston: Houghton Mifflin.

Lucas, J.R., & Freeberg, T.M. (in press). "Information" and the chick-a-dee call: Communicating with a complex vocal system. In K.A. Otter (Ed.), *Ecology and behaviour of chickadees and titmice: An integrated approach.* Oxford, England: Oxford University Press.

Maestripieri, D. (1999). Primate social organization, gestural repertoire size, and communication dynamics: A comparative study of macaques. In B.J. King (Ed.), *The origins of language: What nonhuman primates can tell us* (pp. 55–77). Santa Fe, NM: School of American Research Press.

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

McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters, 1,* 381–385.

Mostrom, A.M., Curry, R.L., & Lohr, B. (2002). *The birds of North America: Vol. 636. Carolina chickadee (*Poecile carolinensis*)* (A. Poole & F. Gill, Eds.). Philadelphia and Washington, DC: Academy of Natural Sciences and American Ornithologists' Union.

Pinker, S. (2003). Language as an adaptation to the cognitive niche. In M.H. Christiansen & S. Kirby (Eds.), *Language evolution* (pp. 16–37). Oxford, England: Oxford University Press.

Shannon, C.E., & Weaver, W. (1949). *The mathematical theory of communication.* Urbana: University of Illinois Press.

Smith, S.M. (1991). *The black-capped chickadee: Behavioral ecology and natural history.* Ithaca, NY: Cornell University Press.

Specht, R. (2002). Avisoft Sound Analysis and Synthesis Laboratory (Version 4.2) [Computer software]. Berlin: Author.

Syntrillium Software. (2002). Cool Edit Pro (Version 2) [Computer software]. Phoenix, AZ: Author.

Templeton, C.N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science, 308,* 1934–1937.

Thirakhupt, K. (1985). *Foraging ecology of sympatric parids: Individual and population responses to winter food scarcity.* Unpublished doctoral dissertation, Purdue University, West Lafayette, IN.

Wilkinson, G.S. (2003). Social and vocal complexity in bats. In F.B.M. de Waal & P.L. Tyack (Eds.), *Animal social complexity: Intelligence, culture, and individualized societies* (pp. 322–341). Cambridge, MA: Harvard University Press.