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MOBBING CALLS OF BLACK-CAPPED CHICKADEES: EFFECTS OF URGENCY ON CALL PRODUCTION

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ABSTRACT.—Many animals advertise the presence of a predator threat through vocal signals. Black-capped Chickadees (*Poecile atricapilla*) use their *chick-a-dee* call as a mobbing call when encountering a perched hawk or owl. This social signal appears to serve as an alert to other chickadees, causing them to rally to the vicinity of the predator and join in a chorus of calling. We asked the question: do chickadees vary the mobbing call in a manner that could convey the immediacy of threat from a potential predator? We examined the responses of chickadees to a taxidermic mount of an avian predator presented at distances of 1 m and 6 m from each subject. Vocal responses were recorded and analyzed for response latency, calling rate, and syllable composition of calls. During 5-min trials, the subjects responded more quickly and produced significantly more *chick-a-dee* calls for predator presentations at the 1-m distance than at the 6-m distance. Alterations of syllable composition of the call also were observed under the two treatments. These results suggest that information about the immediacy of threat or proximity of a predator may be signaled by alteration of the rate of calling, with possible additional information contained in proportional changes in the different syllable types of the call. Studies of referential (symbolic) communication in birds and mammals often have failed to consider the problem of response urgency separately from predator-type labeling in vocal signal design. Received 14 June 2002, accepted 16 October 2002.

The antipredator vocal signaling behavior of birds and mammals offers important research opportunities in the functional analysis of animal communication systems. Observations of the utterances of warning calls or mobbing calls in the presence of predators raises questions about the nature of the information content of such vocal signals. If a vocalization contains variations that inform recipients about environmental events, such as the presence of a predator, the signal is referential (Evans 1997). Mammalian studies, especially of primates, call our attention to questions about the cognitive processes involved in signals that employ acoustically distinct, predator-type-specific calls (Seyfarth et al. 1980, Macedonia 1990, Zuberbühler 2000, Manser 2001, Fichtel and Kappeler 2002). The difficulty in obtaining unequivocal evidence for representational cognition in antipredator signaling has led to the notion of “functional reference,” which directs efforts toward issues that are possible to address by experimental approaches (Marler et al. 1992, Evans 1997). The concept of functionally referential communication causes one to examine behavioral response to vocal signals, testing the hypothesis that the signals encode infor-

mation about environmental events, whether a response to the signal is mediated by internal representation or not (Marler et al. 1992).

A problem often arising in the interpretations of predator signaling is the discrimination of predator class labeling from the immediacy of the predation threat. Two different kinds of signals might be used by small birds: one for a raptor circling overhead and a different one for an approaching fox, but these two kinds of predators differ also in the urgency of response required of the prey. Few studies have examined the possible separate effects of predator type and response urgency (Pereira and Macedonia 1991, Manser 2001). Marler et al. (1992) cast the issue in an important light by arguing that antipredator calls usually will contain both motivational (e.g., urgency) information as well as information about kind of predator stimulus, with the relative amounts of the two types of information lying on a continuum.

It was this latter hypothesis that led us to the present study. Well described in the literature is the variable call of the Black-capped Chickadee (*Poecile atricapilla*), the familiar *chick-a-dee* call, from which the species gets its common name. This call is multifunctional, containing information on flock identity, population identity, and location, but it also serves as a predator mobbing call (Ficken et al. 1978, Apel 1985, Smith 1991, Ficken and

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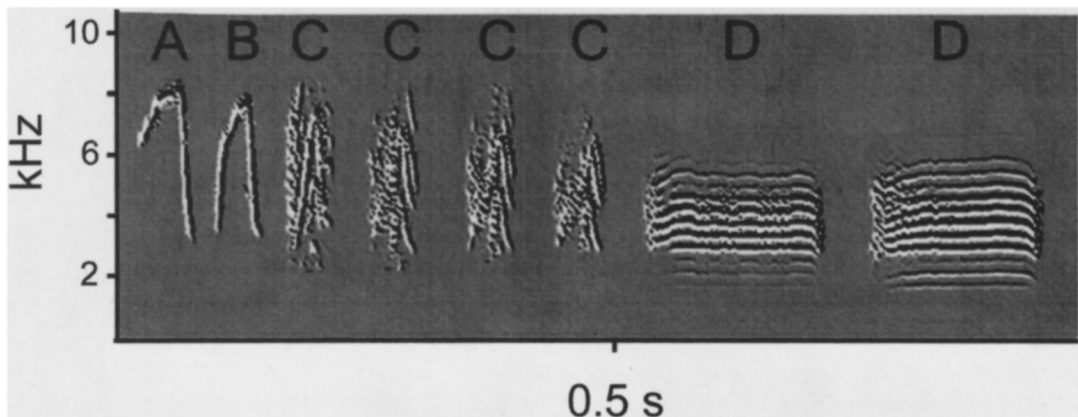


FIG. 1. This *chick-a-dee* call of the Black-capped Chickadee illustrates the four types of syllables (A, B, C, D) usually contained in the call. Each type of syllable can vary in number and this was quantified in calls given by subjects when stimulated by a mount of a Prairie Falcon presented at 1 m and 6 m distances.

Popp 1996, Hurd 1996). During mobbing events, *chick-a-dee* calls are produced as one or more birds approach a predator in a gradual manner, with frequent changes of position, and sometimes attack and dive at the predator, which may induce it to move. Other conspecifics as well as other species are attracted to the site of mobbing. This “harassment” function of mobbing calls has been noted in numerous species of birds (Klump and Shalter 1984, Ficken and Popp 1996).

The *chick-a-dee* call seems well designed for many functions, at least potentially, because the acoustic units that constitute the whole call, the syllables or notes, can combine in various ways numerically to form a very large set of different call types. Although virtually all *chick-a-dee* calls observe the sequential delivery of the four types of syllable in the most complete form of the call (syllable sequence A→B→C→D; Fig. 1), one or more syllable types can be deleted, or produced in differing numbers, indicating a combinatorial signal that has been likened to syntax structures in written language in which letters are recombined to form a variety of different words (Hailman et al. 1985). Therefore, such a variably structured signal as the *chick-a-dee* call encourages one to look for properties of the call that convey different messages. Speculations have been advanced (Hailman et al. 1987) that each of the four kinds of syllables may signal different tendencies for movement. Our study reported here was a first step simply

to determine if the *chick-a-dee* call was broadcast with differing rates or the syllable composition altered in response to predator stimulation that differed only in the urgency of the threat, as indicated by a potential predator presented at two different distances from subjects.

METHODS

We obtained Black-capped Chickadees by trapping in natural populations occupying the riparian habitat zone of the Cache La Poudre River (40° 36' N, 105° 05' W) near Fort Collins, Colorado, between 4 November 2001 and 7 February 2002. During this period, we brought a few birds at a time into the laboratory, held them for approximately one week during testing, and then released them at the site of capture. At the time of capture, we aged the birds by the distribution of the white band on the outer rectrices (Pyle et al. 1987), which we have found to correlate well with the degree of skull ossification in early and late fall juveniles. We banded the subjects for individual recognition, held them in individual cages (46 cm long, 22 cm wide, 26 cm high) in a common room on natural photoperiod, and fed them sunflower seeds and turkey starter daily.

We conducted stimulus presentations in a large room with the subject in its cage positioned in a sound attenuated box 90 cm above the floor. One side of the box was open and facing a table on which a cardboard barrier prevented the subject from seeing the stimulus located immediately behind the barrier. With a subject on its perch in the cage, the base of the stimulus object was 7 cm above the subject when in view. For the near presentation, we presented the stimulus at a distance of 1 m from a subject's cage, and for the far presentation, the table was moved across the room so the stimulus was 6 m from a subject's cage. A microphone

was located near the subject's cage and recorded all vocalizations.

A trial consisted of transporting (<30 s) the subject in its home cage from the holding room to the test chamber, one of us taking a position out of sight of the subject to later present the stimulus, and the other of us operating the recorder and timing the trial. A trial lasted 5 min. We waited to begin a trial until the subject started to move about in its cage, hopping between perches or eating a sunflower seed, which usually took from 0–4 min. Upon this movement, the tape recorder was activated and one of us pulled a string that slowly moved the stimulus from behind the cardboard barrier into full view of the subject. Beginning when the subject gave its first vocalization we recorded calls for 5 min. Our data thus consisted of 5 min of vocalizations of a subject recorded on one day at one distance to the stimulus and 5 min of vocalizations recorded on the next day at the other distance. We tested half the birds ($n = 12$) first at the 1 m distance and half ($n = 12$) first at the 6 m distance.

The predator stimulus was a taxidermic mount of a Prairie Falcon (*Falco mexicanus*) in a natural upright posture as if perched on a branch. Its head was turned toward the cage of the subject so that its face was fully observable. This is a common predator of small birds (Skinner 1938, Bailey and Niedrach 1965) and is seen frequently in the habitats of chickadees in our study area, perched on the buildings and in trees on the campus of the university, and on other commercial buildings in Fort Collins.

We collected an additional data set on eight other chickadees acting as controls for the presentation of the stimulus. We tested these birds at the 1 m distance with the Prairie Falcon and a block of wood of the same size as the predator mount. Four subjects first were presented with the wood block on one day and the predator on the next day, with the reverse order for the other four subjects. This control examined the response of the subjects to a surprising object emerging from behind the cardboard barrier.

From the stimulus sessions, we timed the latency to the first vocalization of each subject, counted the number of calls, and tabulated the constituent syllable types (ABCD) and their numbers in each *chick-a-dee* call. With this matched pairs design in which each subject served as its own control, we examined differences between the two treatments with paired *t*-tests (Sokal and Rohlf 1981) and an alpha level <0.05 for rejection of the null hypothesis. For comparison of age groups of subjects, we used an unpaired *t*-test and an alpha level <0.05.

Whereas D syllables are discretely different from other syllable types in the *chick-a-dee* call, and can be assigned accurately to category, the introductory ABC syllables sometimes exhibit intermediates (Hailman et al. 1985, Nowicki and Nelson 1990). When there were intermediates between A and B syllables we applied an arbitrary rule. Intermediates between these two syllable categories were defined as A syllables if the initial upward frequency sweep (Fig. 1) was less than half

the length of the downward frequency sweep, or as B syllables if greater than half the range of the subsequent downward frequency sweep. Intermediates between B and C syllables were discriminated by the usually more harsh broadband characteristics of the C syllable (Fig. 1). C syllables that were less noisy had a lower peak frequency than B syllables. There were fewer intermediates between B and C syllables than between A and B. Intermediates were less than 5% of the syllables scored. Our observations of the structure of the syllables of the *chick-a-dee* call followed the comments and classifications used in previous studies (Apel 1985, Hailman et al. 1985, Nowicki and Nelson 1990).

RESULTS

Of the 24 subjects presented with the Prairie Falcon mount at two distances, 15 were >1 year old ("old birds") and 9 were fledged during the breeding season prior to testing ("young birds"). Comparing the two age groups at the same distance from the predator showed that they did not differ significantly either on the latency to the first call or the number of calls given; therefore they were combined for a test of the two distance treatments (Table 1). The subjects responded more quickly to the Prairie Falcon mount when presented at 1-m distance than at 6-m distance, and they also gave more *chick-a-dee* calls to the stimulus presented at 1 m than at 6 m (Table 1). The control tests of the wood block versus the predator indicated a nearly complete absence of response to the wood block ($1.4 \text{ calls} \pm 1.0 \text{ SE}$) and a high level of *chick-a-dee* calling to the Prairie Falcon mount ($26.3 \text{ calls} \pm 6.4 \text{ SE}$; $t = 4.0$, $df = 7$, $P = 0.005$).

Differences in syllable composition of *chick-a-dee* calls given in the 1-m compared to 6-m treatments primarily were in the relative proportions of A and B syllables. We found that (1) the number of A syllables per call was greater in the 6-m treatment than the 1-m treatment ($\bar{x} = 2.45 \pm 0.65 \text{ SE}$ and $1.53 \pm 0.41 \text{ SE}$, respectively; $t = 2.43$, $df = 23$, $P = 0.029$), (2) the number of B syllables was fewer in the 6-m treatment than the 1-m treatment ($\bar{x} = 0.83 \pm 0.18 \text{ SE}$ and $1.45 \pm 0.19 \text{ SE}$, respectively; $t = 4.28$, $df = 23$, $P = 0.001$), and (3) the numbers of C and D syllables did not differ significantly between treatments (mean number of C syllables: at 1 m, $0.7 \pm 0.4 \text{ SE}$; at 6 m, $0.1 \pm 0.5 \text{ SE}$; $t = 1.56$, $df = 23$, $P = 0.14$; mean number of D

TABLE 1. The response of Black-capped Chickadees to presentation of a mount of a Prairie Falcon near (1 m) versus far (6 m) from their cage was significantly greater at the near distance as measured by the latency to the first call uttered (all birds: paired $t = 3.7$, $df = 23$, $P = 0.001$), and the number of *chick-a-dee* calls given (all birds: paired $t = 2.8$, $df = 23$, $P = 0.009$). Also, there were no significant differences by these measures when comparing older birds to younger birds at either distance of predator presentation.

Variable	All birds ($n = 24$)		Old ($n = 15$)		Young ($n = 9$)		Old versus young		
	Mean	SE	Mean	SE	Mean	SE	t	df	P
Latency to first call (s)									
Predator near	27.7	13.0	40.7	20.0	6.0	0.8	1.7	22	0.11
Predator far	125.8	28.0	143.0	39.0	86.0	39.0	1.0	22	0.32
Number of calls									
Predator near	24.2	4.9	26.8	7.3	19.9	5.1	0.8	22	0.45
Predator far	13.0	4.5	12.9	5.9	13.9	7.4	0.1	22	0.92

syllables: at 1 m, 2.7 ± 0.4 SE; at 6 m, 2.7 ± 0.5 SE; $t = 0.21$, $df = 23$, $P = 0.84$; Fig. 2).

Using the total number of syllables in each call as a measure of call length, we found that call length of individuals did not differ significantly when the predator was at a distance of 1 m or 6 m ($\bar{x} = 6.4$ syllables ± 0.3 SE and $\bar{x} = 6.1$ syllables ± 0.5 SE, respectively; $t = 0.54$, $df = 23$, $P = 0.60$).

DISCUSSION

We conclude that urgency of response in mobbing calls correlates positively with the rate of calling by Black-capped Chickadees, with possible additional information encoded in the syllable pattern of the *chick-a-dee* call. These findings are consistent with the hypothesis that these call features communicate information about the degree of threat posed by a potential predator. From the lack of response to the wood block, it is also evident that the subjects viewed the Prairie Falcon mount as a significant threat, not simply as a surprising object suddenly entering the visual field. Our results are in accord with observations of Apel (1985), who noted that the presentation of a mount of a Sharp-shinned Hawk (*Accipiter striatus*) elicited the highest rate of calling compared to that elicited by mounts of other potential predators. Sharp-shinned Hawks are well known as important predators of small passerine birds. Thus, the high rate of calling to a known significant predator found in Apel's predator presentations to field populations of chickadees, together with our labo-

ratory findings of the highest calling to the near distance presentation of the Prairie Falcon, suggest that the degree of threat is conveyed by high calling rates.

There is some evidence in the literature that chickadees acquire information about the identity of potential predators through a learning process (reviewed in Smith 1991). In the present case, this might lead to the expectation that young chickadees would not respond to the Prairie Falcon mount but older birds would respond strongly. Our results showing that younger birds indeed did respond to the presentations may therefore indicate that by the time of testing they had acquired sufficient experience to recognize the Prairie Falcon as a threat. Given the prevalence of this raptor in the study area, this result may not be surprising.

It has been hypothesized that the different syllables of the *chick-a-dee* call, in the Black-capped Chickadee as well as in the Carolina Chickadee (*Poecile carolinensis*) and Mexican Chickadee (*P. sclateri*), may encode different information (Smith 1972; Hailman et al. 1985, 1987; Ficken et al. 1994; Hailman and Ficken 1996). Substantial data to examine this idea were gathered previously by Apel (1985) in an experimental study of Black-capped Chickadee responses to different kinds of predators, both live and taxidermic mounts, in several contexts. In field presentations during both summer and winter, different types of predators sometimes elicited different combinations of A, B, C, and D syllables (Apel 1985). Apel concluded that the various sylla-

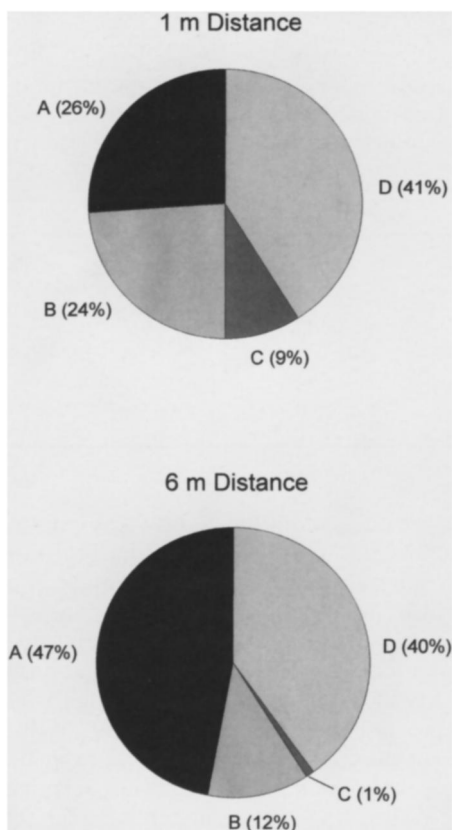


FIG. 2. These pie diagrams illustrate proportional changes in syllable composition of *chick-a-dee* calls given under the two treatment conditions of presentation of a Prairie Falcon mount at a near (1 m) and far (6 m) distance. The data indicate that the chickadees increased the proportion of A syllables and decreased B and C syllables when the predator mount was presented at 6 m compared to 1 m distance. These diagrams summarize the pooled data for all birds, although statistical results (see text) were derived from paired comparisons of each subject's calls under the two treatments.

ble alterations of the *chick-a-dee* call were predator-type dependent and constituted a finely tuned predator recognition response. In particular, Apel hypothesized that an increase in the number of A syllables indicated a higher fear level in subjects, whereas a preponderance of D syllables indicated a less fearful state in the chickadees. In general, the D syllable content of calls was greater in the mobbing context than in nonmobbing situations.

Although we are unable to make conclusions about fear levels in our subjects, the

most intense response, as measured by calling rate, was at the 1-m distance to the predator, and this treatment elicited fewer A syllables and more B syllables than the 6-m treatment. Thus, in contrast to Apel's hypothesis, we conclude that a more immediate predation threat causes a chickadee to shift its call to contain fewer A syllables and more B syllables. Apel also noted that on occasions of natural chickadee encounters with raptor predators, strings of A syllables tend to be heard in birds that have retreated to cover and become immobile, perhaps stimulating alertness in others. This observation may suggest an appropriate interpretation for our results of increased A syllables in the 6-m treatment. Seeking cover and becoming immobile could be a good strategy when a predator is first seen at a somewhat distant location. However, we did not monitor activity levels in our subjects under the two treatments of predator distance and therefore have no data with which to address this idea. Although Apel tested subjects with mounts of different kinds of avian and mammalian predators as well as examples of nonpredators of chickadees, an urgency effect was not examined by direct experimentation, e.g., by varying the distance to a given predator, as a possible factor in the chickadee's responses. This large study (Apel 1985), however, set the stage for a more systematic disentanglement of the possible effects of predator type and response urgency on the chickadee mobbing call.

In the Mexican Chickadee, the equivalent *chick-a-dee* call exhibited differences in syllable composition in undisturbed versus disturbed situations in natural populations (Ficken et al. 1994). Two of the syllable types (A, D) predominated in calls on territory with the mate present (undisturbed), but in a mobbing context the AD combination was greatly reduced while C syllables increased (Ficken et al. 1994). Although these results are not easily compared to ours, they suggest that, as in our findings, A syllables are reduced in number under conditions of increased predator threat.

Results of other research on species closely related to Black-capped Chickadees also are instructive. Studies of the antipredator behavior of the Great Tit (*Parus major*) have addressed the question of vocal signaling in response to predators (Curio et al. 1983, Curio

and Regelman 1985). With restrained live predators at fixed locations as stimuli, Great Tits increased their rate of calling as they approached a predator and decreased the rate as they retreated from the predator. This finding is similar to ours in that calling rate was higher in chickadees for the near presentation of the Prairie Falcon. In other work, a simulated Eurasian Sparrowhawk (*Accipiter nisus*) was presented to captive Willow Tits (*Parus montanus*) at two different apparent distances (10 and 40 m) by use of tiny models (7.2 cm wingspan and 1.8 cm wingspan, respectively) passed over a subject's cage at a height of 2 m (Alatalo and Helle 1990). Only 16% of the birds gave alarm calls to the larger (near) model but 59% gave alarm calls to the smaller (far) model. This simulation of predator distance showed that the propensity to call was low for a more immediate threat, suggesting that calling might increase the risk of predation. No data were provided on the rate of calling or on call structure, so comparisons with our results are limited. However, our subjects all gave mobbing calls at the near distance and did so at a high rate, opposite the general pattern seen in the Willow Tit experiment. A difference of potential significance is that the simulated predator was a moving one in the Willow Tit experiment, whereas the Prairie Falcon, once moved into position, was motionless. This difference could affect the perceived threat of predation.

Alarm call variation in several fossorial mammals appears primarily to be indicative of differing levels of response urgency. Structurally different alarm calls are given by California ground squirrels (*Spermophilus beecheyi*) to approaching aerial and terrestrial predators (Owings and Virginia 1978), but these calls grade into one another and can be given in other contexts (Owings and Leger 1980). These findings led to the interpretation that these variant call structures signal differing degrees of response urgency (Owings and Hennessy 1984). Similar general conclusions have been made for other species of ground squirrels (e.g., Robinson 1981) and marmots (Blumstein and Armitage 1997).

Our results on chickadees parallel these findings in that we view urgency as a descriptor of motivational state, and the differences in calling rate and alteration of syllable com-

position as reflecting different levels of motivation resulting from differences in the immediacy of predator threat. Therefore, results from studies that find structural differences in alarm calls given to two different classes of predator, such as raptor versus mammal, sometimes could be misinterpreted as representing more complex cognition than is warranted, unless the immediacy of the threat is examined experimentally as a possible cause of the observed differences in alarm calls.

The systematic teasing apart of predator labeling and response urgency as causes of differences in vocal signals seldom has been accomplished, in spite of the simple experimental design required: at least two predator classes each presented at two levels of response urgency. Lemurs, for example, make their call selection appropriate to the predator class with only minor vocal alteration signaling urgency in avian predation simulations (Macedonia 1990, Pereira and Macedonia 1991). Other studies also have found predator class labeling independent of urgency (Seyfarth et al. 1980, Fichtel and Kappeler 2002). In social mongooses (*Suricata suricatta*), apparently both predator type and urgency information are contained in their antipredator calls (Manser 2001).

Our results on chickadee mobbing calls suggest that calling rate and some structural alterations vary with the immediacy of predator threat. Whether these variations in call properties represent signals that effect different behavior patterns in conspecifics in the area of the calling bird is unknown. Our results call attention to the need for studies of the responses of receivers to determine if, for example, the intensity of mobbing behavior or defensive escape and hiding are elicited by the call variations.

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LITERATURE CITED

- ALATALO, R. V. AND P. HELLE. 1990. Alarm calling by individual Willow Tits, *Parus montanus*. *Anim. Behav.* 40:437–442.
- APEL, K. M. 1985. Antipredator behavior in the Black-capped Chickadee (*Parus atricapillus*). Ph.D. diss., Univ. of Wisconsin, Milwaukee.
- BAILEY, A. M. AND R. J. NIEDRACH. 1965. Birds of Colorado. Denver Museum of Natural History, Colorado.
- BLUMSTEIN, D. T. AND K. B. ARMITAGE. 1997. Alarm calling in yellow-bellied marmots I: the meaning of situationally variable alarm calls. *Anim. Behav.* 53:143–171.
- CURIO, E., G. KLUMP, AND K. REGELMANN. 1983. An anti-predator response in the Great Tit (*Parus major*): is it tuned to predator risk? *Oecologia* 60:83–88.
- CURIO, E. AND K. REGELMANN. 1985. The behavioural dynamics of Great Tits (*Parus major*) approaching a predator. *Z. Tierpsychol.* 69:3–18.
- EVANS, C. S. 1997. Referential signals. Pp. 99–143 in *Perspectives in ethology*, vol. 12 (D. H. Owings, M. D. Beecher, and N. S. Thompson, Eds.). Plenum Press, New York.
- FICHTEL, C. AND P. M. KAPPELER. 2002. Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. *Behav. Ecol. Sociobiol.* 51:262–275.
- FICKEN, M. S., R. W. FICKEN, AND S. R. WITKIN. 1978. Vocal repertoire of the Black-capped Chickadee. *Auk* 95:34–48.
- FICKEN, M. S., E. D. HAILMAN, AND J. P. HAILMAN. 1994. The "chick-a-dee" call system of the Mexican Chickadee. *Condor* 96:70–82.
- FICKEN, M. S. AND J. POPP. 1996. A comparative analysis of passerine mobbing calls. *Auk* 113:370–380.
- HAILMAN, J. P. AND M. S. FICKEN. 1996. Comparative analysis of vocal repertoires with reference to chickadees. Pp. 136–159 in *Ecology and evolution of acoustic communication in birds* (D. E. Kroodsma and E. H. Miller, Eds.). Cornell Univ. Press, Ithaca, New York.
- HAILMAN, J. P., M. S. FICKEN, AND R. W. FICKEN. 1985. The "chick-a-dee" calls of *Parus atricapillus*: a recombinant system of animal communication compared with written English. *Semiotica* 56: 191–224.
- HAILMAN, J. P., M. S. FICKEN, AND R. W. FICKEN. 1987. Constraints on the structure of combinatorial "chick-a-dee" calls. *Ethology* 75:62–80.
- HURD, C. R. 1996. Interspecific attraction to the mobbing calls of Black-capped Chickadees (*Parus atricapillus*). *Behav. Ecol. Sociobiol.* 38:287–292.
- KLUMP, G. M. AND M. D. SHALTER. 1984. Acoustic behavior of birds and mammals in the predator context. *Z. Tierpsychol.* 66:189–226.
- MACEDONIA, J. M. 1990. What is communicated in the antipredator calls of lemurs: evidence from playback experiments with ringtailed and ruffed lemurs. *Ethology* 86:177–190.
- MANSER, M. B. 2001. The acoustic structure of suricate's alarm calls varies with predator type and level of response urgency. *Proc. R. Soc. Lond. B* 268:2315–2324.
- MARLER, P., C. S. EVANS, AND M. D. HAUSER. 1992. Animal signals: motivational, referential, or both? Pp. 66–86 in *Nonverbal vocal communication: comparative and developmental approaches* (H. Papoušek, U. Jürgens, and M. Papoušek, Eds.). Cambridge Univ. Press, Cambridge, United Kingdom.
- NOWICKI, S. AND D. A. NELSON. 1990. Defining natural categories in acoustic signals: comparison of three methods applied to "chick-a-dee" call notes. *Ethology* 86:89–101.
- OWINGS, D. H. AND D. F. HENNESSY. 1984. The importance of variation in sciurid visual and vocal communication. Pp. 169–200 in *Biology of ground dwelling squirrels: annual cycles, behavioral ecology and sociality* (J. O. Murie and G. R. Michener, Eds.). Univ. Nebraska Press, Lincoln.
- OWINGS, D. H. AND D. W. LEGER. 1980. Chatter vocalizations of California ground squirrels: predator- and social-role specificity. *Z. Tierpsychol.* 54: 163–184.
- OWINGS, D. H. AND R. A. VIRGINIA. 1978. Alarm calls of California ground squirrels (*Spermophilus beecheyi*). *Z. Tierpsychol.* 46:58–70.
- PEREIRA, M. E. AND J. M. MACEDONIA. 1991. Response urgency does not determine antipredator call selection by ring-tailed lemurs. *Anim. Behav.* 41: 543–544.
- PYLE, P., S. N. G. HOWELL, R. P. YUNICK, AND D. F. DESANTE. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, California.
- ROBINSON, S. R. 1981. Alarm communication in Belding's ground squirrels. *Z. Tierpsychol.* 56:150–168.
- SEYFARTH, R. M., D. L. CHENEY, AND P. MARLER. 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* 210:801–803.
- SKINNER, M. P. 1938. *Falco mexicanus*: Prairie Falcon. Pp. 18–42 in *Life histories of North American birds of prey*, part II (A. C. Bent, Ed.). U. S. Natl. Mus. Bull. 170:1–482.
- SMITH, S. M. 1991. The Black-capped Chickadee: behavioral ecology and natural history. Cornell Univ. Press, Ithaca, New York.
- SMITH, S. T. 1972. Communication and other social behavior in *Parus carolinensis*. *Publ. Nuttall Ornithol. Club* 11:1–125.
- SOKAL, R. R. AND F. J. ROHLF. 1981. *Biometry*, 2nd ed. W. H. Freeman, San Francisco, California.
- ZUBERBÜHLER, K. 2000. Referential labeling in Diana monkeys. *Anim. Behav.* 59:917–927.