

## EFFECTS OF GARGLE VOCALIZATIONS ON BEHAVIOR OF BLACK-CAPPED CHICKADEES<sup>1</sup>

MYRON CHARLES BAKER, JEANETTE T. BOYLAN, AND CHRISTOPHER A. GOULART  
*Department of Biology, Colorado State University, Fort Collins, CO 80523*

**Abstract.** In agonistic situations, Black-capped Chickadees (*Parus atricapillus*) utter a short, structurally complex call termed a *gargle*. Previous work has shown that in contests between two birds at food sources the *gargler* always wins. We investigated the establishment of the relationship between *gargling* and dominance by pairing males that were strangers. Our results indicate that dominance is established by fighting and that the dominants are larger than subordinates. In the earliest phase of the first encounter, a dominant bird would utter *gargles* concurrent with aggressive actions whereas a subordinate's *gargling* was suppressed and remained so indefinitely.

We also investigated the separate effects of the *gargle* calls, the partner bird, or both in an experimental presentation. Results indicate that the subordinate was not kept away from a food source by the *gargle* calls of its dominant partner, but it was deterred by the presence of the partner. Dominants, on the other hand, were somewhat deterred by the *gargle* of their subordinate partner but not by the presence of the partner.

**Key words:** *Vocalizations; dominance; Black-capped Chickadee; Parus atricapillus.*

### INTRODUCTION

Contests between birds for access to resources are often characterized by vocal signaling. When the signals are structurally complex and variable among individuals, the possibility arises that the attempted manipulation of an opponent is highly specific and individually distinct. This is especially likely in social species in which the individuals live in stable groups with a history of interactions with one another.

Black-capped Chickadees (*Parus atricapillus*) often produce a brief, complex call, termed the *gargle* (Ficken et al. 1978), in the context of aggressive interactions with conspecifics (Ficken et al. 1987). In observations at outdoor bird feeders, there is a strong correlation between *gargling* and the outcome of an interaction: in 98.9% of 846 cases, the individual uttering the *gargle* displaced the recipient, and within a dominance hierarchy the high ranking birds gave more *gargles* than did the low ranking birds (Ficken et al. 1987).

These observations raise the following two questions which we address in this paper. (1) How is the relationship between dominance and *gargling* established? (2) Does *gargling* serve a deterrent function in a contest situation?

### METHODS

#### GENERAL

Ten male Black-capped Chickadees were obtained from natural populations near Fort Collins, Colorado, in November 1988. Five males were taken from a single site at the Northern Colorado Nature Center, three males were taken from a residential site 6.2 km from the Nature Center, and two males were taken from a riparian site 7 km from the Nature Center and 1.5 km from the residential site. These distances were sufficient to ensure that the Nature Center birds were unfamiliar with birds from the other two areas (Glase 1973). Following capture, the photoperiod was reduced over a two-week period to eight hours of light, and this condition was maintained throughout the study. Sex and size were determined on the basis of wing length (Glase 1973). We kept birds with flattened-wing measurements over 68 mm. A bird with this wing length has greater than 95% chance of being male (Glase 1973). Colorado chickadees have slightly longer wings (Duvall 1945) than does the eastern subspecies for which Glase (1973) made his conclusions. This raises the possibility that we could mistake a long-winged female for a male. All ten of our study subjects produced a large number of *gargle* calls, however, which supports our determination of sex because females very rarely *gargle* (Ficken et al. 1987).

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We formed five pairs of strangers by randomly assigning each of the Nature Center birds to one of the birds from the other two sites. The ten birds were kept in separate cages (46 cm long, 26 cm high, 22 cm deep) in visual isolation until experiments were initiated. Prior to the pairing tests, we tape-recorded the *gargle* calls of all individuals by placing them one-at-a-time in a recording chamber with a mirror adjacent to a perch in the individual's cage. Previous experiments in our laboratory (also M. S. Ficken, pers. comm.) had indicated that a bird will *gargle* at its reflection. We obtained recordings with a Uher 4200 Report Stereo IC at 9.5 cm/sec and Uher microphone mounted 20 cm from the cage of the subject.

#### EXPERIMENT 1

To determine the development of dominance and its association with *gargling*, each pair of males (permanently assigned) was placed in a neutral cage for three or more sessions of approximately 8 min each. Each session was videotaped, tape recorded, and described in a narrative by an observer. We later viewed the videotapes and analyzed the audio recordings to obtain more detailed information than could be observed directly at the initial observation periods. We tabulated information on the time to the first attack and first *gargle*, and the number of attacks, supplants, and *gargles*. In an attack, one bird flew directly at the other and usually made physical contact which resulted in the recipient being knocked off its perch and making rapid escape movements while pursued by the aggressor. Supplanting was a more mild interaction in which one bird moved casually in the direction of the opponent who then moved away. This action avoided physical contact.

#### EXPERIMENT 2

To determine the effects of the *gargle* call in a feeding situation, each individual was tested under four treatment conditions with four repetitions. The four treatments were: (1) silence, (2) partner, (3) partner's *gargle*, and (4) partner plus partner's *gargle*. The testing situation consisted of two adjacent cages and a loudspeaker beside one of the cages. The loudspeaker was connected to a playback system (DSP 5500, Kay Elemetrics). The cage farthest from the loudspeaker contained the subject in each test. On the floor of the subject's cage and close to the cage bars of

the neighboring cage was a dish of ten mealworms. The silence treatment consisted of the neighboring cage empty and no *gargles* broadcast from the loudspeaker. The partner treatment consisted of the partner present in the neighboring cage and no *gargles* broadcast. The *gargle* treatment consisted of the neighboring empty cage but with *gargles* of the partner broadcast from the loudspeaker. The partner/*gargle* treatment consisted of the partner present in the neighboring cage and his *gargles* broadcast from the loudspeaker.

At the start of a five minute test, the mealworm dish was covered. After the first ten *gargles* were played, or 20 sec elapsed, depending on the treatment, the mealworms were uncovered by remote control. We timed the interval to the capture of each mealworm (latency), counted the number of mealworms taken from the dish, and measured the time (out of 280 sec possible after uncovering the mealworms) that the subject spent in the half of his cage farthest from the mealworm dish (and hence away from the *gargles* and partner in those treatments).

Each bird had a repertoire of *gargles*. For the tests, we broadcast the *gargle* most frequently used by the partner during our tape recording sessions (Fig. 1). Sound levels were set at 91 dB (Simpson 885 RMS meter, A weighting, slow) measured at the mealworm dish 33 cm from the loudspeaker, which level decreased to 89 dB at the most distant perch 66 cm from the speaker. Neither subjects nor partners *gargled* during experiment 2.

We conducted four trials with the four treatments on each bird. Each trial was conducted over four days with each bird receiving one randomly assigned treatment each day. There were at least three days without testing between trials. Testing occurred between 08:00–10:00 each day. The experiment was conducted from 23 March to 18 April 1989.

## RESULTS

#### EXPERIMENT 1

*Dominance and gargling.* In four of the five pairs, a dominance relationship was established in the first test (15 December 1988) and remained stable throughout the entire study, which terminated on 18 April 1989. In the fifth pair (WK/MM), the first two dominance tests (15 Dec. and 13 Jan.) gave clear results with one bird (WK)

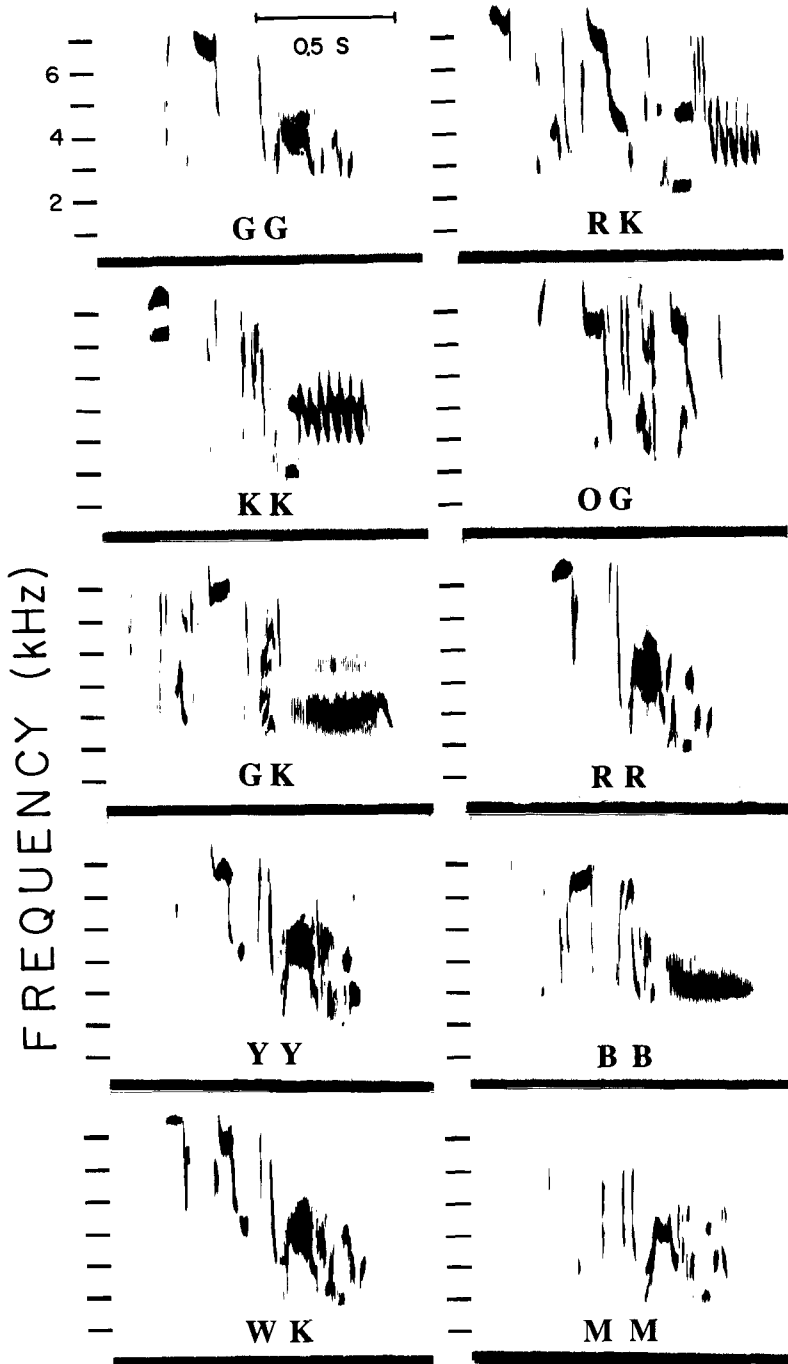


FIGURE 1. *Gargle* vocalizations of each male Black-capped Chickadee used as stimuli in Experiment 2.

appearing to be strongly dominant. Subsequent tests of this pair on 2 and 3 February, however, were inconclusive and suggested a shift in dominance. During the fifth test (8 February), the former subordinate (MM) emerged as dominant and remained so thereafter.

The first two dominance tests (15 Dec., 13 Jan.) were indicative of the general patterns of attacking, supplanting and *gargling* that occurred during the interactions of the members of each pair (Table 1). Typically, one member of the pair performed a large number of *gargles* in the first session, and this same individual did most of the supplanting and attacking. In the first sessions of the five pairs, the mean time to the first *gargle* was 30 sec. Furthermore, in four of the five pairs, the individual that made the first attack and the first *gargle* during the first test was the clear dominant and remained so. In four of the five pairs, *gargling* decreased substantially in session two (13 January), and only the dominant *gargled*. These initial interactions between any given pair were characterized by concordant attacking and *gargling*. Birds did not perch across from each other and *gargle* in a prolonged contest of vocal signaling. Most commonly, one individual made a direct aggressive attack, with physical contact and fleeing by the opponent, which was followed instantly by production of one or more *gargles* by the aggressor. Subsequent to the early interactions in the first and second pairing sessions, the dominant bird often was able to displace the opponent by *gargling* alone, without direct physical attack, although the *gargle* was usually accompanied by a stereotyped posture (Glase 1973). During delivery of the vocalization, the sender was oriented with his head and beak directed at the recipient.

In subsequent pairings for dominance/*gargling* determination, the frequency of *gargling* continued to decrease or it ceased altogether during the behavioral interactions. Dominance was maintained by attacks or, more often, by supplanting. In the case of WK and MM, in which pair the dominance shifted from WK to MM, *gargling* was present in only the first two sessions. Thus, MM became dominant without employing *gargling*.

*Size and dominance.* We examined the relationship between the relative sizes of the two contestants in each pair and their dominance ranking. In four of the five pairs, the dominant

TABLE 1. Number of times per minute each bird displaced (attacked + supplanted) its opponent, number of *gargles* per minute given by each bird, and wing lengths of subjects.

Bird	Wing (mm)	15 December 1988		13 January 1989	
		Displacements	Gargles	Displacements	Gargles
GG	71.0	1.2	5.1	0.6	0
RK	68.0	0.1	0	0	0
KK	69.0	2.4	0.7	4.4	1.5
OG	69.0	0.9	0.9	1.6	0
GK	70.0	3.7	14.8	2.9	8.7
RR	69.0	0	0.1	0.5	0
YY	70.0	4.5	22.0	9.3	0.1
BB	69.0	1.3	0	3.9	0
WK	71.0	8.5	18.4	7.0	0.5
MM	68.5	2.5	0	1.3	0

bird was larger (longer wing length) than the subordinate (Table 1). Furthermore, in the initial two trials for all four pairs, the larger and more dominant bird *gargled* frequently during the encounter. In contrast to this general pattern, one pair of birds (KK/OG) was of equivalent body size and *gargled* few times, even though one bird was clearly dominant on the basis of the outcomes of attacks and supplants.

## EXPERIMENT 2

*Time spent on right side.* Treatment effects were evaluated by calculating the means of four trials for each treatment for each dominant and each subordinate. The mean time that dominants spent on the right side of the cage (away from the neighboring cage and loudspeaker) was weakly heterogeneous over the four treatments (Fig. 2,  $P = 0.07$ , repeated measures ANOVA, Winer 1971). In pairwise comparisons between treatments, there was a significant increase in time on the right when comparing the silence treatment to either the *gargle* or partner/*gargle* treatments (both  $P$ 's  $< 0.05$ , Fisher's LSD, Carmer and Swanson 1973). No other pairwise comparisons were significantly different. The lack of a significant difference between silence and partner treatments suggests that partner alone was not important and explains the partner/*gargle* effect as caused primarily by the *gargle*. Another way to determine the effects of the partner and *gargle* treatments is to compare each to the partner/*gargle* effect. If the *gargle* is the important determinant and the partner has minor influence,

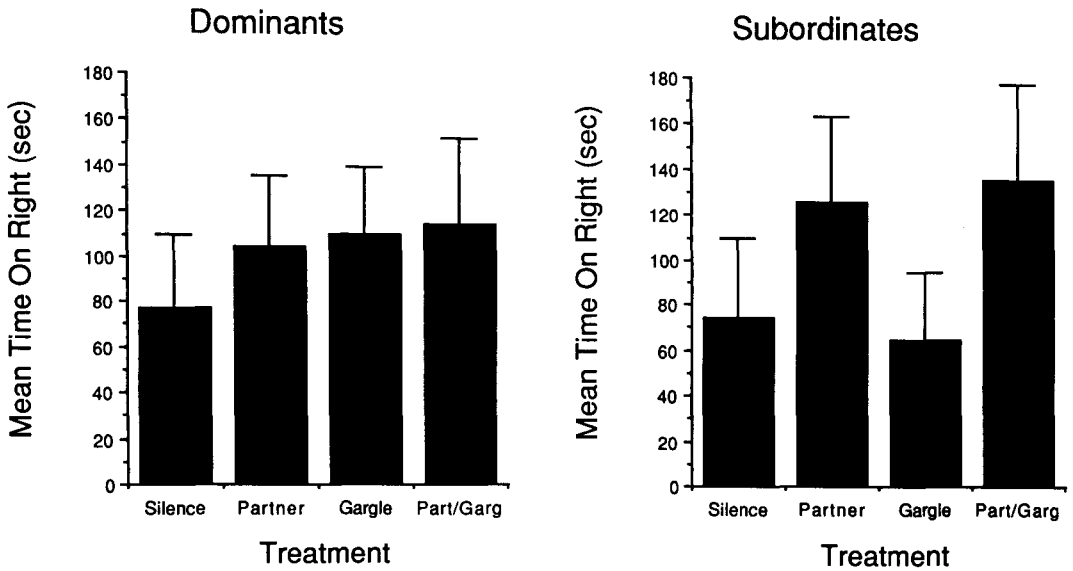


FIGURE 2. Mean ( $\pm$  SE) time spent on the right side of subject's cage (away from stimulus) for (a) dominants and (b) subordinates under four treatment conditions.

then the *gargle* and *partner/gargle* should not differ while the effect of *partner* should be significantly less than that of *partner/gargle*. *Partner* was not significantly different from *partner/gargle*, however. Together with the marginal overall heterogeneity among treatments this analysis suggests that, at best, there is only a small *gargle* effect on dominant birds. Larger samples might solve this issue.

Subordinates exhibited strong overall heterogeneity across the four treatments (Fig. 2,  $P = 0.01$ , repeated measures ANOVA). Pairwise comparisons indicated that the presence of the partner significantly increased the time on right compared to the silence treatment. A similar result was found when comparing the silence treatment to that of the *partner/gargle*. Furthermore, both the *partner* and *partner/gargle* treatments increased the time on right in comparison to the *gargle* treatment. No other comparison was significantly different. The pattern of differences indicates that subordinates were influenced primarily by their dominant partners. The *gargle* treatment alone had little influence, and the *partner/gargle* treatment was no more effective than *partner* alone.

*Number of mealworms.* There was significant overall heterogeneity in the number of mealworms consumed under the four treatments by

the dominant birds (Fig. 3,  $P = 0.004$ , repeated measures ANOVA). Pairwise comparisons (Fisher's LSD) between treatments indicated that dominants consumed more mealworms under the silence treatment than when hearing their partner's *gargle* or when being exposed to their partner in the neighboring cage and hearing the partner's *gargle* from the loudspeaker. The presence of the partner only, however, did not alter the number of mealworms consumed in comparison to the silence treatment. Thus, the pattern of results indicates that dominants were not influenced by the presence of the subordinate partner but were inhibited from obtaining mealworms by the partner's *gargle*. For subordinate birds, there was no overall heterogeneity in mealworms consumed under the four treatments (Fig. 3,  $P = 0.46$ , repeated measures ANOVA) and no pairwise comparisons were significant.

*Time to obtaining mealworms.* The times taken to obtain the first and second mealworms showed no overall heterogeneity across the four treatments for either dominant or subordinate birds. Of the 24 pairwise comparisons possible for the separate analyses of latencies to first and second mealworms, only one was significantly different. Thus, analysis of these variables revealed no patterns of significant treatment effects for either dominants or subordinates.

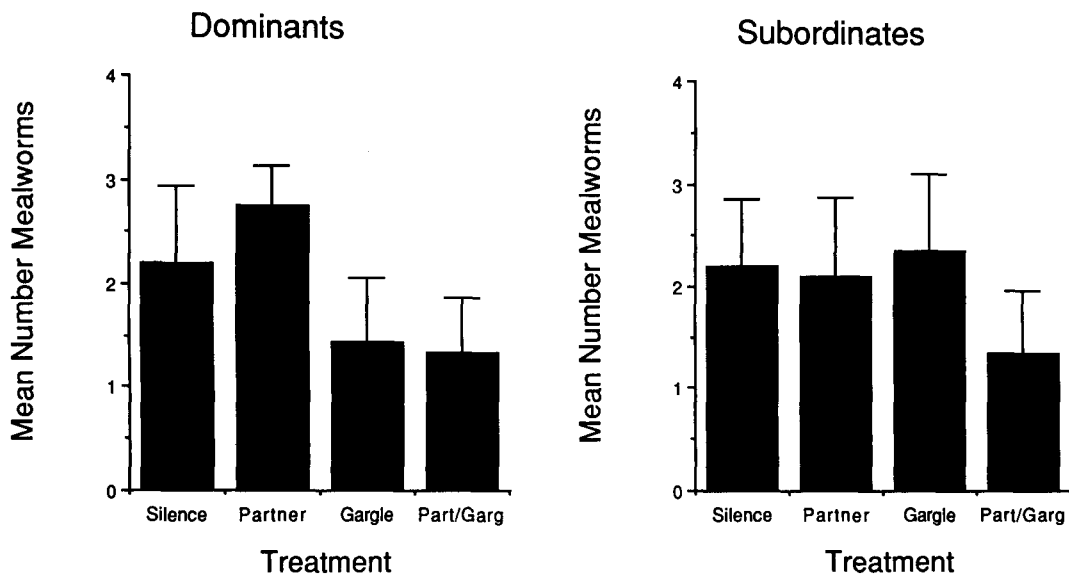


FIGURE 3. Mean ( $\pm$  SE) number of mealworms consumed by (a) dominants and (b) subordinates under four treatment conditions.

## DISCUSSION

Various studies have presented different answers to the question of what information is contained in the *gargle*. Ficken et al. (1978) interpreted the *gargle* as a threat display, signaling the intention of the sender to attack. Further studies (Ficken et al. 1987) suggested that the message was one of "willingness to escalate"; the sender had no intention of fleeing from a potential opponent in a contest situation and would escalate the fight if attacked.

If the *gargle* is a vocal threat display (Ficken et al. 1978), we might expect that the initial social encounters of strangers would involve sustained bouts of *gargling* by both individuals, something like the vocal dueling of territorial neighbors during the breeding season. This, in general, did not occur. It was only in the first session of one pair, KK/OG, that anything remotely resembling a *gargling* duel ensued. In this instance, the eventual dominant gave five *gargles* and the subordinate gave eight, small numbers compared to the early sessions with other pairs in which the dominant gave over 100 *gargles*. In all, there were 34 dominance sessions totaling 249 min distributed among the five pairs of chickadees. In only 12 of these sessions did any *gargling* occur, and 90% of the *gargles* occurred in five

sessions. Dominants gave 574 *gargles* and subordinates gave nine in all the sessions.

The results of this pairing experiment with males from differing locations showed that dominance relationships usually were established rapidly and that the *gargle* vocalization played a role in the social signaling attendant to the establishment of dominance by one bird over another. Fighting with contact typified the onset of the first encounter between strangers and this fighting was accompanied by *gargling*. The fact that usually one bird *gargled* a great deal and the partner *gargled* little or not at all implies that the behavioral dominance by one bird suppressed both visual and vocal display patterns of aggression in the subordinate. Once established, the social dominance relationship between two males was maintained without the use of *gargles*. The major exception to these trends in social dominance and *gargling* was in one pair (WK/MM) that underwent a reversal of dominance after the first 2–3 sessions of testing. In this pair, dominance reversal was achieved without *gargling*, nor did *gargling* emerge in the new dominant at a later time. Thus, although *gargling* was a normal component of the initial aggressive interactions establishing the social relationship between two birds, it was not necessary to the

process. Whether *gargling* influenced how rapidly a stable social relationship was achieved was not evaluated but could be examined in further studies. It is possible also that our forced encounters in small quarters altered the relative importance of fighting versus vocal/visual display in settling disputes. This issue could be addressed experimentally by staging encounters in a large aviary as well as in small cages.

Several authors have discussed the conceptual issues involved in the interpretation of animal signals in fighting behavior (Caryl 1979, Hinde 1981, Caryl 1982, Krebs and Dawkins 1984). In the case of *gargling*, the "traditional ethological approach" would consider that the signal transmits information to the opponent which may indicate, for example, that the signaler intends to stay in place but will attack if approached (Hinde 1981). In such an interpretation it would seem that both animals of a pair would produce copious amounts of *gargling* in some type of ritualized face-off, but this did not occur in our study. Instead, physical displacements (attacks and supplantings) occurred immediately with the emergence of much *gargling*, but only by the bird who proved to be behaviorally dominant. Thus, assessment was accomplished by physical battle with an outcome predicted rather well by size relationships of the contestants. *Gargling* subsequently came into play perhaps as a reminder of status by the dominant directed at the subordinate. In more natural circumstances or at different times of the year, *gargling* duels might occur. We did not examine this possibility.

Our measurements of wing length suggest that contestant pairs exhibited an asymmetry in body size that could be related to fighting ability. If the contestants assess their respective abilities by direct combat in the first few interactions, then the *gargle* emitted by the larger and stronger bird following these initial engagements would signal the dominant's status. It seems likely that in our dominance tests, where no resources were in contention, the pairs settled the contest by the conventions of size and fighting ability.

Wing length has been used as a measure of size in birds by a number of authors (e.g., Lanyon 1960, Hamilton 1961, Johnston and Selander 1964, James 1970, Searcy 1979, Watt 1986). In a recent analysis, however, Rising and Somers (1989) have questioned the accuracy with which wing length indicates overall body size, at least for Savannah Sparrows. Feather wear can con-

tribute greatly to variation in wing length measurements, and thus make wing length an unreliable index of body size if birds are measured at different seasons. Because our measurements were all performed on subjects immediately upon capture, and all birds were captured in a short time span (6–20 November), we believe that our wing measurements are accurate reflections of the sizes of the birds.

The trends in Experiment 2 indicated that dominants were averse to the *gargle* of their subordinate partner but were not averse to the partner itself. This pattern was seen in two of three measures of effect. As indicated by the time on right measure, subordinates were not averse to the *gargle* of their dominant partner but were averse to the presence of their partner. Our expectations, derived from the proposed threat function of *gargling* (Ficken et al. 1978), were that dominants would be unaffected by the treatments but that subordinates would be averse to the dominant and/or his *gargles*.

Smith (1972), working on Carolina Chickadees (*Parus carolinensis*), addressed the question of what information is obtained by the recipient when the sender *gargles* ("rasps") in Smith's terminology). In field situations, the messages encoded in these calls depended upon the context. Most commonly, the calls signaled an aggressive tendency. One distinction made by Smith (1972) concerned the differences in message content when the recipient was a "bonded companion" (such as a flock-mate) or a stranger. In confrontations between flock-mates, the signal appeared to be a reminder of a relationship established previously. In this situation, the sender indicates his dominance and the message that he will fight if approached. Cheating or "bluffing," by the tactic of emitting the first *gargle* in a contest over food, for example, is prevented because the birds within a social group have assessed each other previously, perhaps in physical combat. Confrontations with strangers, on the other hand, usually occur in "patrolling," which brings individuals from different flocks into contact. *Gargle* calls emitted by a resident male during patrolling of his home range signal that an intruder can anticipate attack if transgression occurs.

Smith's (1972) study provides insight into the results of our *gargle* playback experiment. When a dominant hears the *gargle* of its subordinate partner over the loudspeaker, it is likely that this *gargle* is unfamiliar because of the social sup-

pression of *gargling* in the subordinate resulting from earlier dominance contests. The unfamiliar playback *gargle* would simulate the presence of an unknown (patrolling) individual with whom the recipient has had no previous interactions leading to assessment. In this situation, we might expect the recipient to keep away, at least initially. If birds perform this kind of evaluation of unfamiliar *gargles*, it would explain the aversion of the dominants to *gargles* in Experiment 2 for both the measure of time on right and the number of mealworms obtained.

Subordinate chickadees in Experiment 2 were exposed to the visual and/or vocal signals of a dominant partner. Because of prior experience, the *gargle* calls should have been familiar to the subordinates. The subordinate's lack of aversion to the vocal signal alone is intriguing. Clearly, the recipient did not view the *gargle* as a serious threat or intention to attack. Maynard Smith (1979) argued that, because they affect outcomes, displays given during contests should convey information about "resource-holding potential" (RHP, Parker 1974), such as may be indicated by size or strength, and not convey information about intentions. van Rhijn (1980) and van Rhijn and Vodegel (1980), however, pointed out that one might expect conveyance of intention in cases where there is an asymmetry between contestants and this asymmetry is known to the contestants. Interpreting the *gargle* of chickadees in these terms we may imagine that the *gargles* between strangers are about RHP, perhaps loudness or rate of repetition conveying the pertinent information about strength or size. On the other hand, *gargles* directed by one bird toward another from the same flock could well be signals of intention conveying information to a known individual. In the chickadee case, the recipient would be a subordinate member of the same social flock. Perhaps when the *gargle* is that of a familiar bird, it is effective as a deterrent only when the vocal signal is reinforced by the visual component, i.e., proximity of the sender and the motor components of the display. This coupling of visual and vocal components might be necessary for effectiveness within a flock of individuals known to one another, because a bird in a close group often hears *gargles* of flockmates but is not necessarily the target of a particular *gargle* threat. Thus, for a recipient to be threatened, a higher valence stimulus is required which is the combined visual and vocal components of the

signal giving unmistakable directionality to the display.

It remains to explain the result that for subordinates no treatment was aversive as measured by the number of mealworms obtained. A possible explanation of the behavior of subordinates in this situation is that a subordinate may be more likely than would a dominant to undertake a risk-prone response. Subordinates seemed quite willing to move quickly to the mealworm dish to obtain food but then retreated quickly to the perch farthest from the dominant bird or its broadcast *gargle*. On this distant perch the bird would tear apart and consume the mealworm obtained. Dominants may have the luxury of acting more risk averse and be less willing to approach the mealworm dish in the presence of a *gargle* stimulus, not only because it was perceived as the *gargle* of a stranger but perhaps also because dominants may have been in better body condition and less hungry than subordinates (Fretwell 1969, Baker and Fox 1978, Kikawa 1980).

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