

VOCALIZATIONS AND OTHER STIMULI THAT ELICIT GAPING IN NESTLING BLACK-CAPPED CHICKADEES (*PARUS ATRICAPILLUS*)

JANINE R. CLEMMONS

Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, USA

ABSTRACT.—Parental vocalizations that influence the feeding process of nestling passerines have not been well studied. Vocalizations of Black-capped Chickadees (*Parus atricapillus*) were analyzed by audio and video recordings within the nesting cavity. One vocalization, the "squawk," stimulated gaping in nestlings during the feeding process. Parents gave squawks most during the first 48 h posthatching when nestlings were frequently unresponsive to vocalizations and equally or more responsive to vibratory and other stimuli. Contrary to reports about other species, spontaneous gaping did not occur frequently at any age. Within the first 48 h posthatching, however, gapes frequently occurred to "irrelevant" stimuli. As nestlings aged, they gaped more frequently to stimuli directly associated with feeding, such as to squawks at three to seven days of age and to the parents' arrival at older ages. The parents' vocalization plays an important role in coupling the nestlings' gaping response with the appropriate situation, especially during the first days posthatching when nestling responses are coarsely tuned to appropriate stimuli. Received 13 January 1994, accepted 18 June 1994.

AVIAN SPECIES are reported to use a variety of stimuli including special vocalizations to evoke gaping during feeding of nestlings (Kuhlmann 1909, Messmer and Messmer 1956, Collias 1960, Bengtsson and Rydén 1981, Schuchmann 1983, Khayutin 1985, Welty and Baptista 1988). These studies also indicate that nestlings gape to a variety of stimuli other than the parents' vocalization and that patterns of gaping change during development. The timing and frequency of nestling gaping may have important implications for feeding efficiency in terms of the parents' investment of time, as well as the nestlings' rate of feeding and subsequent survival (Perrins 1965, Bengtsson and Rydén 1981). I examine how the parent's vocal behavior is involved in coupling the gaping of nestlings with the presentation of food in the Black-capped Chickadee (*Parus atricapillus*).

Few investigators have studied how parents influence the feeding process with vocalizations, despite the apparently wide occurrence among passerines of a vocalization that elicits nestling gaping (Welty and Baptista 1988). Kuhlmann (1909) examined artificial stimuli and a parental vocalization that elicited gaping in five species of passerines, but the results were not quantified. Khayutin and colleagues (summarized in Khayutin 1985) studied the devel-

opment of sensory organization and reaction to stimuli directly associated with feeding. Bengtsson and Rydén (1981) investigated the use of the parent's vocalization among other factors regulating feeding of asynchronously hatched nestlings. Little is understood, however, about the range of stimuli that elicit gaping in the wild, or how the vocalization is used in a broader context of adult vocal behavior at the nest site.

Despite the number of descriptions and studies of vocalizations of the Black-capped Chickadee (Ficken et al. 1978, Smith 1991), an adult vocalization used to stimulate gaping in nestlings was only briefly mentioned in Clemmons and Howitz (1990). The vocalization, named the "squawk," consists of usually a single note with a broad frequency range and brief duration (Fig. 1a; Clemmons 1993). Experimental analyses of the squawk as a stimulus for eliciting gaping and the possible role of learning are reported elsewhere (Clemmons 1993, 1995). Here, I characterize: (1) the acoustic environment of the nestling with regard to conspecific vocalizations; (2) the range of stimuli to which nestlings gape; (3) the relationship of the parents' vocalization to the nestlings' gaping response; and (4) the changes in all these with age of the nestlings.

METHODS

In May and June of 1991, nestling gaping and other details of the feeding process were videotaped at the nests of seven families (35 nestlings total) at Funic Point, University Arboretum, and Shorewood Hills of the Madison area, Dane County, Wisconsin. Adults were individually identified by colored leg bands with the exception of one pair that was unbanded. Four of the families had excavated their own cavities in snags of rotting wood, and three families nested in wooden nest boxes. Approximately 55 h of video recordings of chickadees at the nest sites were analyzed.

Video recordings were made with an RCA CC520 Proedit Video Camcorder with a 15-mm electret condenser microphone (Sony ECM-150T) placed inside the nesting cavity or box and connected to the camcorder. In order to videotape families inside nest boxes, the box was opened at the top and the camcorder attached to the tree. With families in natural cavities, holes were cut through the snags above nest level and the camcorder was supported by a tripod. A pen light was used to increase illumination when necessary. The camcorder was turned on, and then the observer walked about 10 m away from the cavity and observed the activities of the parents from a distance. When the camcorder was not in use, a piece of bark was wired over the hole.

Observations of behavior inside the nesting cavity were made in conjunction with playback experiments that tested the nestlings' responses to various acoustic stimuli (Clemmons 1993, 1995). Recordings of feedings were made before and between three playback experiments spaced at least 15 min apart on day 0 (day of hatching), 2, 4, 6, and 12 (or within 24 h of these ages). Observations and experiments were repeated on the same day after at least 2 h following the first session, except in cases of inclement weather or equipment failure. One family was lost to predation before day 6. Observations in one family of four nestlings was initiated on day 2 and in another family of seven nestlings on day 6.

The microphone inside the nesting cavity recorded sounds originating from both inside and outside of the cavity, allowing comparison of adult vocalizations in these two contexts and determination of events that were associated with nestling gaping. An event was recorded as being associated with gaping if the event preceded gaping within 1 s. Cases where two or more events occurred within 1 s preceding the gape were classified as "ambiguous" events; cases having unidentified or no apparent events associated with gapes were classified as "unknown."

The events associated with gaping were tallied for each recording session according to frequencies of occurrence. Each event was counted only once per visit to the nest by a parent. For example, if a parent produced squawks that were followed by gaping 10 times during a single visit, the squawk was counted

only once for this visit. The proportion of responses for each stimulus category was determined for each family at each age. The plotted means of each stimulus category and table values represent the average responses of families.

I recorded 620 visits to the nests by parents; 547 of these were feeding trips. Squawks and feeding attempts were counted during each feeding visit of a parent to the nest. A feeding attempt was defined as when a parent placed food in the nestling's mouth or touched the nestling's bill with food. The number of visits to the nest per recording session varied from 0 to 39.

Mean numbers of visits with squawks, squawks per visit, and feeding attempts per visit were determined for each family at each sampled nestling age. The success rate at which squawks elicited gaping was calculated by dividing the proportion of squawks associated with gaping by the number of squawks given during that visit to the nest. Means were calculated for each family at each nestling age. In this analysis, there were 25 visits to the nest in which squawks occurred, and both parents were inside the cavity while the female was brooding. These visits were not included in the analysis because the female was sitting on the young; as a result, whether the nestlings gaped in response to the squawk could not be determined.

Statistical analyses varied according to the type of data and questions being addressed. I employed permutation tests using P-stat written by Bill Engels (Department of Genetics, University of Wisconsin-Madison), Spearman rank correlations, Friedman two-way analysis of variance (Systat 1992), multiple-comparison tests (Daniel 1990), and a variance test for homogeneity of the binomial distribution (Snedecor and Cochran 1967).

RESULTS

The motor response of gaping.—Gaping is the wide opening of the bill with the head and neck extended upwards in a posture to receive food. More specifically, gaping typically involved the following movements and postures: (1) The head was lifted and the neck extended upward, usually with a sudden movement. Lifting of the head occurred in about 57 ms (range 7–133 ms), as measured by freeze-frame counts from video recordings of 28 gaping observations from three families of nestlings at day 0. (2) The head was held up, usually free from contact with surfaces. (3) The mouth was opened widely with the outer membranes forming a nearly complete circle or slight oval. (4) During the upward thrust of the head, the body was kept in balance by bracing the forelimbs on a substrate (e.g. bottom of

TABLE 1. Mean proportion (\pm SE) of gapes following four categories of events (vocalization, parent's arrival, unknown, and other). Proportion of gapes to each category first determined by family, and then mean proportions calculated across families. Friedman analyses of differences among categories by age and pairwise comparisons reported at bottom. Family differences indicated by asterisks (variance test for homogeneity of binomial test): *, $P < 0.05$; **, $P < 0.01$.

| | Age* (days) | | | | |
|-----------------------------------|---------------------|---------------------|---------------------|--------------------|-------------------|
| | 0 | 2 | 4 | 6 | 12 |
| Vocalization | 0.207 \pm 0.084** | 0.678 \pm 0.137** | 0.561 \pm 0.083** | 0.518 \pm 0.061 | 0.243 \pm 0.039 |
| Parent arrives | 0.069 \pm 0.034* | 0.103 \pm 0.049** | 0.208 \pm 0.055** | 0.342 \pm 0.051 | 0.679 \pm 0.031 |
| Other | 0.602 \pm 0.074* | 0.194 \pm 0.097** | 0.193 \pm 0.063* | 0.119 \pm 0.037 | 0.109 \pm 0.043 |
| Unknown | 0.122 \pm 0.089** | 0.025 \pm 0.025** | 0.038 \pm 0.020 | 0.021 \pm 0.021* | 0 |
| Total no. gapes | 138 | 152 | 159 | 136 | 178 |
| Friedman test (P) | 0.030 | 0.051 | 0.003 | 0.002 | 0.001 |
| Multiple comparisons ^b | a | b | b, c, d | b, c, e | b |

* At age 0, $n = 5$ families; at all other ages, $n = 6$.

^b Letters refer to: (a) other \times unknown; (b) vocalization \times unknown; (c) arrival \times unknown; (d) vocalization \times other; (e) arrival \times other.

nest, sides of nest, cavity wall, or on siblings). (5) The gape was held for several seconds ($\bar{x} = 7.52$ s, $n = 28$, range 2.3–22.0 s). At the end of the gape, the mouth was closed slowly while the head was lowered and the neck withdrawn.

Although the above description was the typical pattern of gaping, sometimes one or more of the above components were not involved. For example, the head and neck already may have been extended when a nestling gaped (usually from previous stimulation), or the mouth may have been opened to a lesser degree and for shorter periods of time. Sometimes a nestling displayed all of the above components except opening of the mouth. An action was considered to be a gape only if the mouth was open for more than 1 s.

Events preceding gaping.—Four general categories of events immediately preceded the gaping of nestlings: (1) parental vocalizations in

and near the nesting cavity; (2) parent's arrival at the nest or cavity entrance; (3) unknown events; and (4) other events ("other") of which most were tactile or vibratory (Tables 1 and 2). Often an event was followed by more than one nestling gaping. Because only the first nestling to gape was considered, these categories do not take into account the possibility that the actions or vocalizations associated with gaping of the first nestling may have served as a stimulus for gaping of other nestlings.

On day 0 the most common events preceding gaping were represented by parental vocalizations, as well as various vibratory and tactile stimuli associated with movement of the nest or of birds within the nest ("other" category; Table 2). Multiple comparisons ($\alpha = 0.15$) with the Friedman test indicated no significant differences between the frequency of gapes following the "vocalization" and "other" catego-

TABLE 2. Detailed information on "other" category (Table 1) showing gapes that followed events other than vocalizations, unknown events, or parent landing at the nest or cavity entrance. Values are $\bar{x} \pm$ SD by family (range in parentheses).

| Stimulus | Age* (days) | | | | |
|------------------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| | 0 | 2 | 4 | 6 | 12 |
| Parent leaves nest | 3 \pm 4 (0-11) | 2 \pm 2 (0-6) | 1 \pm 1 (0-4) | 1 \pm 1 (0-3) | 0.8 \pm 1 (0-2) |
| Parent or sibling movement in nest | 5 \pm 3 (1-9) | 0.7 \pm 1 (0-3) | 1 \pm 2 (0-5) | 0.5 \pm 0.8 (0-2) | 0 |
| Outdoor sounds ^b | 0.4 \pm 0.5 (0-1) | 0.8 \pm 1 (0-3) | 0.8 \pm 1 (0-3) | 0.7 \pm 0.8 (0-2) | 0.3 \pm 0.5 (0-1) |
| Movement of nest | 5 \pm 4 (1-10) | 0.8 \pm 1 (0-3) | 0.2 \pm 0.4 (0-1) | 0.2 \pm 0.4 (0-1) | 0.2 \pm 0.4 (0-1) |
| Ambiguous | 3 \pm 2 (1-6) | 0.3 \pm 0.8 (0-2) | 0.5 \pm 0.8 (0-2) | 0.7 \pm 1 (0-3) | 0.7 \pm 1 (0-3) |
| Total no. gapes | 84 | 27 | 26 | 17 | 12 |

* At age 0, $n = 5$ families; at all other ages, $n = 6$.

^b Noise from truck, human voice, etc.

ries ($P > 0.05$), but in four of the five families, the "other" category ranked higher. The frequency of gapes following events from the "other" category was significantly different from gapes following unknown events ($P < 0.05$) and approached significance from gapes following the parent's arrival.

As the nestlings aged, dramatic changes occurred in the relative frequencies of the four categories of events that preceded gaping, except for the unknown category, which was low for all ages. The frequency of gapes that followed events from the "other" category decreased suddenly after day 0, whereas the frequency of gapes that followed vocalizations peaked at day 2 (Table 1). After day 2, the frequency of gapes following vocalizations decreased steadily while an increasing proportion of gapes followed the parent's arrival. The parent's arrival was the most common event preceding gaping by day 12.

Contexts of adult vocalizations inside and near the nesting cavity.—Despite numerous studies on Black-capped Chickadee vocalizations (Ficken et al. 1978, Smith 1991), there is very little published on adult vocalizations of birds around the nest. I recorded six types of vocalizations produced inside the nesting cavity (Table 3). A seventh type, the "hiss," which is typically given to predators near (Clemmons and Lambrechts 1992) or inside the cavity (Odum 1942, Sibley 1955, Ficken et al. 1978), also occurred sometimes while I was setting up the camera and before the recording started.

The squawk (Fig. 1a) was the most frequent adult vocalization inside the cavity at most ages, approaching statistically significant levels on days 0 to 2 and significantly higher than other vocalizations at all other ages (Fig. 2). Other vocalizations inside the cavity included "twitters," "broken dees," notes of the "A-complex," "faint feebees," and "composite" vocalizations (described below). The twitter (Fig. 1b) commonly occurred when the male approached the brooding female and while he gave her the food, a contextual use not previously described for this vocalization. Broken dees (Fig. 1c), analogous to "courtship begging" vocalizations in other species, also were associated with the male feeding the female and sometimes were elicited from the brooding female by the male's nest-approach vocalizations. Faint feebees (soft renditions of the territorial song; Fig. 1h) and A-like notes (A-complex; Fig. 1d-f) have been associ-

ated with approach to the nest hole (Smith 1972, Ficken et al. 1978), but I sometimes recorded them inside the cavity. The "chatter" (Fig. 1f) consists of a series of short duration, rapidly repeated A-like notes that may or may not be preceded with a longer-duration, higher-frequency note, such as pictured in the figure, and is sometimes followed by one or more faint feebee notes. The name "chatter" was borrowed from a similar appearing sonagram recorded from captive chickadees published in Dixon and Stefanski (1970). One type of note in the A-complex, the "peek" note, is previously undescribed; it differs from other A-like notes by having a broad frequency range and strong emphasis in the initial upward frequency sweep (compare Fig. 1g with Fig. 1d-f). The contextual use of this note was not clear; it was given when the caller appeared to be hesitating or indecisive. Composite vocalizations consisted of combinations of notes from the traditional vocalization types described in Ficken et al. (1978) and occurred in a variety of contexts (Clemmons 1993). Although the variable see (Ficken et al. 1978) did not occur inside the nesting cavity in this study, I have previously observed the vocalization in the same context or in combination with the twitter (unpubl. data).

There were nine vocalization types recorded outside but near the nesting cavity (Table 3), including the six types recorded inside the cavity plus three others—the chick-a-dee call (Fig. 1i) given in situations of potential danger, the variable see given during various intrapair interactions, and the gargle, which preceded copulation and occurred in agonistic encounters with nonmates (Ficken et al. 1978, Ficken and Weise 1984, Ficken et al. 1987). There were no adequate recordings of the variable see and gargle.

In contrast to the context within the nesting cavity, squawks were significantly less frequent outside of the cavity than other vocalizations combined at each age sampled (Fig. 2). There was no single dominant type of vocalization, but the faint feebee was the most common, constituting 43.0% of the vocalizations given on day 0 and 38.4% on day 12 (Table 3). Faint feebees were significantly more frequent than squawks outside of the nest at all ages except day 0 (multiple comparisons with Friedman test, $P > 0.05$, $n = 6$). Faint feebees usually were more frequent than other vocalizations except for chick-a-dee calls and the A-complex.

TABLE 3. Overall occurrences of adult vocalizations by family inside and outside of nesting cavity. Values are $\bar{x} \pm SD$ (range in parentheses). Asterisks indicate significant differences among families (variance test for homogeneity of the binomial distribution): * $P < 0.05$; ** $P < 0.01$.

| | Age ^a (days) | | | | |
|---------|-------------------------|--------------------|-------------------|-------------------|------------------|
| | 0 | 2 | 4 | 6 | 12 |
| | Squawk | | | | |
| Inside | 93 ± 57 (48-176)** | 46 ± 34 (3-95)** | 34 ± 29 (3-89) | 22 ± 21 (3-48)* | 10 ± 8 (1-22)** |
| Outside | 19 ± 29 (0-69)** | 9 ± 13 (0-32)** | 3 ± 5 (0-12)** | 0.7 ± 2 (0-4)** | 2 ± 5 (0-13)** |
| | Twitter | | | | |
| Inside | 4 ± 6 (0-12)** | 1 ± 2 (0-4)** | 2 ± 3 (0-7) | 3 ± 4 (0-10)** | 0 |
| Outside | 0 | 0.2 ± 0.4 (0-1)* | 0.2 ± 0.4 (0-1) | 0.7 ± 2 (0-4) | 0 |
| | Faint feebee | | | | |
| Inside | 0 | 0 | 0.2 ± 0.4 (0-1) | 0.3 ± 0.8 (0-2) | 0.2 ± 0.4 (0-1) |
| Outside | 61 ± 33 (25-96)** | 57 ± 35 (12-107)** | 51 ± 50 (0-126)** | 27 ± 17 (2-44)** | 15 ± 13 (1-33)** |
| | A-complex | | | | |
| Inside | 16 ± 32 (0-64)** | 7 ± 15 (0-37)** | 0.7 ± 1 (0-3)* | 4 ± 7 (0-19)** | 0.2 ± 0.4 (0-1) |
| | | 32 ± 38 (2-84)** | 7 ± 10 (0-26)** | 31 ± 48 (1-127)** | 7 ± 6 (3-20)** |
| | Broken dee | | | | |
| Inside | 0.2 ± 0.5 (0-1) | 0 | 0.3 ± 0.8 (0-2) | 0 | 0 |
| Outside | 10 ± 16 (0-36)** | 6 ± 12 (0-30)** | 4 ± 10 (0-24)** | 5 ± 13 (0-33)** | 0.5 ± 1 (0-3) |
| | Composite | | | | |
| Inside | 2 ± 3 (0-7)** | 0.5 ± 0.8 (0-2) | 1 ± 1 (0-3) | 1 ± 3 (0-7) | 0 |
| Outside | 3 ± 2 (0-5)* | 6 ± 11 (0-27)** | 5 ± 9 (0-24)** | 3 ± 5 (0-12)** | 2 ± 4 (0-11)** |
| | Chick-a-dee | | | | |
| Inside | 0 | 0 | 0 | 0 | 0 |
| Outside | 32 ± 40 (1-103)** | 16 ± 21 (0-51)** | 13 ± 14 (0-35)** | 54 ± 93 (0-234)** | 12 ± 17 (0-43)** |
| | Variable see | | | | |
| Inside | 0 | 0 | 0 | 0 | 0 |
| Outside | 0 | 0 | 0.2 ± 0.4 (0-1) | 0 | 0.5 ± 1 (0-3) |
| | Gargle | | | | |
| Inside | 0 | 0 | 0 | 0 | 0 |
| Outside | 0 | 0.3 ± 0.5 (0-1) | 0 | 0 | 0 |

^a At age 0, n = 4 families (inside), n = 5 (outside); at all other ages, n = 6.

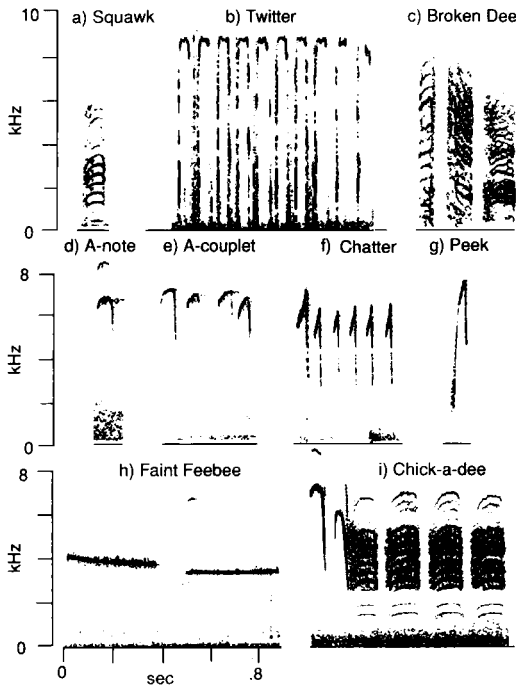


Fig. 1. Sonograms of parents' vocalizations occurring inside and near nesting cavity. Gargles and variable sees not shown.

Comparing the two contexts inside and outside the nesting cavity, there were significant family differences in frequencies of occurrence for most vocalization types with large sample sizes (>15), except for squawks on day 6 inside the cavity ($P < 0.05$, variance test for homogeneity of the binomial distribution). Differences in the proportional frequencies of squawks occurring inside the nesting cavity compared with outside approached significance at day 0 and were significant at all other ages (day 0, $P = 0.068$; all other ages, $P < 0.05$, Wilcoxon matched-pairs signed-ranks test) and for faint feebees at each sampled age except day 0 (day 0, $P = 0.068$; all other ages, $P < 0.05$). The frequencies of occurrences of twitters, A-complexes, broken dees, or composite vocalizations did not differ significantly between the "inside" and "outside" contexts at any age ($P > 0.075$).

Association of squawks with nestling gaping and feeding.—The squawk was the most common vocalization associated with nestling gaping. The difference between the proportion of gapes following squawks compared with other vocalizations approached significance at day 0 and

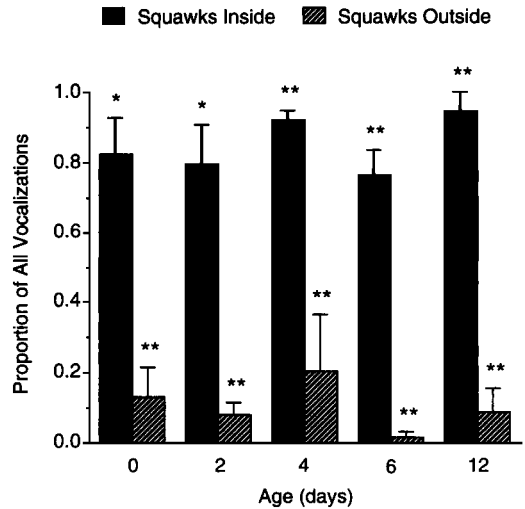


Fig. 2. Proportion of vocalizations that were squawks occurring inside (solid) and outside nesting cavity (hatched). Whiskers indicate SE. Asterisks indicate significance levels testing whether there were differences in frequencies of occurrence between squawks and other vocalizations within each context (Wilcoxon matched-pairs signed-ranks test: *, $P < 0.10$; **, $P < 0.05$). Sample size four families (inside) and five (outside) for age 0, and six for other ages. Total number of each vocalization type for each context provided in Table 3.

was significant ($P < 0.05$) at all other ages (Fig. 3). In three families, gapes followed only squawks. The Spearman correlation coefficient between the total frequency of squawks and the frequency of squawks that preceded gaping was positive in two of the other families and negative in two. Although nestlings gaped mostly at squawks and squawks were the most frequently occurring vocalization in the cavity (Fig. 2), there was no clear association between the proportion of gapes to squawks and the frequency of occurrence of squawks.

Production of squawks was greatest at day 0 (Fig. 4). As nestlings aged, the parents produced fewer squawks per visit ($r_s = -1.0$, $n = 5$, $P = 0.05$; two-tailed Spearman rank correlation test of means at each age). By day 4, squawks occurred in 68.0% of the visits at the rate of only one or two per visit; by day 12, they occurred in 20.0% of the visits, but usually only once.

If the parents use the squawk to activate nestling gaping during feeding, parents should carry food when they squawk, and they should squawk if no nestlings are gaping. A family

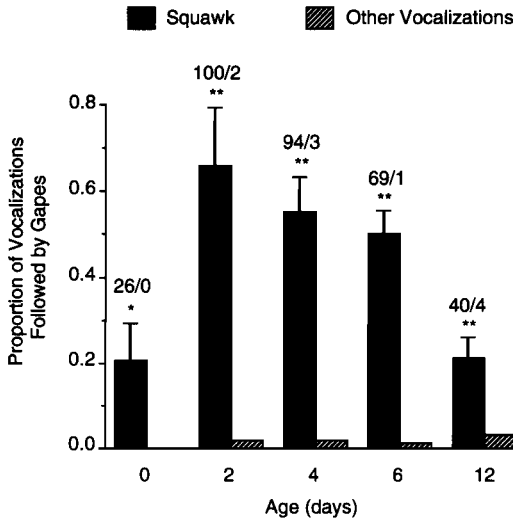


Fig. 3. Proportion of nestling gapes that followed squawks compared with other adult vocalizations (Wilcoxon matched-pairs signed-ranks test: *, $P < 0.10$; **, $P < 0.05$). Whiskers indicate SE. Sample size four families for age 0 and six for other ages. Total number of gapes following squawks (above) and other vocalizations (below) given above bars.

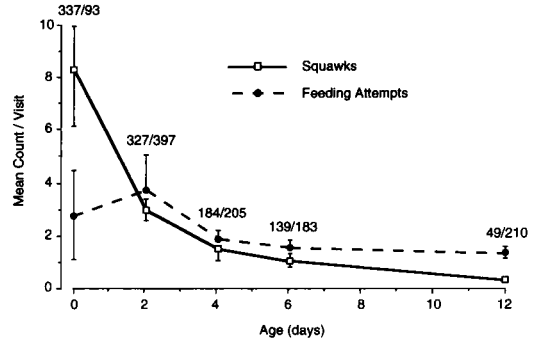


Fig. 4. Family mean rates \pm SE of squawks and feeding attempts by parents with age of nestlings. Feeding attempt defined as touching nestling's bill with food or placing food in nestling's mouth. Sample size four families for age 0 and six for other ages. Total number of squawks (above) and feeding attempts (below) given above data points.

average of $84.8 \pm$ SD of 16.8% of the squawks were given inside the nesting cavity ($P < 0.01$, $n = 7$ families; two-tailed permutation test). Callers carried food in an average of $93.2 \pm 10.8\%$ of the cases where it could be observed whether or not a caller carried food ($P < 0.002$, $n = 7$ families; two-tailed permutation test). That the caller sometimes has an empty bill suggests an alternative use or uses of the vocalization, a possibility analyzed in another study (Clemmons 1993). Although adults possibly could carry hidden food for themselves, whether or not they carry food for the young is reliably observed. Parents with "apparently" empty bills, for example, never fed nestlings during any of the observations.

Usually, a parent with food squawked inside the nesting cavity if there were no nestlings gaping ($P < 0.001$, $n = 7$ families; two-tailed permutation test). Of 1,150 squawks where all of the nestlings' responses were visible in the video recording, only 5.9% were given when one or more nestlings were already gaping. In these cases: (1) the parent was unsuccessful at feeding the gaper and then squawked apparently to stimulate a different nestling to gape; (2) the gape was closing or not fully open; (3)

the parent was positioned so that it could not see the gaper; or (4) a parent could not reach the gaper. In at least one case the squawk resulted in already gaping nestlings extending their heads higher so that the parent could reach.

Most squawks were given upon entry into the nesting cavity or as a parent landed at the entrance. Sometimes the male perched at the entrance and passed food to the brooding female who then sometimes emitted one or more squawks either before or after the male flew off. Older nestlings typically vocalized and gaped vigorously as soon as a parent landed at the cavity entrance. This obviated the need for additional stimuli and may explain why squawks were less common after the first week post-hatching (Table 1). With older nestlings, squawks sometimes were given during the first visits after the camcorder had been set up. Hence, the nestlings may have been in a defense posture when the parent first arrived and the parent used the signal to release them from this posture.

Squawks, gaping, and feeding efficiency.—If squawks are used to sustain the feeding process until successful feeding has occurred, the rate of squawks should decrease as fewer feeding attempts are required. This prediction was supported by observations (Fig. 4; $r_s = 0.90$, $n = 5$, $P = 0.05$; one-tailed Spearman rank correlation test of means at each age). Note that in Figure 4 on day 0, the number of feeding attempts was low relative to the number of squawks. Fre-

quently, at this age, a parent brought food to the nest and squawked numerous times, but the nestlings were slow to gape or none of the nestlings gaped; therefore, the parent could not make a feeding attempt (as defined in this study). In these cases the parent either ate the food or left the nest while still carrying food. At this age of the nestlings, the rate of squawks (which reflects the parent's attempt to stimulate gaping) was a better indicator of the parents' active role in regulating feeding than rate of feeding alone, as sometimes used in other studies.

As the nestlings aged, they not only were more likely to swallow the food presented, but also became more responsive to the squawk, although this difference only approached significance (Fig. 5; $r_s = 0.90$, $n = 5$, $P = 0.10$; two-tailed Spearman rank correlation test of means at each age). The success rate of squawks in eliciting gapes was relatively low at day 0 (<50%) and then increased to nearly 90% by day 4.

DISCUSSION

Many species of passerines reportedly have a "special" vocalization used to stimulate nestlings to gape during feeding. Of the many kinds of vocalizations produced by chickadees near and inside the nesting cavity, only the squawk was regularly associated with the gaping of nestlings. This association was based in part on the frequency of contextual use and in part on the frequency of nestling response. It does not imply that the only function of the squawk is to elicit nestling gaping nor that nestlings have a specific response to the squawk. The squawk occurred, though less frequently, in intrapair interactions and in situations when the nestlings were not present, suggesting a complex role of the squawk in a variety of intrafamilial interactions (Clemmons 1993). Although the proportion of gapes following squawks compared with other vocalizations was not correlated with the frequency of such vocalizations, other reasons could explain the apparent selective response to the squawk, such as the proximity and orientation of the caller to nestlings, or the amplitude of the vocalization. Whereas one of the obvious functions of the squawk is to elicit nestling gaping, the variable uses and responses to the signal require further study (Clemmons 1993).

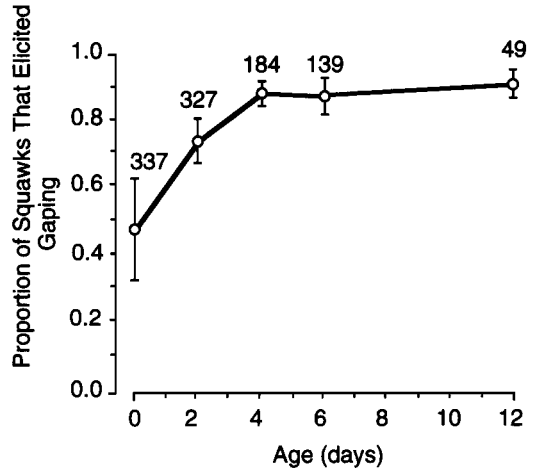


Fig. 5. Mean \pm SE of proportion of squawks for each family that stimulated gaping in nestlings. Sample size four families for age 0 and six for other ages. Total number of gapes provided above data points.

There are at least two characteristics of feeding interactions that are shared widely among passerines, including: (1) the use of an adult vocalization to stimulate nestling gaping; and (2) the replacement of a vocal stimulus with other kinds of stimuli associated with the parent's arrival around the time that the nestlings' eyes open (Kuhlmann 1909, Bengtsson and Rydén 1981, Khayutin 1985, present study). Other common characteristics are that: (1) the feeding procedure is slow during the first few days post-hatching, requiring several feeding attempts by the parents before the food is successfully delivered; (2) the number of vocalizations given by the parents is greatest during the first few days posthatching; and (3) the parent is most likely to give the vocalization when there are no nestlings gaping (Bengtsson and Rydén 1981, present study).

One difference from other studies is that tactile and vibratory stimuli accounted for a large proportion of gapes in Black-capped Chickadees at day 0, whereas other species were reported to be less responsive to tactile stimuli until a later age. In Kuhlmann's study (1909) of the feeding response in nestlings of five passerine species, including the American Robin (*Turdus migratorius*), Chipping Sparrow (*Spizella passerina*), Rose-breasted Grosbeak (*Pheucticus ludovicianus*), Red-winged Blackbird (*Agelaius phoeniceus*), and Brown Thrasher (*Toxostoma ruf-*

um), the parent's vocalization was the most effective stimulus during the first day posthatching and then was replaced by visual and tactile cues associated with feeding in older nestlings. Similar findings have been reported with the Pied Flycatcher (*Ficedula hypoleuca*), Great Tit (*Parus major*) and Redstart (*Phoenicurus phoenicurus*; Khayutin 1985).

Another apparent difference from other studies is the diminished role that spontaneous gaping, or gaping in the absence of external stimuli, plays with hatchling Black-capped Chickadees. For asynchronously hatching species such as the Pied Flycatcher, Great Tit, and European Blackbird (*Turdus merula*) (chickadees are also asynchronous), it has been suggested that spontaneous gaping increases the chance that a younger nestling will be fed when the gaping coincides with a feeding (Bengtsson and Rydén 1981, Khayutin et al. 1988). Bengtsson and Rydén (1981), for example, reported a 40% incidence of spontaneous gaping in the Great Tit when nestlings were one to two days of age, and Khayutin et al. (1988) noted that spontaneous gaping in newly hatched Pied Flycatcher nestlings occurred 80% of the time that parents were away. With chickadees, by contrast, only 13% of gapes occurred without an observable stimulus, and this value is inflated because the squawk as a stimulus was counted only once per visit. Also, it is possible that I did not detect the external stimulus in some cases.

Several reasons could account for the differing explanations among studies about the role of spontaneous gaping. Khayutin et al. (1988) suggested that younger nestling Pied Flycatchers gaped spontaneously because of increased hunger levels. If so, rates of spontaneous gaping will depend on food availability in the habitat or on asymmetry in food acquisition among siblings (and perhaps, on degree of hatching asynchrony). Differences among species in their tolerance for human disturbance during observation also may play a role, thus affecting the rate of parental feeding and subsequent level of hunger in the nestlings. For example, Kluyver (1961), who studied both Black-capped Chickadees and Great Tits, had the impression that Black-capped Chickadees were more tolerant of human disturbance at the nest than their congeners in Europe. Finally, it is not clear from these other studies whether there were specific attempts to document all factors that

stimulate gaping in the natural setting, or even what constituted the definition of spontaneous gaping.

Although spontaneous gaping was not characteristic of newly hatched Black-capped Chickadees, at least 40% of all stimuli that elicited gaping at day 0 were "irrelevant" or less predictive of a feeding. The squawk, therefore, appears to play a critical role in coupling gaping with the presentation of food during a period when nestlings tend to gape inappropriately.

Other studies suggest or demonstrate that parents adjust their feeding rates according to information they receive from nestlings about nutritional status (Kluyver 1961, Henderson 1975, O'Connor 1975, Bengtsson and Rydén 1983). In my study, parents made great attempts to arouse nestlings during the first few days posthatching as demonstrated by the long bouts of squawks used when nestlings were unresponsive. Although I did not consider the degree to which nestlings regulated feeding rate, the frequency of squawks increased when hatchling response decreased (compare Figs. 4 and 5), a result opposite to that expected if nestling responsiveness regulated parental feeding rate alone. At least during the first few days posthatching when nestlings were relatively inactive, the parent's frequent use of squawks and persistent feeding attempts appeared to be major factors driving the feeding interaction. As Figure 4 shows, the number of feeding attempts when measured by bill touches or, in other studies, the rate of visits to the nest (Kluyver 1961, Royama 1966) at day 0 does not accurately reflect the active role of the parents in regulating nestling feeding rates.

ACKNOWLEDGMENTS

I am grateful to: Jack P. Hailman, Jeffrey R. Baylis, Theodore Garland, Jr., Keith R. Kluender, and Charles T. Snowdon for guidance during the study and helpful comments on the manuscript; J. R. Baylis and C. T. Snowdon for loan of equipment; John E. Dallman, Kenneth G. Olesen, and Richard J. Ganje for building nest boxes; Marcel M. Lambrechts for discussions and comradeship in the field; and Hank, Caroline, and Henry Clemmons for assistance in the field and many other kinds of invaluable support. The study was aided by grants from John Jefferson Davis Funds, a Henry Nathan Netzer and Bernard Netzer Brouchoud Scholarship, and a Vilas Graduate Fellowship.

LITERATURE CITED

- BENGTSSON, H., AND O. RYDÉN. 1981. Development of parent-young interaction in asynchronously hatched broods of altricial birds. *Z. Tierpsychol.* 56:255-272.
- BENGTSSON, H., AND O. RYDÉN. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the Great Tit *Parus major*. *Behav. Ecol. Sociobiol.* 12:243-251.
- CLEMMONS, J. R. 1993. Nest-site communication and other behavior between mates, parents and offspring in the Black-capped Chickadee, *Parus atricapillus*. Ph.D. dissertation, Univ. Wisconsin, Madison.
- CLEMMONS, J. R. 1995. Development of a selective response to an adult vocalization in nestling Black-capped Chickadees. *Behaviour* 132:1-20.
- CLEMMONS, J., AND J. L. HOWITZ. 1990. Development of early vocalizations and the chick-a-dee call in the Black-capped Chickadee, *Parus atricapillus*. *Ethology* 86:203-223.
- CLEMMONS, J. R., AND M. M. LAMBRECHTS. 1992. The waving display and other nest site anti-predator behavior of the Black-capped Chickadee. *Wilson Bull.* 104:749-656.
- COLLIAS, N. E. 1960. An ecological and functional classification of animal sounds. Pages 368-391 in *Animal sounds and communication* (W. E. Lanyon and W. N. Tavolga, Eds.). Publication 7, American Institute of Biological Sciences, Washington, D.C.
- DANIEL, W. W. 1990. *Applied nonparametric statistics*, 2nd ed. PWS-KENT, Boston.
- DIXON, K. L., AND STEFANSKI, R. A. 1970. An appraisal of the song of the Black-capped Chickadee. *Wilson Bull.* 82:53-62.
- 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., AND C. M. WEISE. 1984. A complex call of the Black-capped Chickadee (*Parus atricapillus*). I. Microgeographic variation. *Auk* 101:349-360.
- FICKEN, M. S., C. M. WEISE, AND J. A. REINARTZ. 1987. A complex vocalization of the Black-capped Chickadee. II. Repertoires, dominance and dialects. *Condor* 89:500-509.
- HENDERSON, B. A. 1975. Role of the chick's begging behavior in the regulation of parental feeding behavior of *Larus glaucescens*. *Condor* 77:488-492.
- KHAYUTIN, S. N. 1985. Sensory factors in the behavioral ontogeny of altricial birds. Pages 105-152 in *Advances in the study of behavior*, vol. 15 (J. S. Rosenblatt, C. Beer, M.-C. Busnel, and P. J. B. Slater, Eds.). Academic Press, Orlando, Florida.
- KHAYUTIN, S. N., L. P. DMITRIEVA, AND L. I. ALEXANDROV. 1988. Psychobiological aspects of the acceleration of postembryonic development in the asynchronous breeder, Pied Flycatcher (*Ficedula hypoleuca*). *Int. J. Comp. Psychol.* 1:145-166.
- KLUYVER, H. N. 1961. Food consumption in relation to habitat in breeding chickadees. *Auk* 78:532-550.
- KUHLMANN, F. 1909. Some preliminary observations on the development of instincts and habits in young birds. *Psychol. Rev. Monogr. Ser.* 11:49-85.
- MESSMER, E., AND I. MESSMER. 1956. Die Entwicklung der Lautäußerungen und einiger Verhaltensweisen der Amsel (*Turdus merula merula* L.) unter natürlichen Bedingungen und nach Einzelaufzucht in schalldichten Räumen. *Z. Tierpsychol.* 13:341-441.
- O'CONNOR, R. J. 1975. An adaptation for early growth in tits, *Parus* spp. *Ibis* 117:523-526.
- ODUM, E. P. 1942. Annual cycle of the Black-capped Chickadee. 3. *Auk* 59:499-531.
- PERRINS, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. *J. Anim. Ecol.* 34:601-647.
- ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits *Parus major*. *Ibis* 108:313-347.
- SCHUCHMANN, K.-L. 1983. Analyse und Ontogenese des Sperrverhaltens bei Trochiliden. *J. Ornithol.* 124:65-74.
- SIBLEY, C. G. 1955. Behavioral mimicry in the titmice (Paridae) and certain other birds. *Wilson Bull.* 67:128-132.
- SMITH, S. M. 1991. *The Black-capped Chickadee: Behavioral ecology and natural history*. Cornell Univ. Press, New York.
- SMITH, S. T. 1972. Communication and other social behavior in *Parus carolinensis*. *Publ. Nuttall Ornithol. Club*, No. 11.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1967. *Statistical methods*, 6th ed. Iowa State Univ., Ames.
- SYSTAT. 1992. *SYSTAT: Statistics*, version 5.2 edition. SYSTAT, Inc., Evanston, Illinois.
- WELTY, J. C., AND L. BAPTISTA. 1988. *The life of birds*, 4th ed. W. B. Saunders, New York.