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Development of Early Vocalizations and the Chick-a-dee Call in the Black-capped Chickadee, *Parus atricapillus*

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Abstract

The chick-a-dee call of the black-capped chickadee (*Parus atricapillus*) is composed of discrete elements, or notes, that are combined to form hundreds of different calls. To investigate the development of this complex call, 12 families of color-marked chickadees were observed and recorded in the wild. Vocalizations were monitored for 18 d in the nest and 14—18 d postfledging. Most vocalizations of nestlings and fledglings were associated with feeding. At hatching, vocalizations consisted of a structurally simple note type that became more complex and variable with age. Around 9—12 d, the development of the call occurred, when single notes became organized into a multiple-note unit. Notes within the call differentiated into higher frequency, rapidly modulated initial note types and a lower frequency, moderately modulated terminal note type, features also present in adult chick-a-dee calls. Several adult-like calls including chick-a-dee calls, fee-bee songs, and a subsong-like vocalization developed prior to fledgling dispersal. Based on resemblances of note structure and general call structure, the chick-a-dee call appeared to develop from calls of nestlings and fledglings, although not necessarily in a chronologically linear progression. Some features of the chick-a-dee call closely resembled features of older nestling and fledgling calls, while other features more closely resembled the sounds of very young nestlings. Vocal development in the chickadee is compared with song and call development in other species, and the possible significance of acoustic resemblances between chick-a-dee calls and the food-associated calls of nestlings and fledglings is discussed.

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Introduction

One of the best known animal communication systems sharing properties with human language is a call of a songbird, the chick-a-dee call of the black-capped chickadee, *Parus atricapillus*. The call is recombinant, such that discrete note types, referred to as A-, B-, C-, and D-notes (Fig. 1), are variously repeated

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and combined to produce hundreds of different signals, a feature previously considered unique to human language (HAILMAN et al. 1985; HAILMAN & FICKEN 1986). The chick-a-dee call has important social function: it is given by all mature individuals at all times of the year, and it occurs in a wide variety of situations such as pair or flock coordination, mobbing predators, boundary disputes, separation of an individual from a flock, and disturbance at the nest (ODUM 1942; FICKEN & WITKIN 1977; FICKEN et al. 1978). Other studies show that adult chickadees modify the acoustic structure of the D-note in the chick-a-dee call throughout adulthood in accordance with changing social affiliations (MAMMEN & NOWICKI 1981; NOWICKI 1989). Despite the growing interest in the chick-a-dee call as a system for animal communication studies, there is yet no detailed study of its development. This study explores the early structural stages of vocal ontogeny in the black-capped chickadee under natural field conditions with the primary aim of understanding how the adult chick-a-dee call develops from the vocalizations of the young.

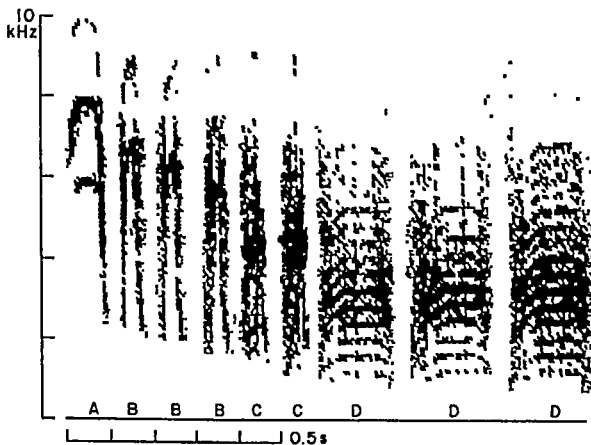


Fig. 1: Spectrogram of an adult chick-a-dee call recorded in the field from one of the parents in this study. A-, B-, and C-notes are collectively referred to as "introductory" notes and have both structural and syntactic properties that distinguish them from the "terminal" D-note (see HAILMAN et al. 1985)

Most studies of avian vocal ontogeny have examined development of song in laboratory-reared birds. Typically, songs are structurally complex signals given by males during the reproductive season that serve to attract unmated females, coordinate reproductive activities, and space territorial males. By contrast, calls are usually brief and simple in pattern and occur under a variety of conditions (THORPE 1956, 1961; MUNDINGER 1970; NOTTEBOHM 1972). The black-capped chickadee, by contrast, has a simple two-note song, the fee-bee, and at least two complex calls, the gargle and the chick-a-dee call (FICKEN et al. 1978; HAILMAN et al. 1985).

In the oscine species so far examined, song development involves a "sub-song" phase, usually within the first month of fledging, when vocalizations are highly variable in structure and include warbling sounds interspersed with call notes (LANYON 1960; MARLER & PETERS 1982 a, b). In the next phase, "rehearsed" (LANYON 1960) or "plastic" (MARLER & PETERS 1982 a, b) song, a variety of identifiable song elements are added, some of which will later compose the adult

song. The final stage involves the elimination of warbling, call notes, and a reduction in the number of song elements.

The development of vocalizations other than song is less well studied. Most species begin vocalizing within the first week of hatching. These early vocalizations undergo substantial change during the first months, and there are numerous examples of adult calls developing from these earlier vocalizations (LANYON 1960; THIELCKE 1965; SASVÁRI 1970; THOMPSON & RICE 1970; WILKINSON & HUXLEY 1978; ANDERSON 1978; COSENS 1981; HOWES-JONES 1984). However, more studies are needed to document these ontogenetic changes using quantitative methods, particularly of multiple-note calls having complex structural properties. The objective of this study was to describe the earliest stages of vocal development in the black-capped chickadee under natural field conditions, and to document the developmental origins of a complex vocalization, the chick-a-dee call.

Methods

Study Area and Subjects

The study was conducted within a 5-km² tract of the Cedar Creek Natural History Area in Anoka and Isanti Counties, Minnesota. The area consists of northern pin oak forests and burr oak savannahs interspersed with abandoned fields and marshes. Winter flocks of chickadees in the Cedar Creek area begin to disband in March. After establishing breeding territories, mated pairs nest in tree cavities, usually of their own excavation, and lay a clutch of 4 to 9 eggs. The parents cooperate in feeding and caring for the young during the 17–18-d nestling period and the 19–24-d fledgling period, until the young disperse (HOWITZ 1981, unpubl. data).

About 360 h were spent in the field from 24 May through 13 July, 1986, recording and observing the parents of 12 families and their 74 offspring (\bar{x} brood = 6 nestlings). Two of the broods, 14 offspring, were lost by predation between 12–15 d. Except for a single nest made in the natural cavity of a living maple, the nests were constructed in cavities excavated by the birds 0.5–5.0 m above ground in decaying hardwood stumps. To enable the recognition of individual birds, the adults were color banded prior to the breeding season, and offspring were banded as nestlings.

Recording and Observations

Nestlings

Before each recording session, a Sony ECM-150T 15-mm electret condenser microphone was placed in the nest hole through the natural entrance. An extension cord connected the microphone to one channel of a Sony TC-158SD stereo cassette-recorder. Through the second channel an observer operating the recorder at about 10 m from the nest maintained a running commentary while watching the adults through binoculars. A second observer with binoculars read leg bands and monitored visits of the adults to the nest. The parents appeared undisturbed by these observations.

A recording session began when a parent with food approached the nest hole. Two feedings and the interval between feedings were recorded in each session. Recordings were made every third day beginning with hatching. Recordings missed because of inclement weather were taken the next day.

Hatching dates were known for 9 of the 12 broods. A brood was aged day 0 on the day of hatching, or when a completely hatched brood was all eggs the previous day. An entire clutch usually hatched over a 24-h period. Hatching was not observed at three of the 12 nests, and ages were estimated by back-dating from the fledging date. The 9 known-aged broods fledged on day 17 or 18 post-hatching.

About d 12, each brood was removed from the nest for color banding and weighing. A hole was cut into the stump at nest level to extract the nestlings. After returning the young to the nest, a piece of bark was wired over the hole.

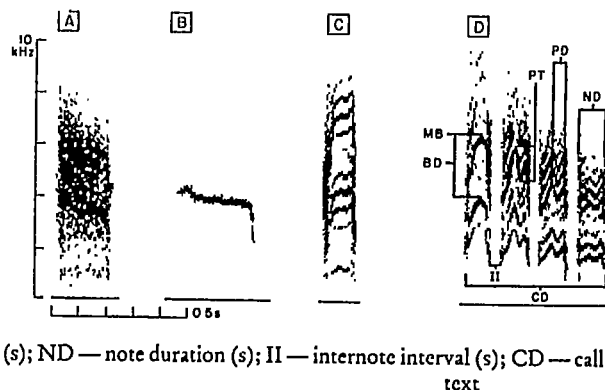


Fig. 2: Spectrograms showing three basic kinds of acoustic structure of notes and the variables measured: A: "noisy", B: pure tone, C: frequency components with side-bands, D: variables measured: MB — maximum energy band (kHz); BD — difference between the two maximum energy bands (kHz); PT — peak-to-trough difference (kHz); PD — duration difference between peaks

(s); ND — note duration (s); II — internote interval (s); CD — call duration (s). For further details see text

Fledglings

After fledging, the families ranged within an approx. 1-km² area, usually including the nest site. Fledglings were recorded using the Sony recorder and the Uher microphone mounted in a 45.7-cm Gibson parabolic reflector. Recordings were obtained every third or fourth d except in a few cases when fledglings were too high to record or families could not be located. Recordings ended after 18 d postfledging because most fledglings had dispersed before the next scheduled recording. Only those recordings of fledglings identified by color bands were used in the analysis.

Analysis

Sound recordings were analyzed on a Uniscan II spectrum analyzer (frequency range = 10 kHz; resolution = 80 Hz). Vocalizations were analyzed by visual inspection and with quantitative measurements made from the printed spectrograms. Because individual nestlings could not be identified, the nestling vocalizations are analyzed by family; fledglings were further analyzed by individual. Although vocal structure varied within and among families, the focus of the description is on common patterns of change.

A *note* is defined as a continuous trace or temporally overlapping traces on the frequency axis that are separated by > 5 ms from other such notes. In nestling and fledgling chickadees, the acoustic quality of notes is variable. A note may be "noisy," having a broad range of frequency components (Fig. 2A). At the other extreme, a note may have only a narrow frequency band resembling a pure tone (Fig. 2B). Alternatively, a note may have temporally overlapping spectral components, each of which will be referred to as a frequency band (Fig. 2C). Finally, a note may have any combination of the above three qualities. A *call*, as defined by HAILMAN et al. (1985) for chick-a-dee calls, consists of a train of notes (refer to Fig. 1) in which the notes are separated temporally by about 0.1 s, although usually less in immature calls of this study. A call is separated from other calls by longer intervals of silence, 2–30 s in adult chick-a-dee calls.

Spectrograms from the 12 families first were visually inspected to make a general record of the types of vocalizations and their ontogenetic changes. Vocalizations were classified according to characteristics exhibiting visually obvious and consistent patterns of change with age, such as frequency-modulation patterns. The classification does not necessarily represent discrete natural categories, but rather it serves to highlight a series of events representing a developmental progression shared by all nestlings and fledglings. The criteria used for classification are provided in Table 1 (below) and are described in further detail under Results.

Once vocalizations were classified, frequencies of occurrence of each type at each age were tabulated to show the ontogenetic replacement of vocal types with age. Four families with the most complete recorded samples were selected for analysis. 20 notes, when available, were selected from each nestling family at each age, as described above, for a total of 447 notes. For fledglings, five notes, when available, from each fledgling were randomly selected for a total of 101 notes. Frequencies of occurrence of individual fledgling call types were calculated from the entire sample. For the

quantitative measurements of nestling vocalizations, 10 notes, when available, were randomly selected from each family at d 0, 3, 6, 9, 12, and 15 from each of two sampling periods: 13 s after a parent entered the nest, and 13 s after a parent left the nest. If the parent's visit to the nest was less than 13 s, the "parent-in" sample ended when a parent left the nest. Vocalizations occurred erratically at other times, but appeared similar to those given during the sampling periods and were not included in the analysis. Except for 0—1-d-old nestlings and some 15—17-d-old nestlings that called incessantly, nestlings tended to remain quiet while the parents were away. For the fledgling analysis, the two individuals having the most complete data set were selected from each of the same four families.

Examination of spectrograms indicated that frequency-modulation patterns and the number and distribution of frequency components in a note were features that changed dramatically with age. Hence, the following variables were selected to reflect these changes. 8 acoustic variables were measured, 6 applying to notes and 2 applying to calls (Fig. 2D, above): (1) MB (maximum band, kHz): the highest frequency peak of the band having the greatest amplitude (in case of a tie between two frequency bands, the highest one was selected). (2) BD (band difference, kHz): the frequency difference occurring where the two maximum bands diverged the most. This point was selected because in some notes the two highest frequency bands were not parallel and merged or diverged irregularly. (3) PT (peak-to-trough difference, kHz): in the maximum band, the frequency difference between the peak and the neighboring trough having the greatest frequency excursion. This variable was selected to measure the maximum contrast of frequency modulation in the note. (4) PD (peak difference, s): the difference in duration between the peak found in PT and its consecutive peak. (5) ND (note duration, s): onset to offset time of the note. (6) PN (peak number): the number of peaks of the maximum band with a peak arbitrarily defined as having a change in acoustic frequency over time greater than 250 Hz (Fig. 2D: one peak for the first and last notes, and two peaks for the other notes). (7) II (internote interval, s): the offset time of one note to the onset time of the next note. (8) CD (call duration, s): the onset to offset time of the call.

All statistical procedures were run with the SPSS-X packaged program (SPSS-X, INC. 1988). A cluster analysis based on the means of four continuous variables for notes was performed to show the structural similarities between note-types of food-associated vocalizations and chick-a-dee calls. The continuous variable, the peak difference, was dropped in this analysis because Spearman correlation coefficients showed that it was correlated with peak-to-trough difference. For the cluster analysis, we used the agglomerative hierarchical clustering procedure and average linkage method between groups based on Euclidean distances.

Results

Nestlings: General Activities

Chicks vocalized on the day of hatching. By the third day, most vocalizations were clearly associated with feeding. When a parent entered the cavity with food, the nestlings responded with a burst of vocalizing, and when the parent left, the rate and amplitude of these vocalizations subsided. Interfeeding intervals during the day varied widely, usually from 2 to 20 min, but sometimes up to 2 h. During the last week before fledging, interfeeding intervals were often less than 1 min. By age 15 d the vocalizations were heard several m from the nest and often persisted throughout the interfeeding intervals.

Vocalizations other than those associated with feeding occurred in presumed defense situations. The hiss, described by ODUM (1942) and FICKEN et al. (1978), was first recorded at 9 d and was elicited when the observers inserted the microphone into the cavity. This call was also given in the same context by the incubating or brooding female and was similar to hers in structure. The call begins with a brief, low-frequency burst produced by hitting the wings against the substrate, and is followed with a broad-band noisy vocalization. A second

defense call, previously called the distress call by ODUM (1942), sounds like a "squeal" and was elicited only when nestlings were removed from the nest for banding. The "squeal" also occupied a wide frequency range but with energy concentrated in one or more narrow bands. These two calls were recorded only in situations of human disturbance and were not included in the analysis.

Despite the seclusion of the nest, sounds of the outdoors could be heard inside the cavity, as evidenced by recordings made with the microphone. Hence, the young nestlings were exposed to a wide variety of adult vocalizations that could have influenced their vocal development from the day of hatching or earlier. Faint fee-bees, fee-bees, gargles, tseets, and chick-a-dee calls, previously described by FICKEN et al. (1978), were commonly heard around the nest and after the young fledged. Broken dees and variable sees were given by the female and were associated with the male feeding the female. Around the first week post-hatching, these two calls were no longer given and the male stopped feeding the female. Other apparently undescribed vocalizations include a note given by parents presumably to elicit the begging response, and calls combining notes from different call-types given primarily around the nest (unpubl. data).

Nestlings: Acoustic Structure and Chronological Changes of Vocalizations

The acoustic structure of vocalizations associated with feeding changed throughout the nestling period. The notes began as simple structures and gained complexity at each sampled age. The following description gives a chronological account of these changes.

Day 0—3

Vocalizations at this age consisted of a single repetitious note-type, referred to as a simple peep. On a spectrogram this note ranged from a nearly vertical downslope to a chevron-shaped figure with a single frequency band and a single

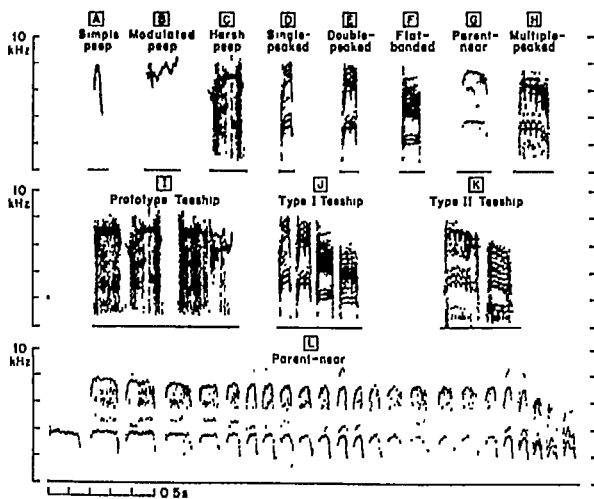


Fig. 3: Spectrograms illustrating the types of nestling and fledgling vocalizations associated with feeding

peak (Fig. 3A, Table 1). Simple peeps usually had longer terminal downsweeps, but there were also notes with longer initial upsweeps and notes with initial and terminal frequency sweeps of equal magnitude. Peak frequencies of simple peeps ranged from 4 to 10 kHz.

Table 1: Criteria used for classifying nestling and fledgling vocalizations associated with feeding

Vocalization type	Classification criteria
Single Notes	
1. Simple peep (Fig. 3A)	Single frequency peak in upper frequency range (>4.5 kHz); chevron-shaped or vertical downslope on a spectrogram
2. Modulated peep (Fig. 3B)	One or more frequency bands with multiple peaks in the upper frequency range; erratic pattern of frequency modulation
3. Harsh peep (Fig. 3C)	Frequency bands in both upper (>4.5 kHz) and lower (<4.5 kHz) frequency ranges; upper and lower ranges usually separated by 1–2 kHz band lacking emphasized frequency components; some notes appear "noisy" with less well-defined frequency bands.
Call Notes	
1. Single-peaked note (Fig. 3D)	Single-peaked frequency bands; at least one emphasized band in the upper frequency range; usually occurs in the introductory part of the call
2. Double-peaked note (Fig. 3E)	Frequency bands with two peaks; upper frequency range or mid-way between first and last notes; follows the single-peaked note or occurs as the first note in the absence of a single-peaked note.
3. Flat-banded note (Fig. 3F)	Bands with reduced frequency modulation appearing nearly flat on a spectrogram; occupies the lower frequency range (<4.5 kHz) in the terminal part of the call
4. Parent-near note (Fig. 3G)	Occurs in the upper frequency range; grades into single- and multiple-peaked notes; longer in duration than single-peaked notes but exhibiting less frequency modulation than multiple-peaked notes (modulation <400 Hz)
5. Multiple-peaked note (Fig. 3H)	Frequency bands with three or more peaks in the upper frequency range; occurs in the introductory part of the call, replacing single- and double-peaked notes.
Calls (multiple note groups)	
1. Prototype tee-ship call (Fig. 3I)	String of harsh peep-like notes
2. Type I tee-ship call (Fig. 3J)	Combination of single-peaked, double-peaked, and flat-banded notes
3. Type II tee-ship call (Fig. 3K)	Combination of multiple-peaked and flat-banded notes
4. Parent-near call (Fig. 3L)	String of parent-near notes, often grading into a tee-ship call

Day 3—6

Three structural developments during this period were (1) an increase in note duration, (2) the addition of frequency bands, and (3) an increase in frequency modulation to form multiple frequency peaks. These notes, referred to as modulated peeps, were irregular in each of these three variables (Fig. 3B, Table 1). In notes having more than one frequency band, the bands tended to be evenly spaced and parallel, but some notes showed merging and diverging of bands.

Simple peeps still occurred but were gradually replaced with modulated peeps. The occurrence of simple peeps decreased from 62.5 % of the vocalizations at 6 d to 6.25 % at 9 d, and disappeared completely by 15 d. Also, as other vocalizations developed, simple peeps were more frequent after the parent left the nest when the vocalizations were subsiding. At 6 d the occurrence of simple peeps increased from 52.5 % during the first 13 s after a parent entered the nest to 72.5 % during the first 13 s after a parent left the nest. At d 9 and 12, all simple peeps occurred only after the parent left the nest.

Day 9—15

Broader-band harsh peeps appeared around 9—12 d, and differed from modulated peeps by the addition of lower frequency components below 5 kHz (Fig. 3C; Table 1). Some bands within the same note differed in duration by dropping out or appearing erratically. In the central frequency range (approx. 4—6 kHz) these notes typically had a gap lacking emphasized frequency components, which was wider than the gaps between consecutive bands of the upper and lower frequency ranges. Other notes had the same general frequency range, but the bands were obscured by frequency components scattered across the entire range, giving the note a "noisy" appearance on the spectrogram.

Modulated peeps still occurred at 9 and 12 d but were gradually replaced with harsh peeps, and totally disappeared from the repertoire by 15 d. After 6 d, modulated peeps were more frequent after the parent left the nest. At 9 d modulated peeps increased from 40 % of the vocalizations given after the parent entered the nest to 47.5 % of the vocalizations after the parent left the nest. At 12 d, all modulated peeps (17.5 % of the vocalizations) only occurred after the parent left the nest.

A major development occurring in 9 and 12 d recordings was the clustering of notes into a call unit and the subsequent differentiation of these notes into two or three types. The formation of the call unit involved stringing together harsh peep-like notes, with the first indication of note differentiation within the call unit involving changes in frequency range and duration: successive notes descended in frequency and increased in duration. This call unit has been variously named the tee-ship call (ODUM 1942) to describe its sound, or the begging dee (FICKEN et al. 1978) because of its apparent effect of eliciting feeding by the parents. Calls comprising harsh peep-like notes are referred to here as prototype tee-ship calls (Fig. 3I) and were relatively uncommon, constituting only about 6 % of the vocalizations of this age group and about 15 % of all nestling tee-ship calls.

In 12 and 15-d recordings, notes were further differentiated into two or three types. Initial notes of the call tended to have fewer emphasized bands and the bands were widely separated in frequency, while terminal notes retained numerous closely spaced bands. Initial notes had a single frequency peak (single-peaked note, Fig. 3D; Table 1), mid-call notes had two broadly modulated peaks (double-peaked note, Fig. 3E; Table 1), and terminal notes ranged from having moderate modulation to being flat (flat-banded note, Fig. 3F; Table 1). The differences among these note types within a call were sometimes distinct, whereas other times the middle notes occupied a range intermediate between the initial and terminal notes. The overall frequency of a call decreased from beginning to end, although an initial increase from the first to the second note was common. Calls with a combination of single-peaked notes, double-peaked notes, and flat-banded notes are termed type I tee-ship calls (Fig. 3J; Table 1).

A variation of the single-peaked note is the parent-near note that occurred in tee-ship calls given when a parent was in the nest, or later when a fledgling was approached by a parent (Fig. 3G; Table 1). Parent-near notes had higher frequency, longer duration, and greater frequency modulation than single-peaked notes but sometimes graded into single-peaked notes toward the end of the call (Fig. 3L; Table 1).

As with simple and modulated peeps, harsh peeps and tee-ship calls also varied with context. At 15 d, harsh peeps were more frequent after a parent entered the nest, decreasing from 50 % of the vocalizations given after a parent entered the nest to 25 % of the vocalizations given after a parent left the nest. Conversely, tee-ship calls were more frequent after a parent left the nest, increasing from 50 % of the vocalizations given after a parent entered the nest to 75 % of the vocalizations given after a parent left the nest.

The last recordings in the nest were on d 15, about 2 d before fledging. By this age 62.5 % of the notes were uttered in call units, but there were differences in rate of development among families. For example, in family R, 75 % of the notes occurred in call units, whereas in family M only about 33 % of the notes were in call units. Differences in structure also occurred among siblings, as demonstrated by the two tee-ship calls in Fig. 4A given by two different nestlings from the same family at 15 d.

Fledglings: General Activities

Parents continued to feed the fledglings during the first few weeks post-fledging. Fledglings gave tee-ship calls (Fig. 3) while perched or foraging independently. When a parent approached with food, the fledgling's call notes increased in amplitude and duration. Older fledglings continued the loud calling after being fed and chased the parents persistently. Calling while a parent was near was often accompanied by wing quivering, which also grew in amplitude and rate of movement as a parent approached.

Adult-like calls were first recorded by some 28-d-old fledglings. Most of these were chick-a-dee calls and soft warbling subsong (described below), and occasionally vocalizations resembling fee-bees. As the day of dispersal

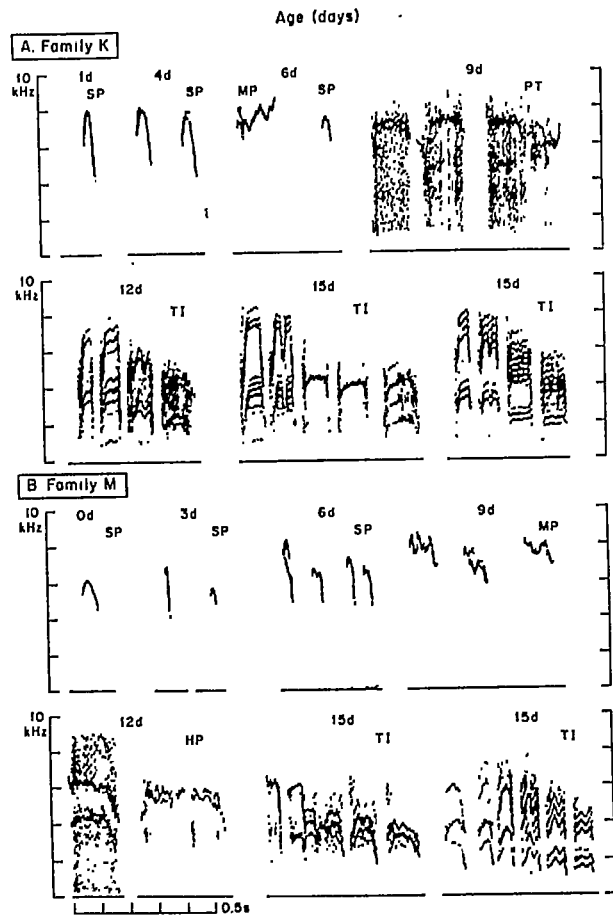


Fig. 4: Spectrograms comparing the longitudinal development of two nestling families from hatching to just prior to fledging (leaving the nest). SP — simple peep; MP — modulated peep; PT — proto-type tee-ship call; TI — type I tee-ship call

approached, fledglings became less dependent on their parents for food and were observed foraging alone or with siblings and newly independent juveniles.

Fledglings: Acoustic Structure and Chronological Changes of Vocalizations

Day 17—22

The dominant vocalizations at this age continued to be type I tee-ship calls. In the calls of some individuals, an intermediate form between double-peaked and the flat-banded note-types still persisted. Also, in some calls, the single-peaked note was absent and the double-peaked note was the first note.

Day 23—29

A new note type, termed the multiple-peaked note (Fig. 3H; Table 1, above), appeared in the tee-ship calls of most fledglings at this age. The note occupied the upper frequencies and consisted of three or more rapidly modulated peaks. The multiple-peaked note usually replaced the initial single- and double-

peaked notes of type I tee-ship calls, and was followed by one to several flat-banded notes. In 24 % of tee-ship calls, the multiple-peaked note was found in some combination with single-peaked or double-peaked notes. Calls containing a multiple-peaked note are termed type II tee-ship calls (Fig. 3 K). As with type I tee-ship calls, these calls were accompanied by wing quivering when a parent approached to feed the young, and the multiple-peaked notes graded into the more shallowly modulated parent-near notes.

Day 30—36

This age period was marked by the appearance of subsong and adult-like vocalizations such as chick-a-dee calls, fee-bees, and tseets, although for some fledglings these calls appeared as early as 28 d. Chick-a-dee calls were recorded from all 8 fledglings, tseets were recorded from seven, subsong from four, and fee-bees from two fledglings.

Fledgling chick-a-dee calls at this age were only approximate renditions of adult chick-a-dee calls (compare chick-a-dee calls in Figs. 5 and 6, below, with Fig. 1, above). Interruptions and irregular modulations of frequency bands in the D-notes were common in fledgling chick-a-dee calls. As compared with adult calls, the introductory notes of fledgling chick-a-dee calls were more variable and often difficult to classify. Some of the pure-tone introductory notes had trailing traces of additional frequency bands, reminiscent of the multiple frequency bands of tee-ship initial notes. Nevertheless, chick-a-dee calls having adult-like struc-

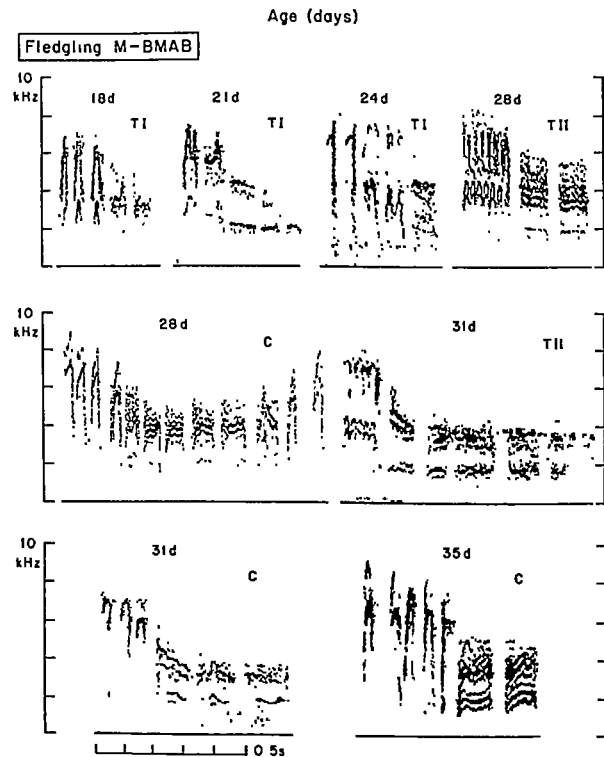


Fig. 5: Spectrograms showing the longitudinal development of an individual fledgling from family M. TI — type I tee-ship call; TII — type II tee-ship call; C — chick-a-dee call

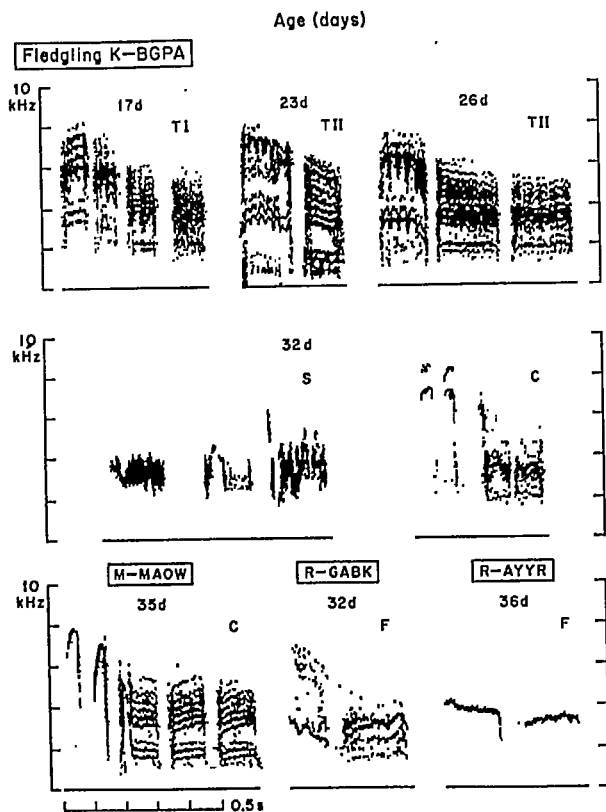


Fig. 6: Spectrograms showing the longitudinal development of a second fledgling from family K to compare with the vocalizations of the fledgling shown in Fig. 5, above. Also shown are spectrograms of other fledgling vocalizations, including an adult-like chick-a-dee call and examples of the fee-bee song. TI — type I tee-ship call; TII — type II tee-ship call; S — subsong; C — chick-a-dee call; F — fee-bee

ture were recorded from one of the 8 fledglings whose vocalizations were analyzed (S-MABY) and at least one other fledgling (M-MAOW) on the last recording prior to their dispersals (compare chick-a-dee call in Fig. 6, fledgling M-MAOW, with Fig. 1).

Subsong was first recorded at 29 d of age (Fig. 6S, fledgling K-BGPA, 32 d). Some subsong elements were erratic and unique in structure, while others resembled notes of chick-a-dee calls, tee-ship calls, and the yet undeveloped gargle call. It was frequently difficult to distinguish on spectrogram whether a vocalization was a rough form of chick-a-dee call or the inventive warblings of subsong.

Two of the 8 fledglings gave imperfect fee-bees or faint fee-bees (Fig. 6, fledglings R-GABK and R-AYYR). In the younger of the two examples, the two long whistled tones had additional frequency components both above and below the main frequency components, perhaps suggesting a derivation from D-notes or the flat-banded note of tee-ship calls. The fledgling had been giving type II tee-ship calls, and then gave this call following a faint fee-bee vocalization given by one of its parents.

Type II tee-ship calls still occurred at this age and parents continued to bring food. Periods when a fledgling foraged independently, however, were more

Table 2: Frequencies of occurrence of vocalizations of nestlings and fledglings at different ages. Percentages refer to the distribution of vocalizations at a given age (rows sum to 100 %). Numbers under percentages: total n of a vocalization-type at a given age for each family. Families progress through similar stages in the same order

Age (d)	Family	Vocalization						
		Simple peep	Modulated peep	Harsh peep	Proto-type tee-ship call	Type I tee-ship call	Type II tee-ship call	Adult-like calls and subsongs
0—1 (n = 47)	K	(100 %) 11						
	R	10						
	M	6	—	—	—	—	—	—
	S	20						
3 (n = 80)	K	(100 %) 20						
	R	20						
	M	20	—	—	—	—	—	—
	S	20						
6 (n = 80)	K	(62.5 %) 10	(37.5 %) 10					
	R	16	4					
	M	19	1	—	—	—	—	—
	S	5	15					
9 (n = 80)	K	(6.25 %) —	(43.7 %) 7	(43.75 %) 12	(1.25 %) 1	(5.0 %) —		
	R	1	6	13	—	—		
	M	—	20	—	—	—	—	—
	S	4	2	10	—	4		
12 (n = 80)	K	(5.0 %) —	(8.75 %) —	(63.75 %) 10	(11.25 %) 8	(11.25 %) 2		
	R	1	5	12	1	1		
	M	3	1	16	—	—	—	—
	S	—	1	13	—	6		
15 (n = 80)	K			(37.5 %) 6	(1.25 %) —	(61.25 %) 14		
	R			5	—	15		
	M	—	—	13	—	7	—	—
	S			6	1	13		
17—22 (n = 24)	K					(95.83 %) 9	(4.17 %) 1	
	R					5	—	
	M	—	—	—	—	8	—	—
	S					—	—	
23—29 (n = 35)	K					(28.57 %) —	(60.0 %) 9	(11.43 %) 1
	R					6	4	—
	M	—	—	—	—	1	6	3
	S					3	2	—
30—36 (n = 35)	K					(5.71 %) —	(31.43 %) 4	(62.86 %) 1
	R					—	1	9
	M	—	—	—	—	—	3	7
	S					2	3	5

frequent, and tee-ship calls occurred less frequently as adult-like vocalizations and subsong developed.

Overview of Nestling and Fledgling Vocal Development

In Table 2 the frequency of occurrence of each vocalization-type is tallied to show the ontogenetic replacement of vocalizations with age. Until about d 28—30, most vocalizations of nestlings and fledglings were associated with feeding. These vocalizations changed dramatically throughout the approximately 36-d period. Just prior to dispersal, 30—36 d, these vocalizations began to be replaced with subsong and adult-like vocalizations, including tseets, fee-bees, and chick-a-dee calls. Each column of the table is subdivided into individual families to illustrate that all families exhibited the same changes in the same order, although rates of development differed. For example, at age 6 d, 95 % of family M's vocalizations were simple peeps, whereas 75 % of family S's vocalizations

Table 3: Frequencies of occurrence of call types of fledglings at different ages. Numbers: total n for each individual during one recording session. Dashes: d for which recordings were not obtained. (I) = type I tee-ship; (II) = type II tee-ship; (A) = adult-like calls and subsong

Individual fledglings	Age						
	17—19	20—22	23—25	26—28	29—31	32—34	35—36
K-BGPA	7 (I)	—	4 (II)	1 (I) 5 (II) 2 (A)	—	5 (II) 1 (A)	—
K-GAOK	6 (I)	3 (II)	2 (I) 2 (II)	12 (II) 4 (A)	—	—	—
R-GABK	—	3 (I)	2 (I)	—	2 (I) 1 (II)	1 (II) 1 (A)	4 (A)
R-AYYR	—	2 (I)	1 (I) 1 (II)	1 (I) 14 (II) 2 (A)	—	5 (II)	1 (II) 11 (A)
M-BMAB	2 (I)	1 (I)	1 (I)	4 (II) 4 (A)	1 (II) 3 (A)	1 (II) 3 (A)	—
M-KARP	7 (I)	—	11 (I) 14 (II)	2 (II)	1 (I) 3 (II) 4 (A)	—	1 (II) 7 (A)
S-YOAB	—	—	11 (I)	—	8 (II)	6 (II) 2 (A)	2 (A)
S-MABY	—	—	—	—	—	7 (I)	—

were modulated peeps. In Table 3 families are further subdivided into fledglings to show that the same pattern of vocalization replacement holds true for individuals. In addition, the fledgling data show that there were periods of overlap where successively developing vocalization types occurred together during the same recording of an individual (also see spectrograms of individual fledglings, Figs. 5, 6, above).

Chick-a-dee calls resemble tee-ship calls in a number of features. Both calls are multiple-note sequences. Terminal notes of tee-ship calls and D-notes of chick-a-dee calls have temporally overlapping harmonic-like bands in the lower frequency range. Initial notes of both tee-ship calls and chick-a-dee calls consist of high, rapid frequency modulations. One difference is that introductory notes of chick-a-dee calls are all single-peaked, whereas those of tee-ship calls usually consist of at least one double- or multiple-peaked note. The single-peaked notes of type I tee-ship calls have one or more harmonic-like bands in addition to the maximum band, while A- and B-notes of chick-a-dee calls usually have only a single band or a second less emphasized band.

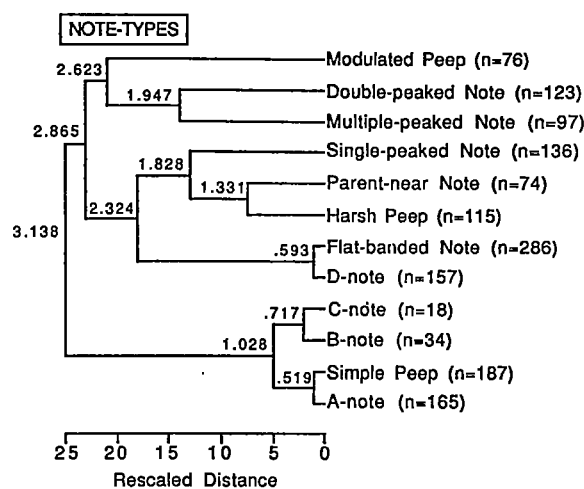


Fig. 7: Cluster analysis showing the structural similarities between A-, B-, C-, and D-notes of chick-a-dee calls and notes of peeps and tee-ship calls

The cluster analysis (Fig. 7) is a quantitative assessment of structural similarities between notes of chick-a-dee calls and notes of peeps and tee-ship calls. The notes are scaled according to degrees of dissimilarity: pairs with the smallest coefficients are more similar in structure based on four continuous variables. In agreement with the qualitative assessment, terminal notes of tee-ship calls and D-notes of chick-a-dee calls are close in structure. The single peep of young nestlings and the A-note of chick-a-dee calls also have a small dissimilarity coefficient; in general, the three introductory notes of chick-a-dee calls more closely resemble the simple peeps of young nestlings than they do the initial notes of later developing tee-ship calls.

Table 4: Variables describing notes of nestling and fledgling vocalizations, $\bar{x} \pm SD$ (n): Maximum band (MB), band difference (BD), peak-to-trough difference (PT), peak difference (PD), note duration (ND), and peak number (PN)

Note type	Variable					
	MB (kHz)	BD (kHz)	PT (kHz)	PD (s)	ND (s)	PN
Simple peep	7.3 ± 1.3 (187)	0.09 ± 0.26 (187)	0.00 ± 0.00 (187)	0.00 ± 0.00 (187)	0.04 ± 0.02 (187)	1.0 ± 0.0 (187)
Modulated peep	7.5 ± 1.1 (76)	0.59 ± 0.52 (76)	0.78 ± 0.58 (76)	0.04 ± 0.03 (76)	0.15 ± 0.06 (76)	3.1 ± 1.8 (76)
Harsh peep	5.9 ± 1.8 (124)	1.5 ± 1.2 (120)	0.54 ± 0.41 (115)	0.04 ± 0.03 (115)	0.18 ± 0.05 (127)	3.0 ± 1.6 (114)
Single-peaked	5.2 ± 1.7 (136)	1.79 ± 1.41 (136)	0.03 ± 0.12 (136)	0.00 ± 0.01 (136)	0.09 ± 0.03 (136)	1.1 ± 0.5 (136)
Double-peaked	5.6 ± 1.9 (125)	1.9 ± 1.4 (123)	1.1 ± 0.8 (125)	0.04 ± 0.02 (125)	0.10 ± 0.03 (125)	2.0 ± 0.4 (125)
Multiple-peaked	6.5 ± 1.6 (98)	2.75 ± 1.24 (97)	1.32 ± 0.71 (98)	0.04 ± 0.02 (98)	0.18 ± 0.05 (98)	4.2 ± 1.2 (98)
Flat-banded	4.0 ± 0.9 (293)	0.64 ± 0.57 (288)	0.23 ± 0.23 (287)	0.02 ± 0.03 (287)	0.14 ± 0.04 (293)	2.2 ± 1.3 (287)
Parent-near	5.4 ± 1.8 (74)	2.56 ± 1.32 (74)	0.30 ± 0.32 (74)	0.02 ± 0.02 (74)	0.16 ± 0.04 (74)	2.2 ± 1.2 (74)
A-note	7.2 ± 0.85 (165)	0.40 ± 0.66 (165)	0.01 ± 0.05 (165)	0.00 ± 0.01 (165)	0.06 ± 0.02 (165)	1.0 ± 0.13 (165)
B-note	6.6 ± 1.3 (34)	0.71 ± 0.77 (34)	0.00 ± 0.00 (34)	0.00 ± 0.00 (34)	0.04 ± 0.01 (34)	1.0 ± 0.0 (34)
C-note	5.8 ± 0.84 (18)	0.57 ± 0.56 (18)	0.00 ± 0.00 (18)	0.00 ± 0.00 (18)	0.05 ± 0.01 (18)	1.0 ± 0.0 (18)
D-note	3.6 ± 0.32 (162)	0.45 ± 0.30 (159)	0.12 ± 0.22 (157)	0.02 ± 0.03 (157)	0.16 ± 0.03 (162)	1.5 ± 0.9 (157)

Table 5: Variables describing call types, $\bar{x} \pm SD$ (n)

Variable	Call type			
	Type I tee-ship	Type II tee-ship	Parent near	Chick-a-dec
No. of notes	4 ± 1 (110)	3 ± 1 (95)	4 ± 2 (23)	6 ± 3 (65)
Call duration (s)	0.58 ± 0.21 (110)	0.57 ± 0.18 (96)	0.73 ± 0.45 (23)	0.84 ± 0.40 (65)
Inter-note interval (s)	0.04 ± 0.01 (110)	0.05 ± 0.01 (95)	0.05 ± 0.02 (23)	0.04 ± 0.01 (65)

Discussion

Based on similarities of both call and note structure, the results suggest that the chick-a-dee call develops from the peeps and tee-ship calls of the young but not necessarily in a chronologically linear fashion. Characteristics of the chick-a-dee call have both continuous and discontinuous developmental origins. Some characteristics of chick-a-dee calls, such as the multiple-note call structure and the structure of the D-note, are present in tee-ship calls appearing in the repertoires of 9–12 d nestlings, while characteristics of introductory notes, particularly of the A-note, resemble an earlier note, the simple peep, given by 0–6 d nestlings. Unlike tee-ship calls, which occur along with chick-a-dee calls during the last week before dispersal, simple peeps drop out of the repertoire after the second week, leaving a 2–3 week period when neither simple peeps nor A-notes are present. The B- and C-notes, on the other hand, appear to develop with the emergence of the chick-a-dee call itself. Continuous development, then, is represented by the similar structure and uninterrupted development of the flat-banded note of tee-ship calls and the D-note of chick-a-dee calls, and of the multi-note call structure in both of these calls; discontinuous development involves a chronological break, or re-access of, an earlier developing form in the case of the A-note, and the sudden appearance or rapid modification of the basic A- and D-notes into B- and C-notes. This pattern of development contrasts with the structurally and chronologically continuous changes exhibited by developing peeps and tee-ship calls, where each stage appeared intermediate in structure between previous and subsequent stages.

Comparison With Song and Call Development of Other Species

In the swamp sparrow (*Melospiza georgiana*) (MARLER & PETERS 1982 a, b) and other oscine species (LANYON 1960), song development begins with a subsong stage where vocalizations are highly variable and lack definite structure. In the subsequent stage, the vocalizations contain identifiable syllable types, including the ones which will eventually crystallize into the adult song. In the final stage, the number of syllable types per song is reduced to just a few types. The development of the chick-a-dee call, by contrast, went from fewer vocalization types to more types with age, except during the later stages when there were three note types in type I calls followed by two note types in type II calls before proceeding to four note types in chick-a-dee calls.

In addition to variation that distinguishes types of vocalizations, vocalization types vary. While variation of vocalization types increased with age during the first month of development in the chick-a-dee call, variation within types sometimes decreased. For example, the apparently variable structure of notes of immature chick-a-dee calls (see Results, above) suggests that further development might lead to the more stereotyped structure of notes observed in adult chick-a-dee calls, although further research is needed to verify this point.

Another difference between song and call development may be the source of variation. MARLER & PETERS (1982 b) found a high incidence of invention of syllable-types (syllables bearing little if any resemblance to those of the tutor)

during plastic song in addition to imitation of types from the tutor vocalizations. They suggested that invention as well as other processes such as improvisation and copy errors may have contributed to the variation of song types found among individuals. In this study, by contrast, the extensive variation that occurred throughout development may have been a source of variation for the production of adult vocalizations. Earlier produced vocalizations do not necessarily disappear permanently from the repertoire, but may be accessible during adulthood, and in some cases, such as with the simple peep and A-note, may be combined with other vocalizations or behavior to increase variation.

The development of adult vocalizations from the vocalizations of nestlings and fledglings has been documented in a wide variety of species (see Introduction). These studies show that adult calls may arise at different points along a developmental continuum (see especially THOMPSON & RICE 1970; WILKINSON & HUXLEY 1978; HOWES-JONES 1984). But it is rarely reported that a single call arises by the combination of elements from different stages of development, such as in the case of the A-note developing from a note of 0—6 d nestlings, and the D-note and call structure developing from the tee-ship calls of fledglings. THOMPSON & RICE (1970) reported that the female solicitation call of the indigo bunting (*Passerina cyanea*) was composed of a combination of visual and acoustic components from different developmental stages: the acoustic component resembled the vocalization of young nestlings, while the posture and movement accompanying the call resembled a visual signal of fledglings.

Other Considerations and Future Study

A better understanding of the development of vocal production may help clarify structural relationships between adult and immature vocalizations. For example, the cluster analysis indicated greater structural resemblance between A-notes and simple peeps, but the single-peaked note of type I tee-ship calls sometimes remarkably resembled the A-note of fledgling chick-a-dee calls (Fig. 5: compare first note of type I call, 24 d, with first note of chick-a-dee call, 28 d). In other cases, slight modification of the single-peaked note, such as elimination of frequency bands, may be all that is required to produce an A-like note. In fact, studies of vocal production in adult black-capped chickadees show that the production and elimination of frequency bands of the D-note depends on the interaction between fundamental frequencies produced by each of the two syringeal membranes (NOWICKI & CAPRANICA 1986 a, b). Other means of dampening or eliminating frequency bands may involve adjustments of a vocal tract filter (NOWICKI 1987). Hence, modifications involving the elimination of frequency bands may have a real basis in the development of vocal production. In terms of vocal production, the step in going from a multiple banded single-peaked note to a "pure" tone A- or B-note may be simpler than what is reflected in a quantitative analysis of the acoustic output itself.

Vocal production may also help explain the differences between A-notes and simple peeps. For example, A-notes sometimes have a second, less emphasized frequency band that is responsible for the "band difference" variable (BD) lacking in simple peeps (compare Fig. 1, A-note, and Fig. 3 A). If the "pure-tone-like"

whistle of the A-note is produced by the attenuation of harmonics (NOWICKI 1987), the difference between the simple peep and the A-note may be the result of different production mechanisms with approximately the same outcome. If the production mechanisms differ, the question of whether these two notes share any semantic component or usage still remains open. Behavioral outcomes during ontogeny may have the same structure and serve the same function, while the mechanisms of their control may change (ALBERTS & CRAMER 1988).

Peeps and tee-ship calls undergo a large degree of ontogenetic change while maintaining the single effect of promoting parental feeding. Structural changes occurring without functional changes during ontogeny are frequently attributed to processes of maturation (SCHLEIDT & SHALTER 1973). In this study, however, these changes are not easily explained by growth processes alone. Individuals can produce either Type I or Type II tee-ship calls as well as adult-like calls during the same recording session (Fig. 5; Table 3). The ability to produce tee-ship calls also extends beyond the period of parental care. Newly dispersed juveniles that were completely independent of parental care sometimes gave tee-ship calls and wing quivered toward an adult, although adults were rarely seen to feed these unrelated juveniles (pers. obs.). Adult females, too, use tee-ship-like begging calls during certain phases of the reproductive cycle (FICKEN et al. 1978). Processes other than maturation should be studied to explain ontogenetic changes of vocalizations, such as whether the changes are adaptations to changing external conditions, or whether the changes are driven by motivational or experiential factors.

Finally, the relationship between the structure of these signals and their semantic contents remains a challenging question. Despite structural similarities between peeps, tee-ship calls, and chick-a-dee calls, behavioral differences associated with these calls suggest differences in the use of these calls. For example, tee-ship calls elicited feeding by the parents and were accompanied by food-getting behavior such as wing quivering and chasing the parent. By contrast, chick-a-dee calls were never accompanied by wing quivering nor followed by feeding from an adult. Nevertheless, it remains to be determined whether similar structural components among different vocalizations represent common denominators in the encoded message. For example, it has been suggested that the four note types of chick-a-dee calls each encode a different message, and that the total message of the call consists of the relative measures of the combined notes (SMITH 1972; HAILMAN et al. 1985). Likewise, if similar message components are encoded in simple peeps and A-notes, and in flat-banded notes and D-notes, the message as a whole would differ with changes in the combinations of notes and other behavior.

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