PARENT-OFFSPRING INTERACTIONS IN ZEBRA FINCHES

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ABSTRACT.—The begging behavior of immature Zebra Finches has both visual and acoustic components. Begging nestlings gape at their parents, exposing characteristic mouth markings and a moving tongue. They also emit begging calls. Both components undergo changes as the offspring mature, and there is a shift from the visual to acoustic modality as the primary stimulus for feeding.

Recorded fledgling begging calls were broadcast inside the cages of Zebra Finch parents with offspring. These begging calls stimulated parental feeding and other behaviors associated with feeding. The offspring also responded to recorded calls by showing begging behavior. Parents were sensitive to recorded begging calls from approximately day 16 to day 28 after the first offspring hatched, although there was substantial variation in these times among pairs of parents.
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AFTER hatching, the offspring of some species of birds are fed by their parents, usually for a period of several weeks. A common feature of the interaction during parental feeding is some type of begging behavior that stimulates parents to provide food to their offspring at a time when it is needed. The details of this communication system can provide information concerning the reproductive strategy of the parents, i.e. the allocation of their "parental investment" (Trivers 1972).

We have determined some of the details of the parent-offspring communication system of the Zebra Finch (*Poephila guttata*). We concentrated on this interaction during parental feeding. Our efforts have followed two approaches: 1) observation of the begging behavior of young Zebra Finches, and 2) observation of the responses of the parents to natural and artificial begging signals.

Immelmann (1965) has summarized the breeding biology of wild Zebra Finches. This species breeds readily in captivity. Pairs of birds will initiate reproductive activity year round and produce several clutches in succession. They are disturbed very little by human presence, and for these reasons are appropriate choices for observation and experimentation of avian parent-offspring interaction.

METHODS

Zebra Finches used in these studies were obtained from several breeding stocks. Breeding pairs were housed indoors in 31 × 43 × 61 cm wooden cages with fronts. A 12/12 light-dark regime was used throughout the study; temperature fluctuated between 20 and 25°C. The birds were fed a commercially available finch seed mixture. Grit and broken eggshells were always available. In addition, germinating seeds, bathing water, and a mixture of boiled egg and bread crumbs were provided daily or every other day. The nests were open-topped round containers 10–12 cm in diameter lined with cloth pads.

Feeding bouts were observed using a video camera system placed in front of the cage. Lighting was provided by a high intensity desk lamp. Feeding behavior could thus be observed on a television monitor and recorded on videotape for subsequent analysis. The birds quickly accepted the presence of the light and camera. Feeding bouts were systematically recorded during the first hour of the light period. Most pairs began feeding during the first or second day of observation.

Prior to many of the recorded feeding bouts, the nestlings were removed, weighed, and placed back into the nest in known positions so that individuals could be identified by position on the television monitor. During feeding bouts nestling begging calls were recorded on a Nagra IV S tape recorder at 19

cm/s using a Sennheiser MD 211 U microphone mounted inside the cage facing into the nest, 10–20 cm from the nestlings. Fledgling begging calls were recorded using either a SONY model ECM22P or Sennheiser MD 211 U microphone located in front of and just outside the cage.

Spectrographs of selected recordings were made on a Kay Vibralyzer, model 5030A, with a wide band filter setting (300 Hz at 80–8,000 Hz, 600 Hz at 160–16,000 Hz). Begging calls were periodically tape recorded during feeding bouts in 15 nests. This permitted comparison of the changes in begging calls during development for young in different nests. Recorded begging calls were broadcast through a speaker inside a cage during 21-min observation periods, consisting of three consecutive 7-min periods. Each period consisted of 2 min of taped calls followed by 5 min of silence. The same calls were used for all three of the 2-min periods. The interval between tests in an individual cage was always at least 24 h.

Observations of responses to calls were conducted at the same time each day in any one cage and started either at 4.5 or 5.5 h after the onset of the light period. These periods were chosen because little feeding was normally observed at these times. It was assumed that most of the feeding observed during the observation periods would be caused by the recorded begging calls. A maximum of two tests were conducted in the laboratory on any one day. All tests utilized a 10-cm speaker (Realistic model 40-1197) placed directly beneath the nest in each cage. Behavior was observed directly or with a closed circuit television system.

The main categories of behavior observed and scored during these observation periods were:

1) *Feeding*.—The regurgitation of food to the young birds by their parents. Each insertion of the parent's bill into the mouth of one of its offspring was counted as one feeding.

2) *Begging*.—Gaping and/or emitting begging calls by the young birds.

3) *Regurgitation*.—"Choking" or pumping movements by the parents that preceded feeding. These movements sometimes occur without subsequent feeding, and were only counted if they were not followed by feeding. They were recognized by the characteristic pumping of the head and often by the presence of regurgitated food in the partially opened mouth of the parent.

4) *Eating seeds*.—By the parents.

5) *Other*.—Behavior such as approaches of parents to their offspring or of fledglings to parents, pecking on the fledglings to induce begging, grooming, and sitting in the nest were also recorded.

Observation periods were scored by the presence or absence of the types of behavior within each minute of the 21-min observation period. The scores of all observation periods were combined. The resulting histograms represent the total number of observation periods in which a particular behavior was shown within each minute of the sequence (Fig. 5).

RESULTS

Both of the parents brood and feed nestlings. Feeding takes place in bouts. Parents begin by eating seeds or egg food and, after several minutes, begin to feed their young. They may walk on the nestlings or peck lightly at their heads to induce begging. The parents insert their bill into the open mouth of their offspring and regurgitate the partially digested food. The young birds grasp the bill of their parents and swallow the regurgitated food with front to back movements of their tongue. Each insertion of the parent's bill into the mouth of a nestling may last for a period of several seconds.

VISUAL COMPONENTS OF BEGGING

Color patterns.—Gray-colored adults, which have coloration most similar to wild Zebra Finches (Delacour 1943, Steiner 1960), have complete mouth markings. There are five black areas on the palate, two black areas on the dorsal side of the tongue, and eight black areas on the periphery of the mouth. "White" Zebra Finches, however, have no pigmented mouth markings when they are nestlings. Their mouths lack the black pigmentation on the palate, tongue and sides of the mouth as well as the white pigmentation on the edges of the beak. Nestlings of color varieties between these two extremes have intermediate mouth markings with only some of the color

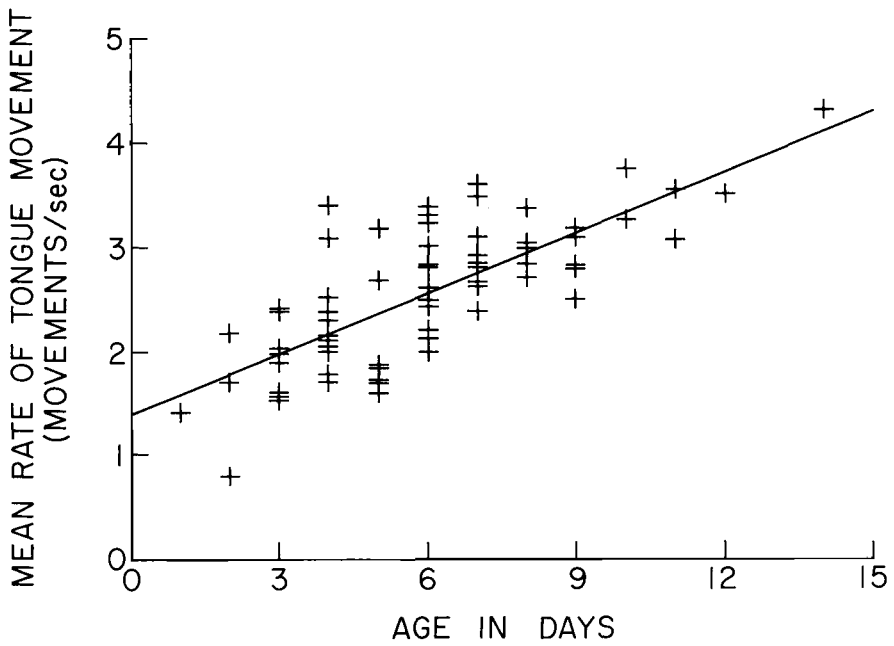

Fig. 1. Mean individual rate of tongue movement vs. age of offspring. The data were collected from 22 individuals. Each point represents the mean rate of movement for one individual during one observation period. $R^2 = .56$.

pattern present. Usually one or more dark areas are missing from the tongue and/or palate.

The color patterns inside the mouths of nestlings are closely correlated with structural patterns present in the adults as well as the nestlings of these finches.

Behavior.—Begging Zebra Finch nestlings open their mouths exposing their mouth markings. They initially orient their open gapes upward, but at around 8 days of age their eyes open and nestlings begin orienting their begging toward their parents. The most prominent motion accompanying this gaping in nestlings is the lateral movement of the tongue. The tongue has three dark spots on its surface, two on the dorsal side and one on the ventral side. The rate of motion of the tongue is related to the age of the nestlings. (Fig. 1).

There are qualitative differences in this motion that are also related to age. Nestlings less than 5 days old have very stereotyped motion with continuous tongue movement. Nestlings older than approximately 7 days move their tongues only during periods when parents are feeding. In addition, older nestlings often move their tongues in directions other than side to side, and as vocalization increases in frequency and amplitude, movements associated with sound production replace side to side tongue movements during begging.

Tongue movements observed during recorded sessions were divided into two categories: 1) those that were observed during feeding bouts, and 2) those observed at all other times. The mean rates of tongue movement in these two categories were compared using a one-tailed signed rank test (Sokal and Rohlf 1969). During feeding bouts the rate of tongue movement of nestlings is increased a small but significant amount (mean difference = .06 movements/s, SD = .05, $P < .05$). However there

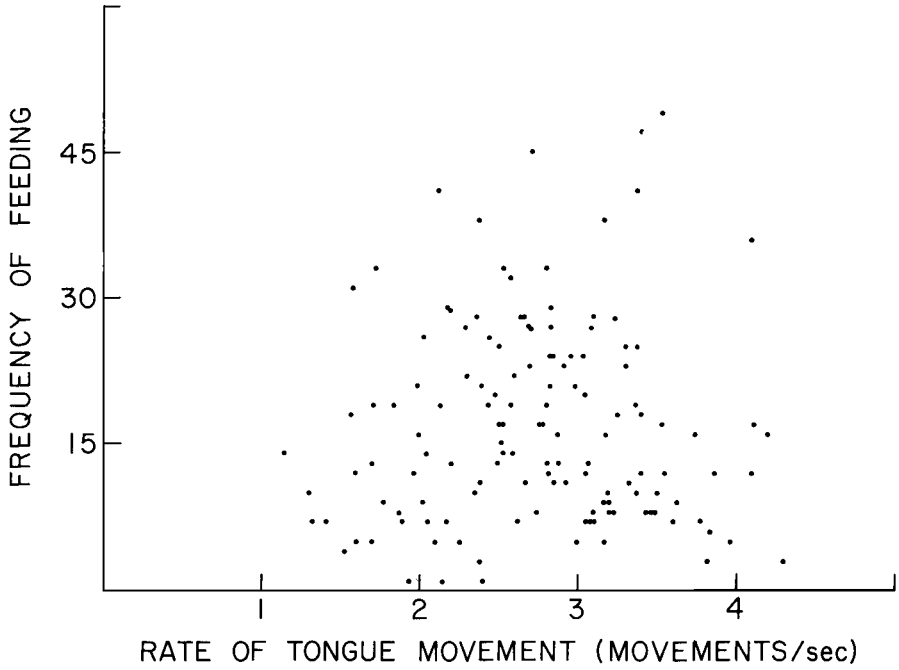

Fig. 2. Frequency of feeding vs. rate of tongue movement. Each point represents the values for one individual during one observation period. Correlation coefficient = .10.

was no significant relationship between the mean rate of tongue movement for an individual nestling and the frequency of feeding of that nestling (Fig. 2). The data do not support the hypothesis that the parents are more intensely stimulated to feed by an increased rate of tongue wagging.

Acoustic Components of Begging

Because of the variations that might have resulted from the recording technique and because of the variations between individuals, only the most general properties of begging calls will be discussed here. The most obvious characteristic is that begging calls vary with the age of the young birds. The first sounds that we could detect came on day 3 of the nestling's life. These calls were of very low intensity and we could not hear them outside the cage; they were detected using the audio system. Begging calls continued to be given during feeding bouts until the fledglings were approximately 30 days old and were feeding independently. During these 27 days, begging calls, which vary in intensity within any one feeding period, progressively increased in average sound intensity. The increase just prior to the time when the birds fledge is especially noticeable.

The spectral properties of the calls also changed with the age of the young birds (Fig. 3, A–F). It appears that the changes that occur from 3 days of age to around 17 days of age are a lowering of the fundamental frequency with the appearance of more harmonics, and the increase of a "noise" component of the sounds.

It must be emphasized that there is variation in begging calls within and among individuals. This variation is present in the timing, amount of the "noise" compo-

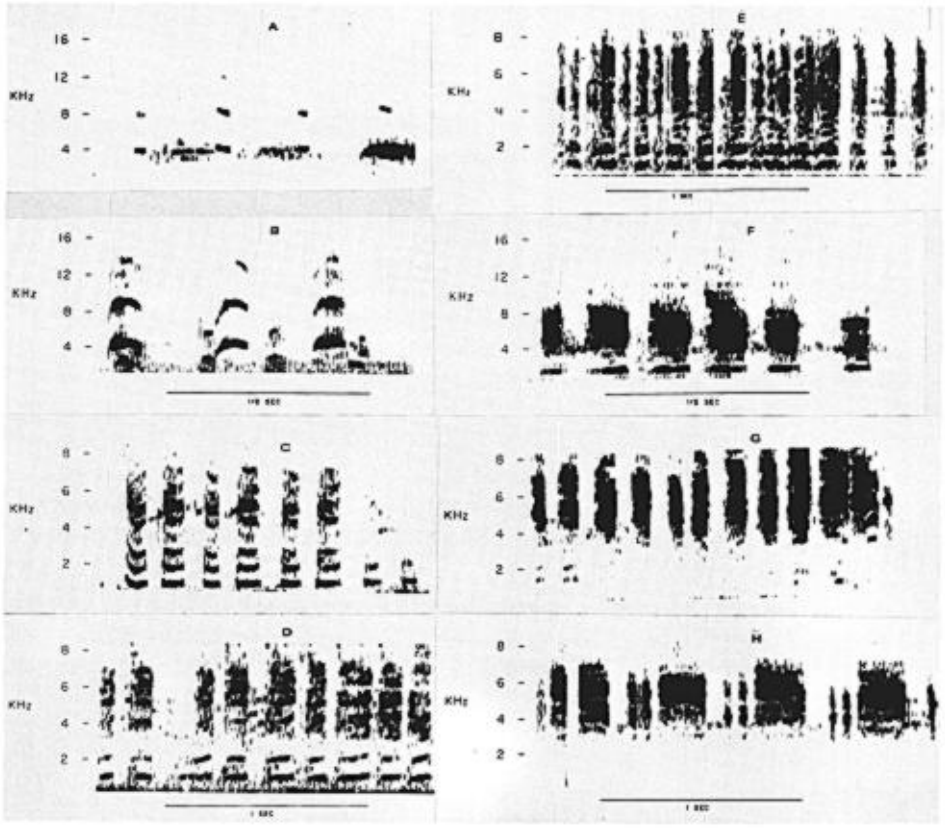

Fig. 3. Spectrographs of Zebra Finch begging calls representative of: A, 5-day-old nestlings; B, 8-day-old nestlings; C, 12–14-day-old nestlings; D, 15–17-day-old fledglings; E, 17–19-day-old fledglings; F, 23-day-old fledglings; G, 25-day-old fledglings; and, H, Type II begging calls.

nent, and energy distribution at different frequencies. Figure 3B shows that even within one syllable the amount of modulation can be varied. Figure 3 presents a representative developmental sequence of begging calls.

There is one other change in calls that occurs in older fledglings as they approach independence. There is an appearance of a call which we have named the Type II begging call. Calls previously described are all Type I begging calls that occur during feeding bouts and are given with the mouth open and oriented up and toward the parent. Type II calls, in contrast, are given with the mouth only slightly open and fledglings may or may not be oriented toward the parent. They are usually given prior to feeding bouts, when parents are eating, and they change into Type I calls once feeding of the young commences. The frequency spectrum of Type II calls is very similar to that of Type I calls. The temporal properties, however, are different. Figure 3G and 3H illustrate these differences.

The timing of the begging calls in relation to feeding bouts also changes as the young birds develop. When begging calls first appear (usually on day 3), only the nestling who is being fed vocalizes, and it only vocalizes while it is in the process of being fed. From about day 4 to day 12, all nestlings vocalize during feeding bouts. However the begging is still silent before and after feeding, and the nestling who is

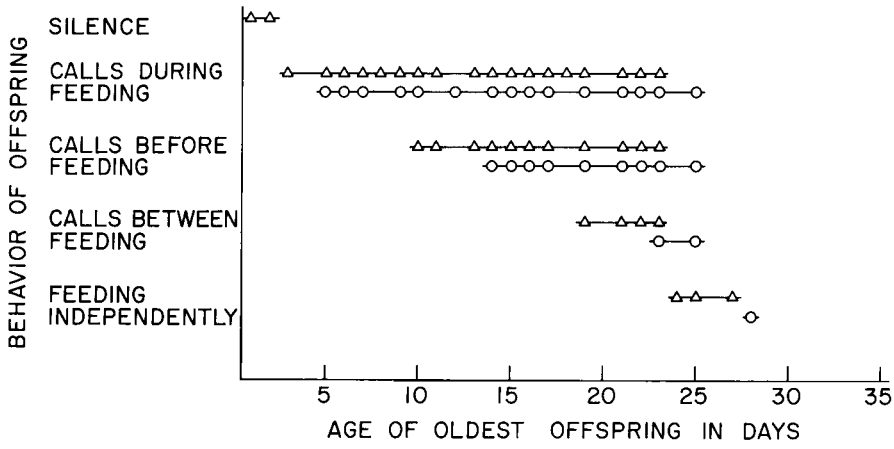

Fig. 4. The begging behavior of immature Zebra Finches during feeding bouts vs. their age. The two symbols represent the behavior of two different clutches. Observations of one clutch (delta) were begun on day 1 after hatching. Observations of the other (circle) were begun on day 5 after hatching. Silence = offspring gaped silently during the entire feeding bout; Calls During Feeding = offspring emitted begging calls after feeding had begun; Calls Before Feeding = offspring emitted begging calls before feeding had begun (calls were given after the parent had approached to initiate feeding); Calls Between Feeding = offspring emitted begging calls without being approached by a parent; Eating Independently = offspring began a feeding bout by eating rather than begging.

actually being fed at any time vocalizes loudest. At the end of this period, vocalizations may continue after feeding bouts. At about day 13 to 15, just prior to fledging, the behavior of the nestlings changes. The nestlings will now start vocalizing prior to feeding when a parent comes into the nest. Calls continue through and between feeding bouts and become louder as feeding progresses. This pattern continues after fledging when young birds will call loudly and persistently prior to any feeding. These changes are plotted in Fig. 4, which illustrates the behavior of two clutches of Zebra Finches.

Responses to Recorded Begging Calls

Figure 5A shows the frequency of feeding within each minute of the observation periods. There are peaks in feeding frequency during the three 2-min periods when begging calls were played. The probability of being fed was significantly greater ($P < .025$, Mann-Whitney U-test) during the times when begging calls were played and the 1 min immediately after (min 1–3, 8–10, 15–17) than at other times during the observation period (min 4–7, 11–14, 18–21).

Figure 5B shows a similar frequency distribution for begging by the offspring. Notice that this also has peaks during the minutes when recorded begging calls were played in the cage. The frequency of begging during min 1–3, 8–10, 15–17 was significantly higher ($P < .001$, Mann-Whitney U-test) than at other times during the period.

There are several explanations for the observed frequency distributions. The parents could be responding to recorded begging calls by initiating a feeding sequence that resulted in begging calls being given by the offspring. Or the offspring could be responding to the begging calls by initiating begging behavior, which induces a

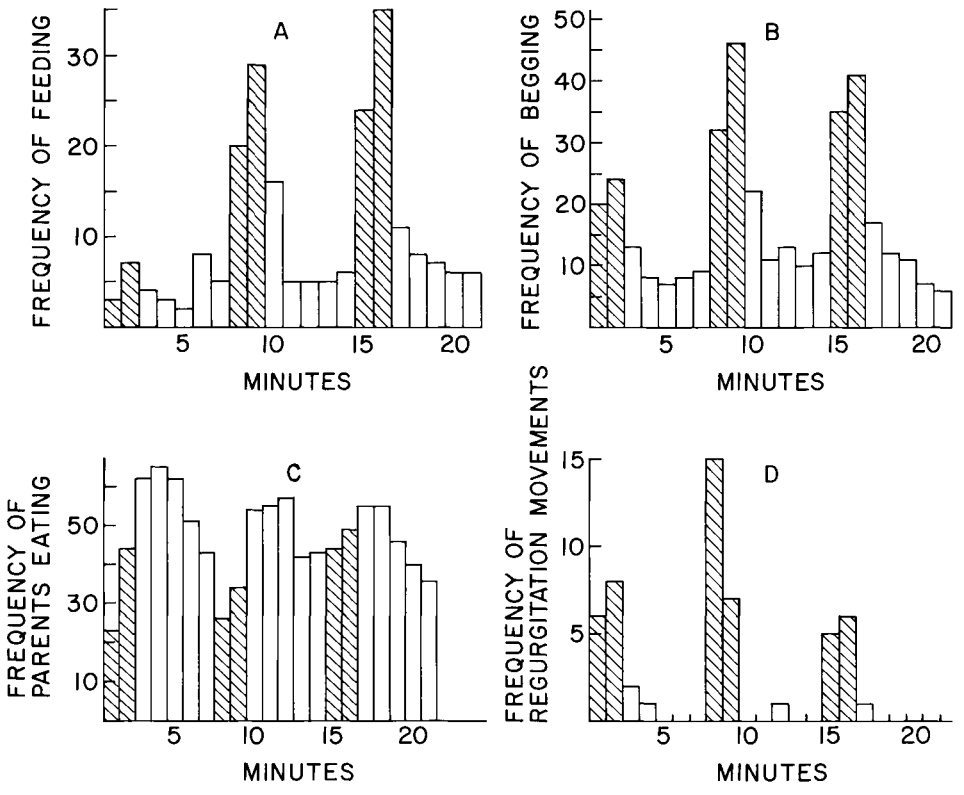

Fig. 5. The frequency of four behaviors during observation periods. Frequency represents the total number of observation periods during which the behavior was observed. Hatched bars represent the frequencies of behavior during the min when recorded calls were broadcast in the cage. The data were collected during 149 observation periods involving 19 pairs of parents.

feeding sequence. There could also be a combination of these—begging calls might affect both parents and offspring to initiate a feeding sequence. We believe that the latter explanation best accounts for the results. The frequency distributions of both feeding and begging have peaks during the 2-min periods when calls are played. However, the distributions do differ (Figs. 5A, B).

The offspring often began begging immediately after the recorded begging calls began playing during min 1 and 2. However, the parents did not usually begin feeding at that time. They often waited until the calls stopped and then began eating seeds. Figure 5C shows the frequency of seed eating by parents within each min of the observation periods. The largest peaks follow the periods when begging calls are being played. The 3 min after each interval of recorded begging calls had significantly more seed eating than the 12 other min ($P < .001$, Mann-Whitney U-test). This demonstrates that the common parental response to recorded begging calls was to eat seeds, which they could later regurgitate and feed to their offspring. After several min of eating seeds parents would usually stop eating and approach and remain close to their offspring. This usually occurred before the second 2-min period of recorded begging calls. If the offspring begged during this time they would almost always be fed immediately, and the parents sometimes pecked at their fledglings, which normally induced begging.

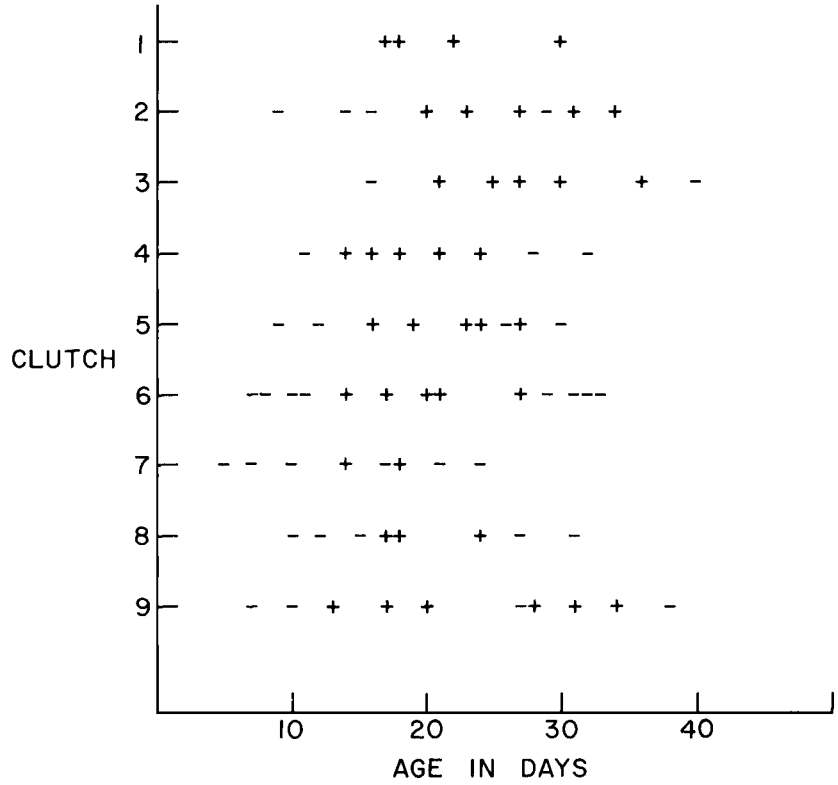

Fig. 6. Responses of parents to recorded begging calls vs. the age of the off-spring. A "+" indicates that feeding occurred during at least 1 min within the observation period during which recorded calls were being played; a "−" indicates that no feeding occurred at these times.

Most feeding, however, was delayed until min 8 and 9 or 15 and 16, when begging calls were again played. The parents initiated feeding sequences during the periods when begging calls were played by approaching their offspring and pecking at them. There were 219 min during which feeding sequences took place. During 61 of these sequences (28%), the parents initiated the feeding bouts. In addition, of 380 min during which the offspring showed begging behavior, 181 (48%) were not followed by feeding. Parents also displayed regurgitation movements in a temporal pattern that was related to that of the recorded calls (Fig. 5D). The frequency of regurgitation movements during min 1–3, 8–10, and 15–17 was significantly higher than that in the other min ($P < .001$, Mann-Whitney U-test). This behavior was often given in the absence of begging by young birds.

Thus parents responded to the recorded begging calls as well as to the begging behavior of their offspring. However, the young birds began begging during the periods when the recorded calls were played even if the parents did not approach them. This was also interpreted as a response to the sound of recorded begging calls. The recorded begging calls had a longer term effect on feeding as well as an effect within each 2-min period. The frequency of feeding increased progressively from the first to the third 2-min period during which calls were played, and most feeding took place during min 15 and 16 (Fig. 5A).

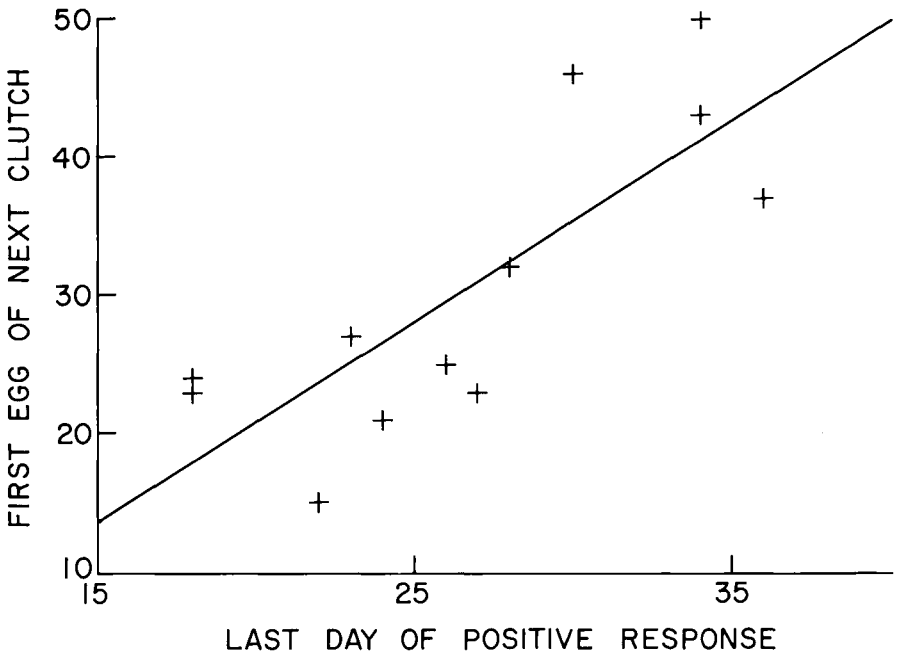

Fig. 7. Day on which the first egg of a clutch was laid vs. the day on which the parents showed the last positive response to recorded begging calls in the previous clutch. Both were measured from the day on which the first egg from the former clutch hatched. $R^2 = .79$.

The responses by parents to recorded begging calls were only seen during one phase in the reproductive cycle. Figure 6 shows the responses of parents plotted with respect to age of the offspring. A positive response indicates that feeding took place during at least one of the min when begging calls were being played. Feeding at other times did not constitute a positive response. However, feeding seldom occurred only during the silent portions of the observation period. The parents began to respond to begging calls around the time when their offspring fledged (between 13 and 19 days post-hatch). The age of the offspring on the day on which positive responses were first elicited was variable and ranged between 13 and 21 days post-hatching. In several cases there was a positive response during the first observation period involving a particular parent-offspring group In other cases the first few responses of one pair of parents were negative. Those cases of initial negative responses occurred when the offspring involved were relatively young. Those pairs that displayed positive responses within the first observation period had offspring that were relatively old. The initial negative responses in some cases are thus related to the age of the offspring rather than a period of adjustment to the test situation. The end of the period of positive responses was even more variable than its beginning. When it occurred the offspring were able to feed themselves. There is a high degree of correlation between the appearance of begging and feeding, but there were observation periods when only begging occurred. Of the 13 times when this occurred, 10 involved old fledglings whose parents no longer responded to recorded begging calls. This suggests that the parents cut off feeding of fledglings before the fledglings stop begging.

Those pairs that stopped responding to recorded begging calls when the offspring were younger tended to lay the first egg of their next clutch earlier than those pairs that stopped responding when the offspring were older (Fig. 7). This suggests that physiological changes that are involved in courtship and ovulation within the parents may be related to a parent's responses to older offspring.

DISCUSSION

The begging behavior of immature Zebra Finches contains visual and acoustic components that change qualitatively and quantitatively as the young grow and develop. Nestlings less than 3 days old beg silently, suggesting that the mouth markings and tongue movements constitute the primary signals for feeding at this time. Over a period of days calls appear and increase in sound intensity. The timing of these calls with respect to feeding also changes. Calls are first given by nestlings after a feeding bout has begun. When the nestlings are older (approximately 13–15 days) they begin to vocalize prior to feeding bouts. Fledglings (approximately 15–30 days) commonly vocalize prior to and during feeding bouts. The responses of parents to begging calls also change with the age of the offspring. Recorded begging calls are sufficient to initiate feeding by parents only when the offspring are approximately 12–16 days old or older. These factors all suggest that acoustic signals become important in initiating feeding only after the nestlings reach a certain age. Prior to that time visual cues seem to be most important in initiating feeding.

The importance of visual cues is suggested by the fact that wild Zebra Finches will not feed nestlings of other species, which have different mouth markings (Immelmann 1962; Nicolai 1964, 1974), and domestic Zebra Finches will often discriminate against nestlings with unusual mouth markings (Muller 1975).

Several species of birds are known to have nestlings that, like Zebra Finches, at first beg silently (Collis 1952, Marler 1956, Eisner 1960, Snow 1974). However nestlings of other species vocalize immediately (Odum 1941, Spencer 1943). This suggests that the relative importance of visual and acoustic cues probably varies among species.

Other studies have demonstrated the importance of acoustic cues in eliciting parental behavior. Using Pied Flycatchers (*Muscicapa hypoleuca*), von Haartman (1953) arranged a double nest box in which one of the nestlings was accessible to the parents and six other nestlings could be heard but not seen by the parents. The calls of the six hungry nestlings stimulated the parents to feed the single accessible nestling more than twice the normal amount of food. Nottebohm and Nottebohm (1971) found that surgically deafened Ring Doves (*Streptopelia risoria*) do not feed their squabs enough to sustain them, and deafened turkeys will kill their offspring when they hatch out of the eggs (Schleidt et al. 1960). Betts (1954, 1956) found that the begging calls of its own young were necessary to induce parents in several species of passerines to feed an artificial nestling. These studies on three different orders of birds, as well as the use of some type of begging call by most species of birds, suggest the widespread importance of acoustic signals in the parent-offspring interaction.

Trivers (1974) has examined the parent-offspring interaction from a theoretical viewpoint considering probable selection pressures on parents and on offspring. He has proposed that at all times the offspring will ". . . tend to favor greater parental investment than the parent is selected to give." A further prediction is that at some time during the reproductive cycle the parent should cut off parental care to maximize its reproductive output, but the offspring should continue to seek parental

care. According to Trivers the offspring could increase parental attention by not only begging when it is very hungry but also when it wants more food than the parent has already given. Zebra Finch fledglings were observed to respond to recorded begging calls by begging to their parents. Presumably they were not very hungry in these cases or they would have been begging before the calls were played, but they increase their individual benefits by begging whenever the parents were feeding or when other nestlings were begging. Our data also suggest that Zebra Finch parents cease to respond to begging calls before fledglings stop begging. It thus appears that the parents cut off parental care and force the fledglings to feed independently.

The communication system that functions between parents and offspring is a dynamic one. The signals that offspring generate to elicit feeding from their parents change substantially as the offspring grow. In addition, the responsiveness of parents to different types of begging signals changes over a period of days. The result seems to be an interaction in which the parent's responsiveness changes in parallel with the changing signals emitted by its offspring. Different modalities function as the major communication channel during different stages in this sequence.

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