

BEHAVIORAL ADJUSTMENTS OF CUCKOO NESTLINGS (*CUCULUS CANORUS*) TO FOSTER PARENTS

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ABSTRACT: The behavior and adjustments of a cuckoo nestling developing in a redstart nest were studied. High acoustic sensitivity was found in the range of non-species-typical components of the sonic feeding complex of the host species. The general tendency of avian hearing development, accelerated formation of low-frequency range, also plays an important role in the biology of the parasite species. A constantly increased level of feeding motivation along with the high acoustic sensitivity are basic for the 100% responsiveness to arrivals of adults with food. Vocalization matching, that is, a coincidence of the frequency band limits and of the intensity of vocalization of a cuckoo chick and redstart brood ensures the equal frequency of feedings. The coincidence of sequence and timing of the periods of nest life of cuckoo and redstart young that were determined with respect to the change of the modality stimulating feeding behavior increases the feeding competition abilities of a cuckoo nestling in the case of forced coexistence with the young of the host species.

The most prominent and well-known characteristic of the behavior of the nestlings of the nest parasite, the common cuckoo (*Cuculus canorus*), is the fact that immediately after hatching they start throwing the eggs and nestlings of their foster parents out of the nest. This behavior has been observed in all sub-species of the common cuckoo that parasitize the nests of different passerine species, both open- and hole-nesters. The adaptive meaning of this behavioral pattern, the elimination of competitors for food, seems so obvious that time has failed to affect this view postulated decades ago (Promptov, 1941; Malchevsky, 1954, 1987; Gould & Marler, 1987). This is probably because the behavior of cuckoo nestlings has remained the subject of naturalistic description (Malchevsky, 1987) rather than the focus of an experimental analysis. The majority, if not all, researchers concentrated their attention on the egg-throwing behavior itself. According to the logic of the traditional

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approach, a cuckoo nestling would starve if it did not successfully dispose of its possible future "nest-mates." However, in two cases foster parents were seen successfully feeding their own young and a cuckoo chick in deep tree-holes where the latter could not effectively dispose of the foster species' eggs (Malchevsky, 1954; Shkatulova, 1970). These are the only reports we know of the adjustments of cuckoo nestlings to the nest-life of their foster parents other than the behavioral pattern of eggs and/or nestling removal.

The present study was designed to analyze the sensory basis of the main behavioral patterns of the postembryonic ontogeny of common cuckoo nestlings reared by redstarts (*Phoenicurus phoenicurus*). The focus of the study was on the adjustive characteristics of the behavior of the young throughout the period in the nest, 20 days for the cuckoo and 14-15 days for the redstarts. Our analysis of the organization of feeding behavior of the young was aimed at the evaluation of the probability of a feeding reaction by the young to an arrival of an adult with food and the probability of reinforcement of these reactions (begging success) for each nestling during each day of nest life. In the studies of the families in which cuckoo nestlings were reared, special attention was paid to the stimuli eliciting feeding and defense reactions in cuckoo and redstart chicks and to the organization of their behavior.

METHODS AND PROCEDURES

All field and laboratory studies were carried out in the Oka-Terrace State Reserve (120 km south of Moscow).

Field Studies

Artificial wooden nest-boxes (13 x 13 x 30 cm) were set up 1.5-2 m above the ground on tree trunks in the mixed forest. From May through July these nest-boxes were used for breeding by various hole-nesters: pied flycatchers (*Muscicapa hypoleuca*), different tits (*Parus spp.*) and occasionally by redstarts. Birds constructed their nests in the center on the bottom of the nest-boxes, approximately 15 cm below the entrance hole.

To study the nest behavior we constructed a wooden light-protected experimental chamber (1.5 x 1.5 x 1.5 m) that housed researcher and all necessary equipment near the nest to be studied. The experimental nest-box that was fixed in the wall of the chamber differed from an ordinary one only in that its back wall could be easily removed to observe the nest. During the observation period adult redstarts (both male and female) were foraging on their own. The observer and the equipment in the dark experimental chamber did not in any way influence the normal nest life of the birds under study.

The only criterion for a choice of a given redstart family from the local population was the presence of a cuckoo egg in the clutch. One such family was found and studied each season. Observations were made during two breeding seasons successively throughout the period of cuckoo nest life (20 days). Nest behavior was observed during the light hours (10 to 12 h) of continuous observation starting every day at 0600-0700 h.

Each nest was divided into 13 zones: a central zone and 12 sectors, numbered clockwise. In all families studied the following data were recorded daily in the protocol: the time of hatching of each nestling; stimuli eliciting feeding and defense reactions of the young; sectors occupied by the parents on the nest edge during feeding the young; zones of the nest where begging of each of individually marked chick took place; number and position of the nestling that got food during each feeding act; and nestling body weight.

Sounds emitted by the young and their parents were tape-recorded. The microphone of the tape-recorder and the 1.5 cm microphone of a Bruel & Kjaer (Type 2203), SPL-meter to measure intensity of vocalization were placed 15 cm above the center of the nest. Sounds were analyzed on a Kay Electric 7029A sonograph with narrow-band filter in the frequency band of 0-16 kHz.

Each season one family with only five redstart chicks and a family with one cuckoo chick to which one redstart chick was later added were studied. These were obtained in the following way. A few days before hatching a redstart nest with six eggs, including one laid by a cuckoo, was removed from the nest-box on a tree into the experimental chamber. After the cuckoo young had hatched, the redstart eggs were moved to the redstart nest in the other experimental chamber. The redstart eggs of the second family were distributed among other redstart broods. In both cases redstart young hatched 1-1.5 days after the cuckoo; thus, cuckoo nestlings were 1-1.5 days older than their redstart "siblings" in the study. When the cuckoo was six days old and had stopped attempting to throw redstart nestlings out of the nest, a 4.5 day-old redstart chick was returned to its native nest to join the cuckoo chick; thus the original age difference was maintained.

Laboratory Studies

Laboratory studies were performed in the laboratory building containing all necessary equipment. Nestlings to be observed were brought from their nests, which usually took 5 to 15 min. After the procedures that lasted 20-45 min, chicks were quickly delivered back to their nests.

Auditory Sensitivity. The range of auditory sensitivity of cuckoo and redstart nestlings was measured daily between days 1 and 6. Nestlings were placed one by one in the nest 15 cm from the loudspeaker.

Gated signals from the sound generator were used. After testing each nestling, the microphone of the Bruel & Kjaer SPL-meter was placed in the nest in the position of a nestling's head to measure the threshold intensity.

Monotonic signals 100 ms duration, 5 ms rise/fall, in the frequency range 0.1–6.0 kHz, in steps of 100 Hz, were presented in a quasirandom order. The criterion of auditory sensitivity was feeding reactions by nestlings at the highest level of feeding motivation to 90% of the presented stimuli.

Other Stimuli Eliciting the Feeding Reaction. Nestlings were presented with soundless light flashes of varying intensity and duration generated by an FS-2 photostimulator. The vibration sensitivity was tested by means of shaking the nest with a chick in it, with special precautions taken against rustling of the nest material that was an effective stimulus by itself for begging. Sensitivity of the nestlings to an air flow from a bicycle pump was tested.

RESULTS

Development of Behavior in Redstart Young. The dominating behavior pattern in 1–5 day old nestlings was feeding. Under natural conditions begging was elicited by a cluster of stimuli which may be called the sonic feeding complex: 1) the sound made by the feet of an adult bird landing on the nestbox; 2) the rustle of the material in the nest caused by the bird's landing on the nest edge and 3) the species-typical food call, emitted by a bird. The characteristics of redstart parental signals are presented in Table 1 and Figure 1.

Beginning with the first day of life, the feeding reaction of the nestlings was accompanied by their vocalizations. By day 4 it reached a level high enough for measurement and recording by the equipment used. Sonographic analysis revealed (Fig. 2) that these sounds were in the wide frequency band between 4.0 and 8.0 kHz, the borders shifting towards the low-frequency part of the spectrum as the chicks grew. Changes in the integrated level of the vocalization intensity of the redstart brood consisting of 5 chicks are illustrated in Figure 3. In response to the sonic feeding complex nestlings changed their posture: the body was oriented vertically, the neck was stretched upward, the beak was opened wide. The very first begging response included a vocalization component of low intensity. The parents stayed in the nest-box when the young did not need warming after one of the chicks had received a portion of food as long as the chicks vocalized and moved in the nest (4.6 ± 0.3). The adult bird left the nest after picking up the fecal capsule of the young or after there was no chick movement. Movements and vocalizations ceased simultaneously.

When the modality and the parameters of stimuli effective for begging in 1-5 day old young were studied in the laboratory it was found out that begging could be elicited *only* by the *acoustic signals*. Begging in chicks with the highest level of feeding motivation (Khayutin, 1985) could be provoked in the laboratory not only by playing a tape recording of the sonic feeding complex but also by a rich assortment of sounds, e.g., human whistles and speech. No other stimuli, such as tactile (e.g., air flow), vibrational or visual could elicit begging in the young at that stage. Khayutin (1985) also found this to be true of other hole-nesters, such as *Erethacus rubecula*, *Ficedula hypoleuca*, *Parus major*, and *Parus atricapillus*.

When feeding sounds were imitated in the laboratory by a wide range of signal tones, auditory sensitivity was found in the range of 0.1-5.1 kHz. The lowest thresholds were in the 0.1-0.2 and 1.5-2.5 kHz

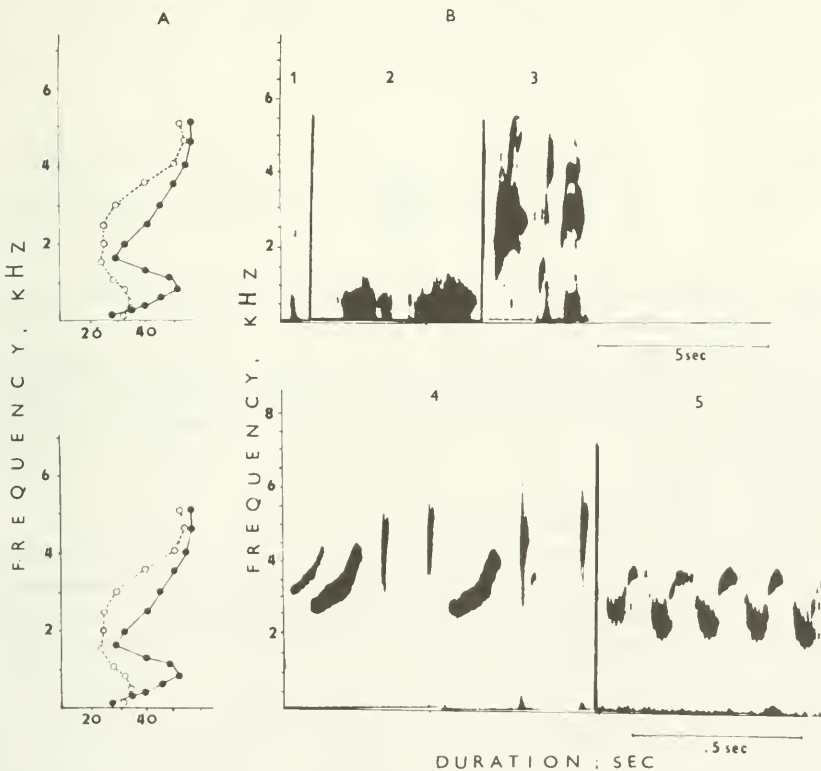


FIGURE 1. A. Auditory thresholds of 5-day nestlings: 1. redstart; 2. cuckoo; dB above the background noise level. B. Sonograms of sounds produced by parental redstart behavior meaningful for young behavior. Sonic feeding complex; 1, parent feet tapping; 2, rustling of nest; 3, variations of the food call. 4. Alarm call. 5. Species song.

TABLE 1
Characteristics of Parental Acoustic Signals of
Redstarts Recorded in Natural Nests

<i>Signals</i>	<i>Main energy maxima (kHz)</i>	<i>Duration (ms)</i>
Sound of feet tapping on a nest-box	0.2-0.75	50-75
	1.5-2.50	
	3.5-4.00	
Rustle of nest material from landings on a nest	0.2-1.25	200-500
Food call	0.2-0.80	50-100
	2.0-3.50	
	3.5-5.50	
Alarm call	2.5-3.50	25-150

ranges. A comparison of the hearing range of the young with the spectrum of the sonic feeding complex (Figure 1B, 1-3) revealed that the first of these sensitivity peaks corresponded to the maximum energy of the first two components of the complex, while the second peak corresponded to the high-energy part of the food call (Figure 1A, 1). The first two components of the sonic feeding complex have characteristics that are not restricted to redstarts, while the third, the food call, is characteristic only of the redstart species.

Beginning with day 5, nestlings started to show a passive-defense reaction, that is, a cessation of vocalization and freezing, in response to the alarm call. On day 5-6, the nestlings' eyes opened and the modality of the stimulus for feeding behavior changed significantly. Beginning with days 5-6 and until day 8, when the visual system responded only to diffuse light, the diffuse luminosity change caused by the arrival of the adult bird with food that closed the entrance hole with its body became the dominant component of the complex of feeding stimuli in the natural nest box. As a result, the frequency of occurrence of the food call was reduced greatly; it was observed in 10% of the feedings only. In spite of the significant increase of the variety of feeding stimuli, i.e., the appearance of a new stimulus modality, no changes in the pattern of feeding took place until day 8-9.

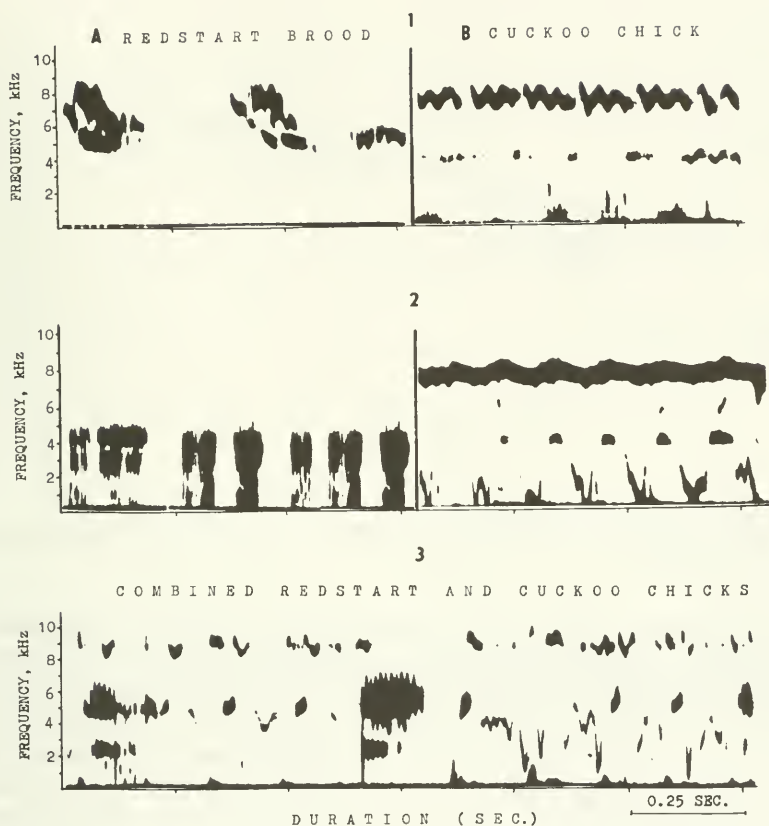


FIGURE 2. Vocalization component of begging behavior of redstart brood (A) and of cuckoo chick (B). A, 5-day old chicks; 12-day old chicks; 3, vocalization accompanying begging of redstart chick sharing the nest on 8-day old and 9.5-day old cuckoo chick.

On day 8 the feeding reaction was transformed from passive begging to active food-acquisition. The young turned their heads to the head of the parent and tried to snatch the food from its beak. Until day 11, this behavior followed a change in diffuse luminosity and was guided by the moving silhouette of the adult. Food acquisition was elicited and guided by the moving bird silhouette after this and until fledging.

In general, the distribution of food in the brood of redstart young was like that described for some other species (Khayutin & Dmitrieva, 1976; Best, 1977; Khayutin, 1985). Even distribution of food among the young was due to their relatively regular circular movement in the nest. Each nestling periodically occupied the zone with the highest probability of begging success as it moved around the nest. These zones were connected with the places taken by the parents for feeding the young, the places being fixed in any given nest (Khayutin & Dmitrieva, 1981).

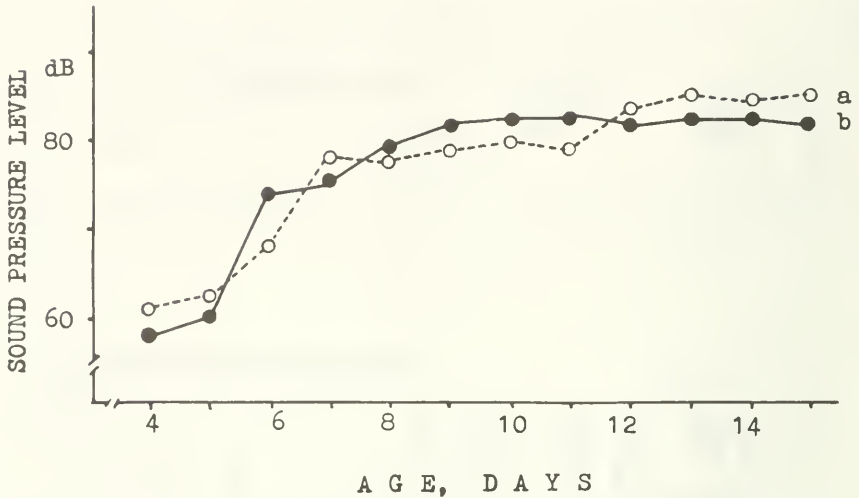


FIGURE 3. Intensity of vocalization of redstart brood of five nestlings (a) and cuckoo chicks (b).

Most arrivals of adults provoked begging in at least four chicks or in all young, i.e., the probability of begging for each nestling in response to each arrival of a parent was 70-90% (Fig. 4A, 2) but only one chick got food. After a chick in the optimal zone got food, it left the area and, by the time of the next arrival of a parent, this zone was usually occupied by another young. Thus in a brood of five, each nestling got 20% of all food brought by the parents, each of the young having only one of four or five beggings reinforced. The fact that the probability of reinforcement of each nestling was slightly higher than 20% (Fig. 4B, 1) might be due to two reasons: a) the probability of begging for each young was somewhat below 100%; b) sometimes, though rarely, that is, in 2-3% of all feedings, birds did feed more than one nestling at a time.

Body weights of nestlings yielded the S-shaped curves typical for altricial birds (Poznanin, 1979; Khayutin & Dmitrieva, 1981). By day 11, the young reached the maximal mass of 15 g that varied only slightly during the last days in the nest (Fig. 5, 1).

Behavioral Organization of the Cuckoo Nestling. Immediately after hatching the cuckoo young was observed begging and throwing eggs and/or nestlings out of the nest. The latter pattern has been described in numerous studies (Promptov, 1941; Numerov, 1978).

The analysis of the feeding behavior in the cuckoo nestling revealed that the redstart sonic feeding complex elicited its begging. The motor organization of begging in the cuckoo young differed from that of the redstart: the reaction was tonic and included no apparent movements of body and limbs. The neck was bent backwards and the position of the

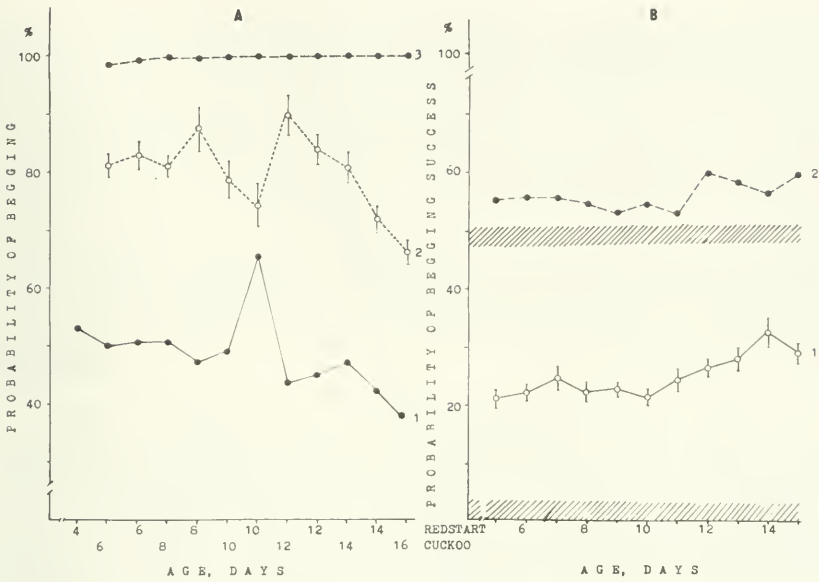


FIGURE 4. A. Probability of the feeding reaction (begging) in 1) redstart chicks ($n=2$); 2) 5 redstart chicks in a normal brood sharing one nest ($n=10$); and 3) cuckoo chicks ($n=2$). B. Probability of begging success for a redstart nestling developing 1) with 4 siblings ($n=10$); and 2) with a cuckoo chick ($n=2$). Area between hatch lines = expected probability of begging success for a redstart developing in a nest with a cuckoo chick.

head was fixed with the beak wide open. This posture was maintained until the adult left the nest-box. Begging included a vocalization component that reached a measurable level by day 4-5 (Figure 2B, 1). The vocalization of a 4-5 day-old was frequency modulated, narrow-banded with two marked energy maxima at 4.0-4.5 and 7.0-9.0 kHz and with a low-frequency component of 0.1-2.5 kHz. The latter is a sonographic representation of a click. As the nestlings grew older, the low-frequency component became more marked and its structure more complicated (Figure 3, B).

The auditory sensitivity of 1-6 day-old nestlings was in the range of 0.2-5.1 kHz; sensitivity peaks corresponded to 0.2-0.4 and 1.6-2.0 kHz. Comparison of the hearing range of cuckoo young with the spectrum of the sonic feeding complex of the foster parents revealed that the low-frequency sensitivity peak corresponded to the energy maxima of the first two components of the complex while the second peak corresponded to the high-energy part of the species-typical redstart food call (Fig. 1A, 2).

We also tried to find some other stimuli eliciting feeding behavior in cuckoo chicks: light flashes of varying intensity and duration, air flow,

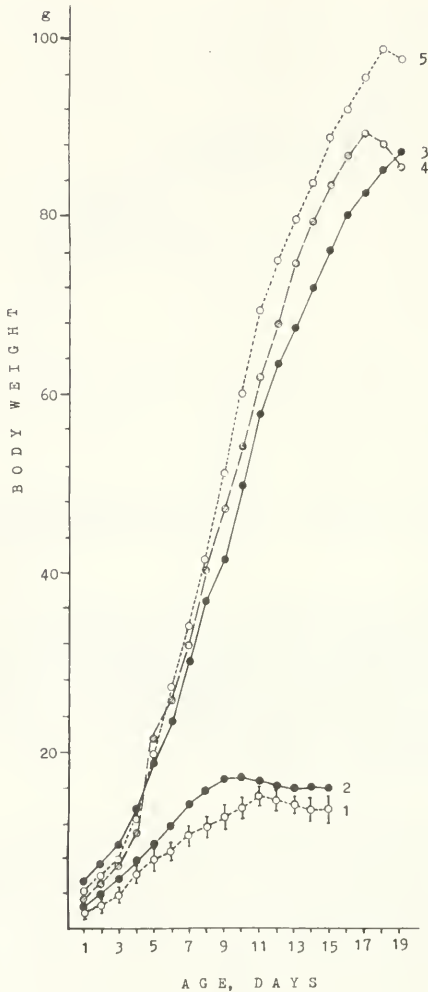


FIGURE 5. Body weights of nestlings. Redstart chick: 1. in a normal brood ($n=10$); 2. sharing a nest with a cuckoo ($n=2$). Cuckoo chick developing alone 3) after Promptov (1941) ($n=12$) and 4) after Numerev (1978) ($n=8$); and 5) developing with one redstart chick ($n=2$).

shaking of the nest. Only the latter, of all stimuli used, elicited begging in the cuckoo chick.

Cuckoos opened their eyes on day 6. This was accompanied by the emergence of a feeding reaction in response to a diffuse luminosity change. However, the sounds produced by the arriving adult bird remained very effective stimuli for begging until the end of the nest period. From day 6 the cuckoo chicks stopped vocalizing and froze to the alarm calls of foster species and some other birds (passive-defense

reaction). But if a parent arrived with food, or if the feeding stimuli were reproduced artificially while an alarm call sounded outside the nest-box, the cuckoo chick immediately started to beg, either in complete silence or with barely audible vocalization. In response to repeated stimulation this reduced begging was quickly substituted by a normal one. In redstart chicks such suppression of defense reactions was observed very early.

On day 11 the moving parent started to provoke a very active food-acquisition response. No changes in the behavior of the young were observed from day 11 to the end of the nest period (day 20). Begging was elicited by the sounds produced by the arriving bird and by its moving silhouette.

Development of Cuckoo and Redstart Chicks in a Shared Nest. In an attempt to understand what made the foster parents feed cuckoo chicks that differed greatly from their own young in body size, feather coloring, as well as in size and color of the oral cavity, we analyzed the behavior of adult birds and cuckoo and redstart nestlings sharing the same nest. When the cuckoo was 6 days old, a 4.5-day old redstart was placed in the nest. By that time both had their eyes open and thus begging was adequately stimulated by the luminosity change as well as by sonic stimuli. Although the hearing range and sensitivity peaks of the cuckoo chicks matched those of the redstart young, its low-frequency thresholds (corresponding to energy maxima of the nonspecific components of the complex) were 1.5–2 times lower than those of redstarts. However, in the high-frequency range corresponding to the spectrum of the redstart food call, the cuckoo's absolute thresholds were a few times higher than those of a redstart chick of the same age. Cuckoo chicks responded by normal begging to the same set of sounds that caused a feeding response in redstart young.

Feeding was organized as follows. All arrivals of an adult elicited begging in the cuckoo chick, but only 45% of the arrivals elicited begging in the redstart (Fig. 4A, 1, 3). Thus, in 45% of the cases, the nestlings responded in a chorus. Here it is worth noting that in normal redstart broods of five, each young reacted to 70–90% of the arrivals while the probability of begging success could not significantly exceed 20%. From this the following somewhat arbitrary conclusion may be inferred: if redstart parents feed each of the two chicks with equal willingness, as in the case with a normal brood of five redstart chicks, the probability of reinforcement of a feeding reaction in each of two different young must be about 50% (Fig. 4B, upper hatched line). Reports from other studies, however, challenge such an oversimplification. Adult birds are known to put food selectively in the most widely opened beaks when feeding differently-aged nestlings (Lohrl, 1968; Illies, 1975). Considering the great differences between the cuckoo and redstart nestlings in the body

size and the size of the opened beaks, it may be supposed that the redstart's begging should practically never be reinforced (Fig. 4B, lower hatch lines). Thus the probability of begging success for a redstart sharing the nest with a cuckoo must be confined within the limits of 0-50%.

The analysis of the distribution of food between two different chicks in each of the nests during the two seasons throughout their joint stay in the same nest revealed, however, that the probability of reinforcement of the redstart's feeding response reached 60%, that is, it exceeded the expected level (Fig. 4B, 2). How can this high probability of the redstart's begging success be explained in view of the fact that the redstart's feeding reactions themselves occurred much less frequently than did those of the cuckoo as well as less frequently than those of the other redstart chicks (Fig. 4A, 1, 2 and 3).

As noted above and elsewhere (Khayutin & Dmitrieva, 1981; Khayutin, 1985) the existence and location of the zones of the highest probability of begging success was determined in each nest by the places taken by the parents on the edge of the nest when feeding the young and by the adult's physical ability to bend its neck and put food into an open beak of one of the young. When a cuckoo chick and a redstart chick were begging, in spite of the fact that the central part of the nest was occupied by the cuckoo, and the redstart chick was pressed into a distant sector of the nest with the most unfavorable position for feeding, the redstart chick was fed more often. Moreover, when feeding its own young, an adult bird was often carrying food right in front of the open beak of cuckoo young

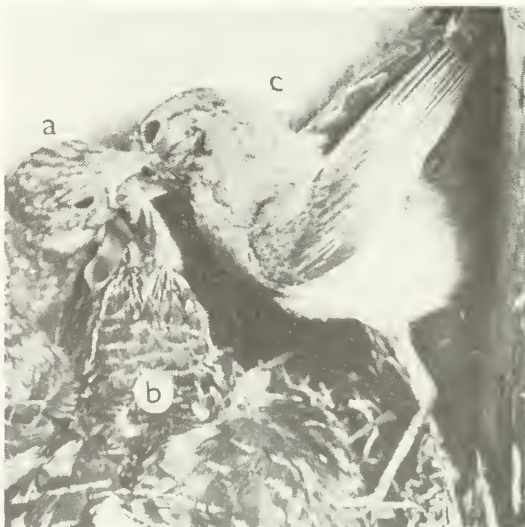


FIGURE 6. Redstart (C) selectively feeding its own nestling (A) developing in the nest with a cuckoo chick (B).

provoking its violent attacks (Fig. 6). On many occasions (55%) the sounds produced by an arriving parent that always elicited a feeding response in the cuckoo, appeared ineffective for the redstart chick because of its constantly decreased level of feeding motivation. In those cases, the parent emitted the food call that was never used when feeding the young with open eyes in normal broods. This call provoked a very slow feeding response in the redstart chick that was immediately reinforced (Fig. 6). Sometimes adults even tried to force food into the beak of their own chick.

DISCUSSION

Our observations indicated the existence of a very finely-tuned parental behavior manifested in the selective feeding of the young of its own species by the parent. As the foster parent's chicks have the "first turn" during feeding, the specific behavior pattern in which cuckoo young throw out the eggs and/or nestlings of the parasitized species may be considered an elimination of the competitors for food that are preferred by the cuckoo's foster parents, rather than resulting from hypothetical limitations of food resources or from the limited physical capabilities of the foster parents.

The unique role of these two factors, the availability of resources and parental prowess, are widely accepted and cited in the ornithologic and behavioral literature. For example, Manteifel says (1980, p. 16), "This whole complex of behavior of a newborn cuckoo is unequivocally inborn and was developed in the evolution of the parasitic species as a necessary adaptation, because a pair of small passerine foster parents is barely able to feed one very voracious cuckoo chick which grows extremely quickly. They cannot feed and raise their own brood in addition to the adopted child." This viewpoint is contradicted by the data of Malchevsky (1954) and Shkatulova (1970) who observed foster parents successfully feeding cuckoo chicks as well as their own young. Our own data (Figure 5) demonstrate that the body weights of cuckoo young raised with redstarts are no less than the body weights of cuckoos raised alone and that the body weights of redstarts raised with cuckoos are also less than those raised with other redstarts.

Marked parental preference for their own young results in an apparent ignoring of the cuckoo chick during its life in the same nest. From this observation it may be supposed that foster parents probably do to some extent ignore a cuckoo chick even when the foundling is alone in the nest. Consequently, cuckoo nestlings must possess a set of adaptations that can counteract this tendency. On the basis of our observations the following traits may be suggested as the possible candidates for such adaptations:

1. High sensitivity of sensory mechanisms to the feeding behavior stimuli addressed to the young of the host species.
2. A constantly increased level of feeding motivation that along with the sensitive sensory mechanisms ensures the 10-80% responsiveness of the cuckoos to the arrivals of the adult birds.
3. The match between the upper and lower limits of the frequency bands and amplitude of vocalization of one cuckoo chick and of a brood of five redstart chicks, which is most marked at the early age. Khayutin & Dmitrieva (1981) have shown that the vocalizations of an entire brood of chicks acted as an index of the integral level of the feeding motivation that regulated the frequency of feeding. The equivalent intensities of the vocalization of a cuckoo chick and five redstart nestlings may determine the similar frequency of the feeding episodes in both cases.
4. The bright coloring and larger size of the cuckoo oral cavity may partly counteract the tendency of the redstart parents to feed their own young selectively. Thus the cuckoo can take advantage of the basic "conservatism of parental behavior" that leads to the selective feeding of bigger nestlings.
5. The match of the succession and timing of the stages of nestling development that are related to the changes of the modalities of the stimuli that elicit feeding behavior in cuckoo and redstart young. This match may be considered to be a *super-adaptation* that is realized in case of the failure of the cuckoo's first adaptive behavior pattern, i.e., throwing out eggs and/or nestlings. This superadaptation increases the cuckoo's feeding competitiveness significantly when it has to share the nest with the young of the foster parents, but is not necessary in the case of solitary development.

SUMMARY

The survival of the parasite species, *Cuculus canorus*, is based not only on the efficacy of the behavioral adaptations of adult cuckoos (e.g., the selection of adequate nests and the timing of egg-laying) but also on the adaptational mechanisms that their young possess. Some of these mechanisms have been revealed in this study. The most widely known pattern is throwing eggs and/or nestlings out of the nest. Other behavioral and physiological mechanisms may also play an important role in the survival of a cuckoo in the nest of foster parents. The first concerns the timing of maturation and the range of thresholds of cuckoo auditory

sensitivity. Our comparison of the cuckoo chick's hearing range and the spectrum of adult redstart feeding sounds has demonstrated that the peaks of auditory sensitivity matched the energy maxima of those components of the sonic feeding complex that were not species-typical, the thresholds in that range being two times lower than those of redstart young. The well-known general tendency of the hearing development in the low-frequency range (Golubeva, 1978; Konishi, 1973; Saunders, Cole & Gates, 1973; Ryden, 1980) and the relation of hearing to early behavior patterns including feeding (Milyagin, 1957; Gottlieb, 1971; Khayutin & Dmitrieva, 1981), increase the efficacy of the organization of feeding behavior in parasitic nestlings ensuring their adequate reaction to the nonspecific as well as to species-typical components of the sonic feeding complex of the foster parents.

Along with the characteristics of hearing, we studied other sensory factors of cuckoo chick feeding behavior and found that they were sensitive to vibration (soundless shaking) of the nest. No other nestling of any hole-nester species studied displayed begging in response to shaking in spite of the highest possible level of feeding motivation. On the other hand, this factor was described as an element of a signal complex of feeding response in rook nestlings by Milyagin (1946) and in blackbird young by Manteifel (1980). These findings suggest that the sensitivity to vibration and its relation to feeding behavior is a common characteristic of the nestlings of big open-nesters with nests on branches, for only then would the arrival of parents with food result in nest shaking.

Thus, cuckoos parasitizing redstart nests possess in their early ontogeny a capability to display a feeding behavior pattern in response to a wider complex of stimuli of different modalities than is necessary for survival; an adequate feeding response not only to sounds but also to vibration might theoretically help its nestlings survive not only in the nests of hole-nesters but even in the nests of big open-nesters that make nests in the trees.

In spite of the fact that after the cuckoo's eye had opened, and the modality stimulating feeding behavior changed, so that chicks started to respond to luminosity changes, sounds still remained highly effective and were related to begging until fledging. Such a high degree of efficacy of acoustic signals for the realization of feeding behavior until the end of nest life is also atypical for redstarts and any of the hole-nesting species studied by us (Khayutin & Dmitrieva, 1981; Khayutin, 1985).

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