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PSYCHOBIOLOGICAL ASPECTS OF THE
ACCELERATION OF POSTEMBRYONIC
DEVELOPMENT IN THE ASYNCHRONOUS
BREEDER, PIED FLYCATCHER
(*FICEDULA HYPOLEUCA*)

S.N. Khayutin, L.P. Dmitrieva and L.I. Alexandrov

ABSTRACT: The nest behavior of the pied flycatcher nestlings was studied in the artificially formed broods. Each of two groups of nestlings with an age range of four days were studied. Under optimal food conditions, the last of the nestlings to appear shortened the incubation period by 20-25% so that the whole brood fledged relatively synchronously. During the first half of nest life in the mixed broods younger nestlings got food mainly due to their constant motor activity, manifested in unceasing spontaneous begging, resulting from the constantly increased level of feeding motivation. During the second half of the nest life younger nestlings, due to their high activity level, get even the greater amount of food than the elder chicks. The long-lasting contact of the nestlings of both age groups is necessary for the selectively accelerated development of sensory and motor components of functional systems of early behavior that ensure the survival of younger nestlings and their fledging, synchronous with the older ones. It is suggested that all factors promoting the accelerated development of younger nestlings are present in the natural habitat.

Numerous investigations of the ontogeny of early forms of behavior in animals with different ecological adaptations have shown that late embryonic and early postembryonic sensory experience greatly influences their behavioral organization. Studies of newly-born mammals have demonstrated the necessity of early stimulation for the development of selective attention as well as for the maturation of the respective information processing systems (Creighton and Tees, 1975; Imbert and Buisseret, 1975). Sarrow, et. al. (1972) found that the odor of male mice stimulates ovulation in young females and reduces significantly the time of their sexual maturation. Moreover, additional physical and social contact in the mouse colony accelerates sexual maturation by 18-20% compared to control isolated mice (Drickamer, 1974). The accelerated development of sexual behavior in male rats was observed under the influence of specific olfactory, tactile, visual and auditory stimulation

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by others (Gruendel and Arnold, 1974). We consider that set of influences to be a social one.

The accelerated development of different functions under the influence of additional specific afferentation is much more pronounced in avian ontogeny. In experiments with laughing gull chicks Impekoven (1976) discovered that exposing embryos to adult conspecific signals, characteristic of the incubation period, resulted in the appropriate reaction by one-day-old chicks to these signals, unlike the incubator bred gulls that started to respond to these signals much later. Adam (1975) found a significant effect of acoustic as well as light stimuli on the development of chicken embryos—they hatched earlier. Even 10 hours of light stimulation (with flashes or with constant light) reduced significantly the duration of the incubation period in chickens. Stimulation during the first week and between days 17 and 20 proved to be the most effective (Siegel et. al. 1969). Acoustical stimulation (clicks) during the last few days of incubation synchronized hatching in quail broods (Vince, 1966, 1968).

Stimulation of avian embryos at late stages of development with the attraction calls of adults or with sounds imitating these calls, accelerated and synchronized hatching in many orders of precocious and in some semiprecocious (grebes, rails, oystercatchers) birds (Vince, 1969, 1973; Impekoven, 1971; Tikhonov, 1986). The most pronounced capability of hatching synchronization is that of the rhea (Vlack and Vlack, 1985; Tikhonov, 1986). The eggs are laid during 3-14 days, incubation is started with the second or third egg laid in the clutch, but all nestlings, nevertheless, hatch synchronously with intervals of 1.0-2.5 hours. The maximal "acceleration" in rhea embryos may reach seven days. Investigations have shown that the "younger" embryos are stimulated during incubation by the clicks, produced by the "elder" embryos at the final stage of incubation and with the signals of the incubating rhea males. The synchronous hatching in precocious birds is a basic condition for the brood to leave the nest region as soon as possible.

In some semiprecocious (gulls, auks, storks), and in most altricial bird species synchronous hatching is almost never observed. The degree of asynchrony varies from few hours to 4-5 days (Clark and Wilson, 1981).

Few theories have been proposed to explain the adaptive value of asynchronous hatching. The most commonly accepted one is the hypothesis of adaptive brood reduction (Lack and Lack, 1951; Lack, 1954). It treats asynchronous hatching and the resulting difference in the size of the young as an adaptation to match the size of the brood to the available food resources. In the species utilizing the brood reduction strategy, the relation of the original clutch size and the number of the fledged nestlings may be considered as an indication of the gradual

process of adaptation to the food conditions including two phases: a) asynchronous hatching, preadapting the brood to the possible future reduction, and b) selective feeding of the most active and largest chicks, regulating the growth of the young with respect to fluctuations of the food resources.

Clark and Wilson (1981) suggested another interpretation of the asynchronous hatching. In terms of their modal asynchronous hatching is seen from the viewpoint of the breeding success, i.e., the probability of the brood survival. Synchronous hatching is more common among species more subject to predation during the nest period, i.e. open-nesters; it is more "advantageous" for these birds to prolong the period during which they have only eggs in the nest. Nestlings are a demasking factor, attracting the attention of predators to the nest. Such species (approximately 30% of the passerines) usually start the incubation after the last egg is laid, so nestlings hatch more or less synchronously.

Asynchronous hatching is most often observed in hole-nesters with their clutches protected against predators. Considering the variety of nest conditions, Clark and Wilson (1981) selected a few factors affecting the onset of incubation, and thus, the succession of hatching of the young. Northern species start incubation before the clutch is completed to protect eggs from freezing; some species have to start incubation before the last egg will have been laid because of the competition for nest sites, robbing of nest material or the necessity to protect the nest against predators. Asynchronous hatching is most pronounced in the late or repeated clutches, during the period of increasing food deficiency. In the latter case the early onset of incubation and the resulting hatching asynchrony may be considered as the parents' attempt to raise some nestlings before the food resources will become sparse. Gibb (1950) noticed that in late and repeated clutches, egg size grew with each successive egg. This observation does not fit the Lack hypothesis, but it may be explained in terms of the breeding success model as the parents' "attempt" to compensate for the difference between chicks that's due to the asynchronous hatching.

The variety of situations affecting the breeding behavior of birds is not so easy to analyse but the aforementioned facts enable us to state that nest adaptations are formed due to the complicated compromise between differently directed pressures of the selection. Later hatched nestlings due to their small size may, indeed, be involved in the competitive struggle, but the unfavourable position of one or a few nestlings is an inevitable price of brood adaptation. Lori (1968) and Illies (1975) found that parents tend to feed selectively the young with the most widely open beaks. Investigators believe that this "conservatism of parental behavior" is one of the basic mechanisms determining the better chances to survive of the elder nestlings. Also, in several bird species (hawks,

gulls) the younger nestlings' mortality rate is additionally affected by the aggressive behavior of older siblings that is directly related to their level feeding motivation (Meyburg, 1974; Dennis and Proctor, 1975).

Thus, asynchronous hatching may sometimes lead to the elimination of the younger chicks in the brood. Their mortality rate, according to different investigators, may vary between 1% (Gibb, 1950) and 55% (Parsons, 1975). The reasons for death may be different but for small passerines it is usually starvation (O'Connor, 1984). Nevertheless, even under the worst food and weather conditions the mortality rate of the later hatched nestlings never reaches 100%.

The duration of the nest period in different avian species varies between 10 and 40 days and does not depend upon the degree of asynchrony of hatching. All siblings (synchronously or asynchronously hatched) fledge, separated by the intervals from few minutes to few hours, during the 10th-40th day of life of older nestlings. Since this is the case nestlings that were last to hatch obviously pass the nest stage of development over a shorter period than their older siblings.

It is believed that nestlings of many species must possess some mechanisms, basic for the accelerated development of sensory and motor components of the main behavioral patterns of the nest period (feeding and defence behavior); normal functioning of these mechanisms provides for a synchronous termination of nest period by all nestlings, whatever the succession of their hatching.

MATERIALS AND METHOD

The data were collected in the Oka-Terrace Biospheric Reserve (120 km south of Moscow) during the study of 30 pied flycatcher (*Ficedula hypoleuca*) families. They were divided into 4 groups. Group I consisted of five families in which the nestlings hatched during a single day ("natural synchronous hatching"). Group II included five broods that hatched during 1-4 days ("natural asynchronous hatching"). Group III included five families in which the nestlings were mixed artificially irrespective of the duration of the brood hatching. The last group consisted of 15 families: Four broods were transferred into experimental chambers for a thorough study of nest behavior, 11 others were used for control studies. In groups I-III the following parameters were recorded for each chick: time of hatching (each chick was marked with individual color mark right after birth), the time and the degree of eyes opening, daily changes in body weight and the time of fledging. The nest behavior of four families with eight nestlings in each was constantly (10-14 hours a day) observed. One to two days before hatching, the nests were transferred from the ordinary nest-boxes into experimental ones (without a back wall) that were fixed on the wall of a light-protected experimental chamber which housed a researcher with cameras and tape-recorders. Two experiments

(2 families in each experiment) with mixed broods were designed as follows: In each two families nestlings hatched during one day, but in the first family four days earlier than in the second. A few hours after the last chick of the second family had hatched nestlings were mixed between the two nests, so that each brood contained eight chicks, four of each age group.

The observations of nest behavior of nestlings and adult birds yielded the following data: intervals between feedings of each nestling during each day and all nest life, changes in chick's movements in the nest, factors determining each nestling's probability of receiving food during each day and all nest life. To create an exact reference system for recording the position of the young and parents during feeding, the nest was divided into 12 sectors corresponding to the numbers on a clock face, with zone 12 situated right under the entrance-hole. An additional thirteenth zone was the center of the nest. The probability of a nestling receiving food after begging in a certain zone was calculated in the following way: $p = m/n$, where p is the probability of reinforcement of a feeding reaction of a chick begging in a given zone, i —the number of the zone, m —number of reinforced beggings in the given zone, n —total number of reinforced beggings. The interior of the experimental chamber is shown in Fig. 1.

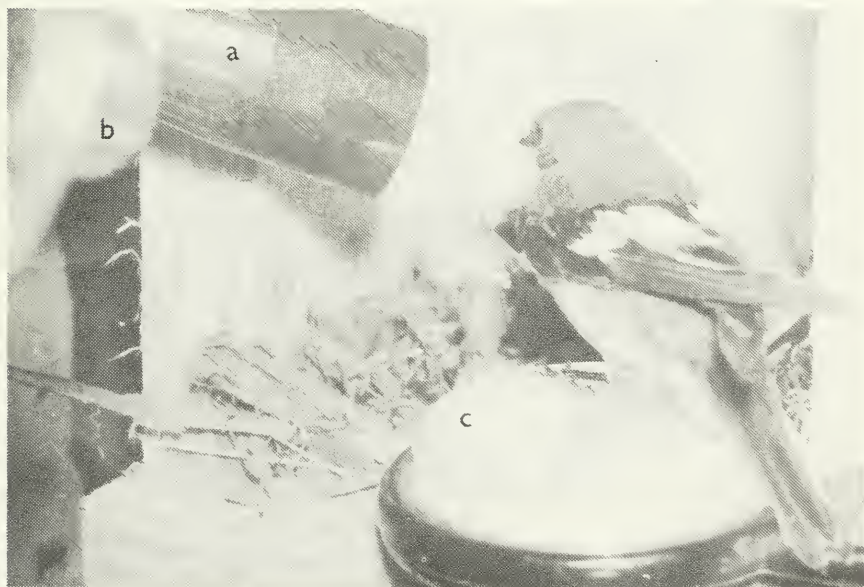


FIG. 1. Interior of an experimental nest-box with the nest of pied flycatcher. (a) Microphone of the tape recorder; (b) microphone of the sound pressure level meter; (c) photoelectric element.

RESULTS.

The analysis of nest behavior of the synchronously hatched nestlings of pied flycatcher revealed that, with respect to the triggering afferentation of feeding behavior, the nest life of the young can be subdivided into distinct stages (Khayutin and Dmitrieva, 1978a, 1981b; Khayutin, 1985; Fig. 2).

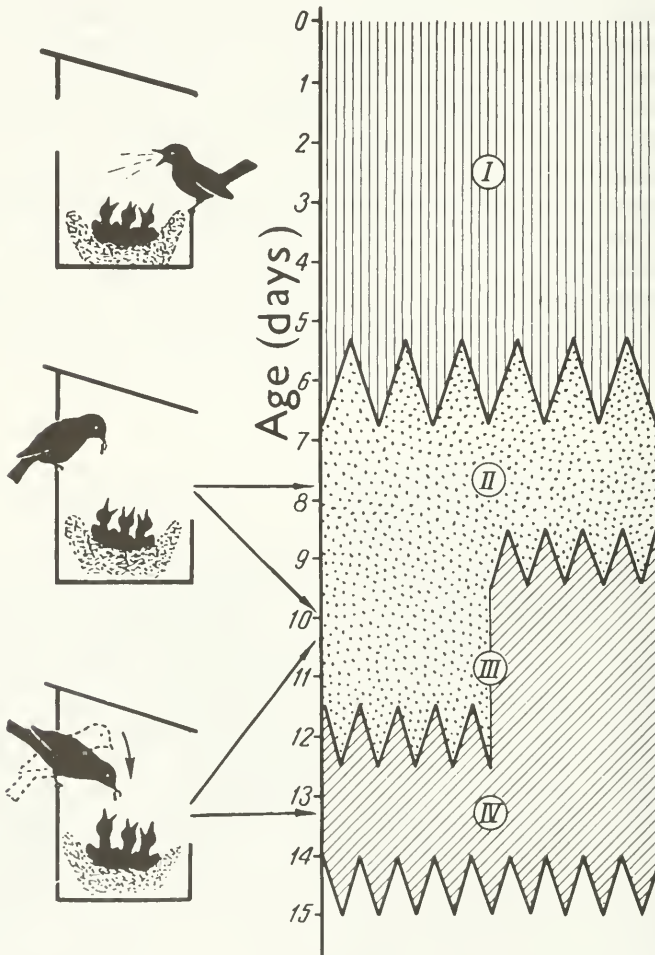


FIG. 2. Periods of nest life as determined by the triggering stimuli of feeding behavior. I. Feeding reactions elicited by the complex of auditory stimuli; II. Feeding reaction elicited by the short-term luminosity change; III. Feeding reaction organized on the basis of two visual stimuli: triggering and guiding ones; IV. Feeding reaction elicited and directed by the silhouette of the moving bird. Figures to the left of the schema—age of nestlings in days.

- I. From the moment of hatching until the onset of eye opening, i.e., until day 5-6, begging is elicited by a complex of acoustic stimuli: feet tapping on the wall of the nest-box as the bird arrives, the rustle of the nest material as the bird perches on the edge of the nest and the species-specific "food" call, emitted by a parent (Fig. 3). The analysis of feeding behavior revealed that there were fixed zones in the nest that adults occupied during feeding and zones that were characterized by the maximal probability of begging reinforcement. A statistically equal number of feedings of each nestling during the first half of nest life is determined by a specific behavioral phenomenon—the more or less regular circular shift of the chicks in the nest (Khayutin, 1963, 1985; Khayutin and Dmitrieva, 1976; Best, 1977). The optimal feeding zones are believed to be determined by the position adopted by the parent for feeding the young (always the same for a given bird in a given nest). The position of the adult determines whether food will be placed in the open beak of a nestling that is begging in a certain zone.
- II. From day 5-6 nestlings' eyes start to open and, accordingly, the set of stimuli eliciting begging changes. The luminosity change caused by the parent bird's body closing the entrance hole becomes the leading factor in feeding behavior. These luminosity changes are about 1-2 log. units and 100-150 msec long. After the nestlings' eyes open the circular shift of the young loses its even character—they start to move along the luminosity gradient that is determined

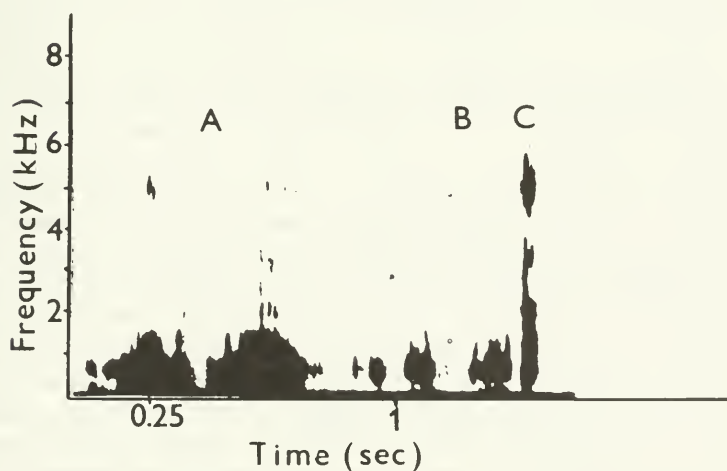


FIG. 3. Sonograms of the signals of adult birds affecting the feeding behavior of nestlings: the sonic complex of feeding. (a) Foot tapping on the nest-box; (b) rustle of nest material; (c) species-specific food call.

by the nest-box construction. At the same time their behavioral repertoire is enriched: the level of vocalization, both background and evoked, increases and the passive-defence reaction appears. The latter consists of the cessation of vocalization and freezing in response to the alarm call emitted by the parents outside.

- III. From day 8-9 feeding behavior is modified significantly. Upward neck stretching and beak opening (characteristic of nestlings during the first half of the nest period) is replaced by active food seizure, i.e., passive feeding behavior is transformed into active food-acquisition. Chicks turn their heads towards a parent, attacking its beak and snatching away food. It was found that this behavior pattern is organized on the basis of two kinds of visual stimuli: triggering (luminosity change) and guiding (moving silhouette of the adult) ones.
- IV. From day 12 and until the fledging of nestlings the moving silhouette of the adult plays the role of both triggering and guiding stimulus. Diffuse luminosity change loses its importance.

Thus, with respect to the change in sensory stimuli that are basic for the occurrence of nestlings' feeding behavior, there are several successive stages separated by 1-2 day transition periods in the nest life of flycatcher young.

The analysis of the behavior of naturally asynchronously (during 3.5-4 days) hatched nestlings confirmed that the adults selectively fed the older nestlings with beaks more widely opened during begging. When nestlings of two age groups (age difference 3.5-4 days, each group including 4 siblings) were experimentally mixed in the same nest, mean intervals between two feedings of the same chick were 13.3 min. for the older group and 37.5 min.—for the younger one. During the two days preceding the change of nestlings (when each of the broods consisted of 8 siblings of the same age) those intervals equaled 18 min. (Fig. 4, B).

Feeding behavior of nestlings in the two age groups differed significantly. During the first 4 days of life in the mixed brood older nestlings begged spontaneously very rarely, whereas the younger ones demonstrated almost unceasing spontaneous feeding reactions—when the parents were away about 80% of the time was filled with spontaneous begging of one or more chicks. Younger nestlings got food only in two cases: 1) the arrival of an adult coincided with their spontaneous begging, while the sounds accompanying the arrival either failed to elicit a feeding response in the older nestlings or elicited it with too long a latency; 2) when the feedings by two parents were separated by only a very short interval then the begging of younger nestlings was maintained due to the vocalization of the older ones, responding to the first arrival of the parent. Even these favorable situations, however, did not always

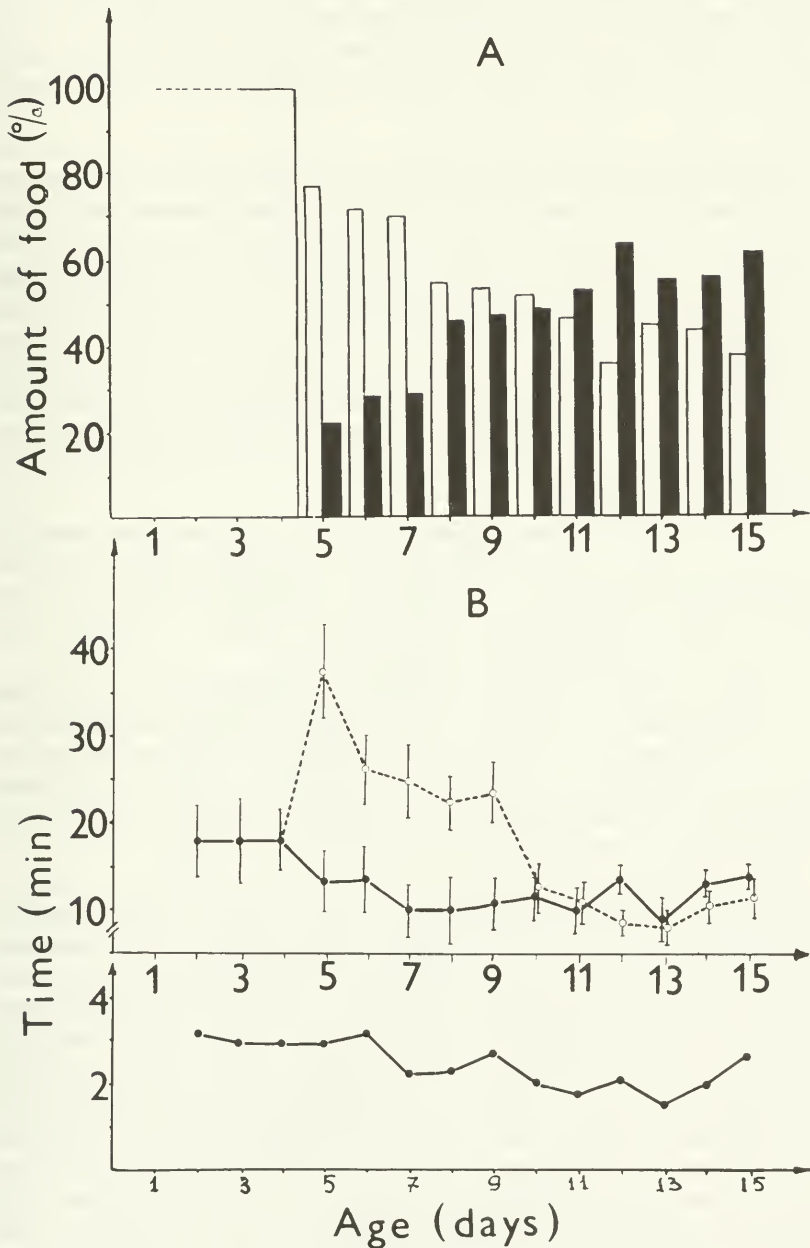


FIG. 4. Distribution of food among the nestlings of two age groups during their life in the mixed brood. (A) Relative amount of food received by the nestlings of older (open bars) and younger (black bars) age groups; (B) mean intervals between feedings of the same chick in the older (solid line) and younger (dashed line) age group; (C) mean intervals between the arrivals of adults with food.

result in the feeding of the younger chicks. In approximately 10% of the cases an adult bird, after a few unsuccessful attempts to feed the younger nestlings, gave food to the older one, who happened to be begging at this time. In other cases, the food was given directly to the older chicks.

Comparison of the daily number of feedings of each chick in the younger age group with that of a nestling of the same age in the natural "synchronous" brood demonstrated that the former received only about 75-80% of their normal food ratio. The analysis of changes in the body weight of the nestlings in the mixed broods proved, however, that during the first days after hatching the body weight of the chicks of the younger age groups is much closer to a normal value than would be expected judging by the insufficient number of feedings they received (Fig. 5). Moreover, unlike the synchronously hatched nestlings that get their food "automatically", younger chicks in the asynchronous broods, to get even a smaller amount of food, have to spend much more energy in frequent, almost unceasing, begging.

Thus the great number of spontaneous feeding reactions, resulting from the increased level of feeding motivation, which, in turn, is due to the 20-25% decrease in the number of feedings, appears to be an important factor helping the younger chicks to get food during their first days of life together with the older nestlings.

Another important factor helping the younger chicks to get food is an interesting modification of the circular shift reaction in the asynchronous broods. It differed from that in the synchronous broods and was quite alike in all 4 mixed nests that were under constant observation. For this reason we will present here the data on the organization of the circular shift in only one brood.

Zones used by the parents for feeding the young were 1 and 11 and did not change even if both parents were in the nest-box simultaneously. As Fig. 6 shows, during the first 4 days (from the moment of hatching until the moment when part of the brood was changed) zones 5, 6, and 7 were optimal for the chicks to get food and zones 1, 9 and 12 were suboptimal. When begging in other zones, nestlings either never got food or got it very rarely. On the morning of day 3 in this brood (the day before the broods were mixed), the full cycle of the shift of a nestling from the optimal zone through all intermediate ones and back to the optimal was 35-37 minutes. During the very first day after the partial change of nestlings the circular reaction shift underwent significant modification. Movements of the younger chicks were relatively independent of the activity of the older ones. As a result, during four days we could observe two cycles of rotation that overlapped only partially. Younger chicks huddled in the suboptimal zones: in the center of the nest, zones 12 and 1 (Fig. 6, B), and did not leave it, having received food. Their movements were quite local, i.e., they moved one

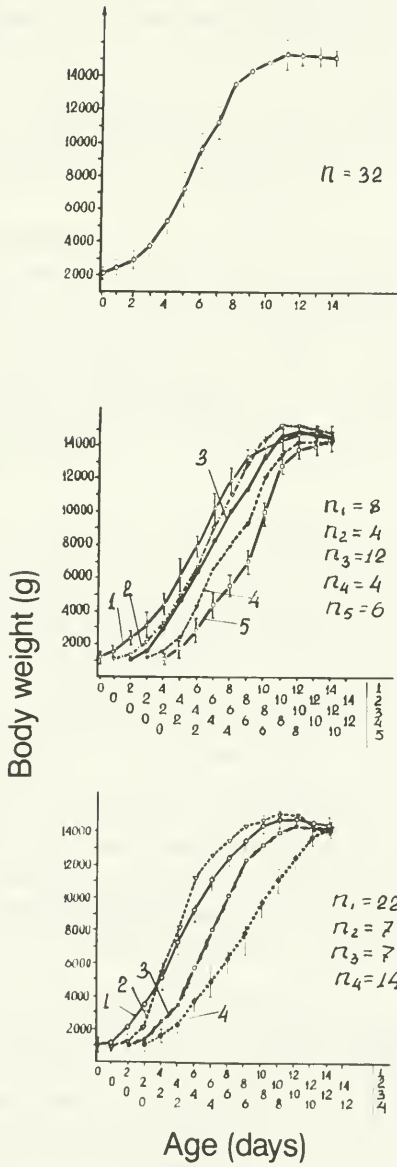


FIG. 5. Changes in nestlings' body weight during the nest life. (A) Natural "synchronous" broods; (B) natural "asynchronous" broods; (C) artificially mixed broods. n—number of nestlings in each age group.

around the other but strictly within this area, while the older nestlings moved all around the nest and sometimes got food in the zones with a low probability of reinforcement. The full cycle of rotation for the older nestlings during the fourth day of their life in the mixed brood (day 8 of life) was 28–30 min. The mean interval between two feedings of the same chick of the younger group had decreased by that time 1.5-fold (Fig. 4, B).

On day 5 of life the eyes of older nestlings began to open. The eyes of younger nestlings opened during day 4 of their life. In spite of this no significant changes in the organization of feeding behavior were observed.

From day 9 of the older nestlings' life the guiding stimulus was included in the organization of their feeding behavior, so their begging was transformed into food-acquisition behavior—now they didn't raise their heads up, but stretched them in the direction of the parent's head, actively attacking its beak even before it would take its place on the nest edge. Since that day, elder nestlings started to get food from the adult that was sitting in the entrance-hole. The distribution of the zones, optimal for begging reinforcement, that was settled during that day is presented in Fig. 6, B.

Younger nestlings also started to get food from the entrance-hole 24–30 hours later (Fig. 6, B). Thus on the 10th day of older nestlings' life two relatively independent rotation cycles merged into one general cycle of movement along the luminosity gradient: the zones located right under the entrance-hole (11,12, 1) became optimal for all nestlings. The mean intervals between feedings of the same chick in both age groups became equal (Fig. 4, B). During this and the following day all nestlings in both age groups received equal amounts of food. Later on, however, mean intervals between two feedings of the same younger nestling became shorter than those for the elder ones. Accordingly, the amount of food received by the younger nestlings exceeded that received by the elders (Fig. 4, A). The higher level of constant movement activity and, therefore, the shorter latency of begging must be the factors ensuring the greater amount of food received by the younger nestlings during the last days of nest life.

The dynamics of the nestlings' body weight during the nest period is described by a S-shaped curve (see Fig. 5). During a good part of nest life the body weight of the chicks that hatched last (Fig. 5, B) is lower than that of their older siblings. The same holds true for the artificially-mixed broods (Fig. 5, C). Body weights of nestlings of different age become equal only during the last days of nest life, when the weights of older nestlings are stabilized or even decreases slightly while the weights of the younger nestlings are still growing. The youngest chicks practically do not have a "plateau" phase. Body weights of the fledglings are equal and do not depend on age. In spite of this, in most of the broods studied

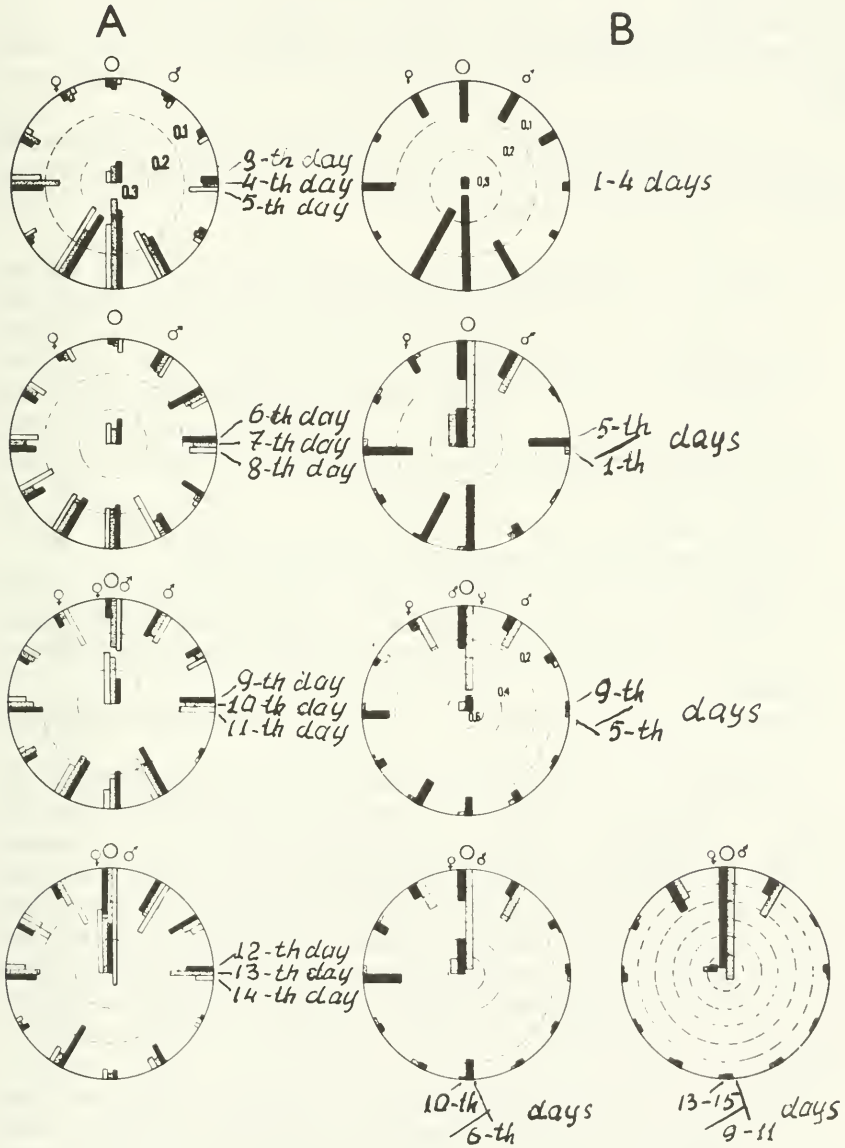


FIG. 6. Probability of the begging reinforcement in each zone of the nest. (A) synchronous broods, (B) asynchronous broods. Fractions in B: numerator—age of older nestlings, denominator—age of younger nestlings. O, Places taken by the parents during feeding; (e), entrance-hole. The probabilities are represented by the figures in the upper diagrams.

with asynchronously hatched nestlings where they could fledge during several hours, the first young to leave the nest were always the older nestlings. Often, right after the very first fledgling had left the nest-box, the intervals between the arrivals of the parents with food increased greatly and continued to lengthen as other nestlings were leaving the nest.

Thus, preliminary analysis of our material makes it possible to consider the following factors responsible for the synchronization of fledging of different-aged nestlings:

- A. A high level of feeding motivation throughout the entire nest period. Due to this, a constantly increased level of movement activity. At the earliest stage of nest life, this is manifested in the great number of spontaneous beggings, while at the final stage, it is seen in the increased number of stimulus—elicited beggings and in the great number of movements around the nest between feedings. During the final stage this helps younger nestlings to get more food than the older ones.
- B. Younger nestlings live in the environment, constantly enriched due to the vocalizations and movements of elder nestlings.
- C. Stabilization of body weight of older nestlings (the same for the synchronously hatched chicks) before their fledging. Nestlings that hatch later reach the same weight and fledge without the “plateau” phase.
- D. Increased intervals between feedings after the older nestlings fledge.

To estimate the individual role each of these factors plays in this complex an additional study was designed. First of all, counting the number of feedings of nestlings that hatched as late as can be observed in the wild (with maximal possible lag) showed that during nest life each of them received less food than older nestlings or synchronously hatched ones (Fig. 7). Although it is greater during the entire nest life, movement activity does not help younger nestlings to receive normal food rations but it apparently improves both food utilization and the accelerated development of motor components of early functional systems.

In the series of control experiments with eight broods we varied the time of mixed life of differently aged nestlings in the mixed brood. An age difference of 3.5–4 days was created not 10–10.5 days before fledging, as the situation occurs in the wild, but eight, six, four or two days before. It was found that in the first two cases body weights of younger nestlings at the moment of the fledging of the older ones had reached “fledging” value, but, nevertheless, they stayed in the nest after the older ones fledged. In the third case, the difference in body weight between the fledged chicks and those that stayed in the nest was

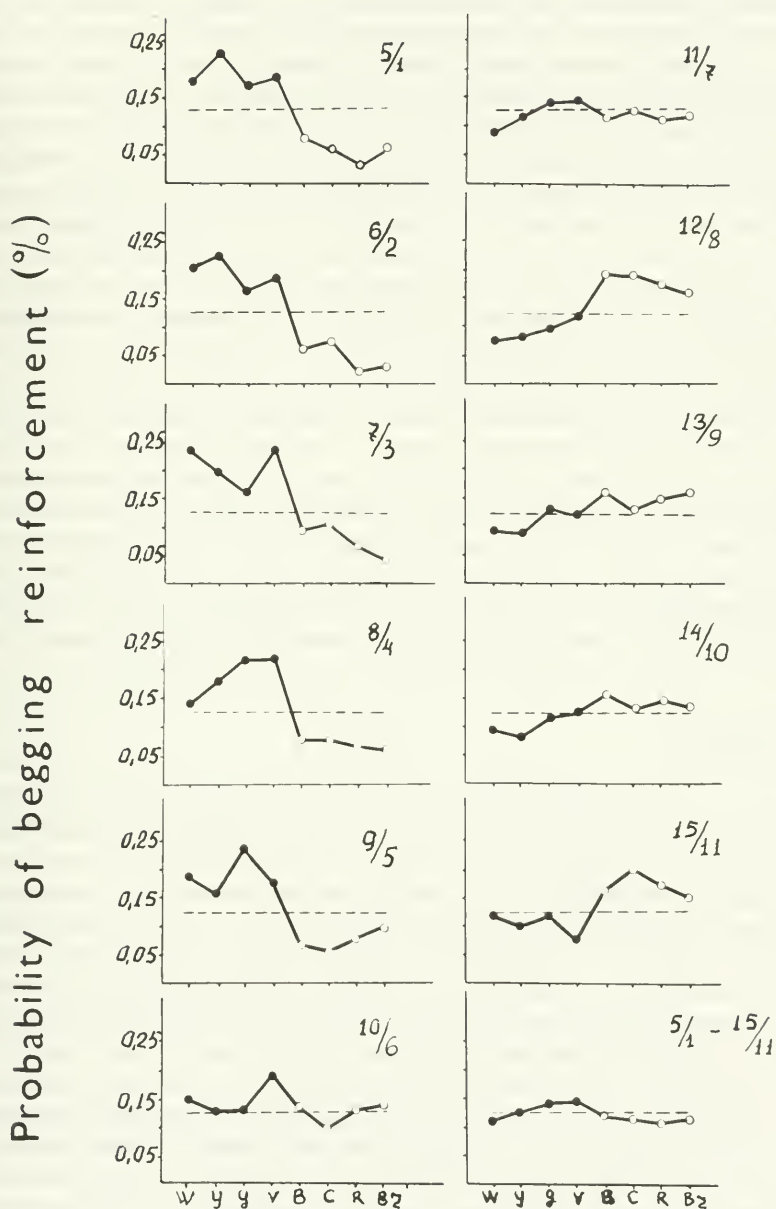


FIG. 7. The probability of getting food for each nestling of both age groups during each day and the entire life of the mixed brood. Ordinate—the probability of getting food for each nestling; abscissa—chicks' individual marks (W, Y, G, V—elder nestlings, B, C, R, Br—younger nestlings). Dashed line marks the level of equal probability to get food. Fraction in each graph: numerator—age of older nestlings, denominator—age of younger nestlings.

statistically insignificant; in the last case body weight of younger chicks was significantly lower than that of the older ones at the moment the latter fledged. Besides, it was found that right after the first nestling had fledged, the mean and individual intervals between feedings increased dramatically. These intervals grew still longer after all older nestlings had left the nest. During the first day after the last older nestling had fledged, the mean interval between feedings of the young remaining in the nest was 47 min., unlike 2.1 min. the day before the fledging, some intervals reaching 2.5–3 hours: they continued to increase until the brood left the vicinity of the nest and adults ceased to feed the chicks in the nest. During the first day after fledging by the older nestlings body weights of the young ones in the nest decreased by 8–10%. An attempt to continue the experiment would have resulted in the death of the chicks.

Thus, the experiments proved that neither "fledging" weight, nor the increase in the intervals between feedings, taken by themselves, determine the premature leaving of the nest. At the same time this study provides another example of the conservatism of parental behavior—adults stop feeding the younger nestlings in the nest after the fledging of the older ones. This, in turn, leads to the hypothesis that the synchronization of the fledging of differently-aged nestlings is also an adaptive factor determining the accelerated maturation of sensory and motor components of the leading functional systems of nest life.

DISCUSSION

Our experiments revealed several behavioral mechanisms ensuring the survival of all nestlings in the brood in spite of their initial differences in age and, accordingly, in the physical state and sensory experience. It must be noted here that the tendencies determining the survival and the synchronization of development are, to some extent, contradictory and equivocal. As it may be inferred from our experiments, the survival of the nestlings, initially lagging behind in the level of their physical development during the first half of the nest life, is insured only by their own activity that compensates even for the conservatism of parental behavior. This conservatism manifests itself in the selective feeding of the chicks with bigger and wider opened beaks, i.e., of the older nestlings.

Our observations are in agreement with those of Illies (1975). He found that the thrush female ignored her own young trying to feed the dummy if it had a wider beak that was constantly opened and if the inner surface of its mouth was more brightly colored. The author proposes that this behavior of the female is inborn and has, under normal conditions, a selective function. An alternative interpretation of the conservatism of parental behavior is suggested elsewhere (Khayutin *et al.* 1982).

In our experiments it was found that younger nestlings received the food providing for their survival during the first half of the nest life owing to, first of all, a great number of spontaneous feeding reactions determined by the high level of their feeding motivation. Some spontaneous reactions may, in fact, not be endogenous, but elicited by the sensory stimuli that are subthreshold for older nestlings due to the lower level of their feeding motivation. The influence of the high and low level of motivation on the perception thresholds and the reaction time was proved by many investigations.

Another factor ensuring that younger nestlings will receive food during the first half of their nest life is their constant remaining in the zones with relatively high probability of begging reinforcement. The same observation was made by Lebedeva and Lomadze (1986) who repeated our study, having investigated the artificially-mixed broods of the great tit (*Parus major*). From the analysis of feeding behavior in the "synchronous" broods we inferred (Khayutin, Dmitrieva, 1976) that the principle factor which determines whether a nestling receives food is his begging in the zone of high probability of reinforcement. The present study demonstrated, however, that within the natural limits, the great differences in the ages of the chicks cannot affect the equal distribution of food among all the chicks. In strong opposition to it is the conservatism of parental behavior directed at selective feeding of larger nestlings. Moreover, today we cannot answer the question what makes the younger chicks, huddle in a compact group before their eyes open and immediately afterward, within the fixed region of the nest and not move through all other zones. It may be supposed that this huddling is based on thermal and tactile stimulation.

We call attention to the following fact in our experimental material. In spite of a daily food ration decreased by 20-25% during the first days of the younger nestlings' life, the difference in body weight between chicks of the groups compared does not increase but, on the contrary, has a tendency to decrease, though younger chicks obviously spend more energy because of the great amount of spontaneous begging.

From the point of view of Arshavsky (1975), the increased movement activity of young animals leads to a more effective food utilization that not only compensates for energy losses but also provides for the plastic needs of the growing organism. Saraev's (1974) experiments proved the positive effect of partial undernutrition during limited period on the future growth of animals, their physical activity and an index of food utilization for growth. This author believes this positive effect is due to the influence of physiologically active metabolites formed in the process of undernutrition-induced histolysis.

The increase in movement activity of younger nestlings caused by their constantly increased level of feeding motivation during the first

half of nest life is also observed later on. This must be an important factor helping the younger nestlings obtain a greater amount of food (as compared with older siblings) during the second half of nest life. Moreover, as ensuring the normal physical state of the nestlings, basic for the accelerated formation of sensory and motor mechanisms necessary for the transition to life in the open, synchronous with the older siblings.

Comparison of the stages of maturation of the sensory systems at different ages shows that the progressive shortening of the periods of each stage successively changes the stimuli adequate to elicit feeding behavior.

Comparison of the results of the main series with the control experiments demonstrated that the normal physical maturation of the younger nestlings during the shorter time demands a sufficiently long contact with older nestlings. It is this contact that must create the necessary bases for the selectively-accelerated (heterochronous, according to Anokhin, 1974) formation of the leading sensory and motor capabilities in the younger nestlings. The following factors may be considered as the principal ones, determining the accelerated development of nestlings: their increased movement activity; an additional complex of tactile and thermal influences which is due to the movements of the older nestlings; vocalization of the older nestlings accompanying their begging from the earliest days of life of younger chicks. The complex of these factors, determining the accelerated maturation of sensory and motor components of the functional systems of the chicks' nest life, is considered as a physically and socially enriched environment.

The study of Vlack and Vlack (1985) showed that rhea embryos also needed sensory and social stimulation for normal development. The rhea's incubation period may vary between 29-43 days. The investigators believe the mechanism promoting the accelerated development to be the acoustic communication among embryos confined to the last stage of incubation. The metabolic processes of "older" embryos (oxygen consumption, growth of embryonic tissues) increase exponentially until day 29, then tend to decrease. In the "younger" embryos in the clutch this stage of metabolic decrease may be shortened or eliminated due to embryonic communication, thus promoting the synchronized hatching.

Our earlier data (Khayutin, 1978b, Dmitrieva, 1981b) on the heterochronous development of pied flycatcher nestlings were later confirmed by Lebedeva and Lomadze (1983, 1986) who analysed the natural development of two other passerine species *Parus major* and *P. coereleus*. Applying numerous physiological and behavioral criteria to the natural asynchronous broods they found that the maturation of acoustic and visual analysers and the formation of orienting and defense

reactions in older nestlings of asynchronous broods lag behind, while in the younger chicks they are accelerated as compared with the middle-aged ones. This finding was further developed in a study of a set of morphometric indices (mean growth constants, weight, length of wing and beak, etc.) of great tit nestlings whose relative age was changed by means of transferring them from one nest to another. In one series the nestlings that were older in their own brood were transferred to the broods where they became the younger. The transferred chicks were found to develop according to their new age status as typically young ones—their development was accelerated. In another series younger nestlings were transferred to a still younger brood where they appeared to be the older. As a result, their development decelerated. The authors concluded that the nestlings develop in their new broods according to their new age status, i.e., the pace of their development depends on their age status in the given system and serves the interests of synchronization of the brood as a whole.

The role played by the above-mentioned factors in the accelerated development of sensory and motor components of the principal functional systems of bird nest life is confirmed by many investigations of the effect of sensory deprivation and additional stimulation on the bird embryonic development. Additional stimulation proved to play an important role in the development of the adaptive traits of the embryos of many avian species and to influence significantly the nestlings' behavior after hatching. The experiments of Gottlieb (1968) who paralysed chicken embryos at the early stage of development demonstrated the necessity of movement activity, that is, from the author's viewpoint, the main form of stimulation that muscles and skeleton demand for their normal development.

Thus, our results indicate that the pace of maturation of the sensory and motor components of the early behavioral acts' systems may be determined, to a great extent, by the changed environmental factors. The succession of the maturation of sensory mechanisms must be genetically determined (Gottlieb, 1971) whereas the pace of this maturation is apparently subjected to the influence of physical and social environmental conditions. At the same time, the sensory-enriched environment created by the activity of elder nestlings is the necessary natural factor promoting the accelerated development of the younger chicks.

These mechanisms are to some extent natural for the flycatcher species. The aforementioned studies by many researchers prove that in many species the hatching of the clutch may take as many as several days. Our own data show that the flycatcher is not an exception to this tendency. In other words, under natural conditions the nestlings that were the last to hatch and that, accordingly, lag behind in their physical state and sensory experience, have the mechanisms for the

accelerated maturation of the sensory and motor components of the main nest-life functional systems functioning, thus matching these systems to the level of those in nestlings that hatched earlier.

From our point of view, our results which demonstrate the significant effect of additional stimulation on the accelerated maturation of a number of functions in the developing organism may be best interpreted in terms of the concept of the ontogenetic consolidation of functions (Anokhin, 1964, 1974; Shuleikina, 1973; Kiselev, 1978). Embryogeny is considered by this concept not only as a stage of development of this or that functional system but at any moment as a stage of a certain dynamically developing condition of readiness to realize these systems. For at certain stages of ontogeny, the immaturity of functions is manifested not in the inability to perform them but rather in the fact that "the given function needs some additional facilitating influences to manifest itself" (Shuleikina, 1973, p. 285). It is important to stress here that the degree of maturity of the central structures at the final stages of the embryogeny and at early stages of postembryonic development is not the absolute determinant of the ability of the executive mechanisms and systems to function. An important role is played here by the consolidating effect of additional and probably specific stimulation on the final arrangement of a system, i.e., on its functional readiness to be performed. The present study demonstrated that the factor consolidating and accelerating and facilitates the formation of sensory and motor mechanisms of the leading functional systems of early avian behavior is the specific acoustical, visual and tactile stimulation. It was also found that the synchronization and acceleration of the development of sensory and motor components of the main functional systems under the influence of a specifically enriched environment is the necessary factor for the progressive acceleration of the change of developmental stages and the obligatory factor of systemogenesis (term after Anokhin, 1964, 1974). In connection with this the concept of development of the early behavioral functional systems may be extended to include also the supraorganismic level with the obligatory consideration of mutual social influences among individuals in the micro- and/or macropopulations.

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