

zoals STEGMANN veronderstelt, zal moeten worden afgewacht. Op grond van welke argumenten KIST STEGMANN'S veronderstelling à priori als onaannemelijk verklaart, is niet duidelijk. Op de bastaardering van de geelpotige vormen, zowel in het Oosten als in het Westen van hun verspreidingsgebied, met de rosepotige vormen, berust de opvatting, dat beide groepen de soortgrens nog niet hebben overschreden en het beste als één soort kunnen worden opgevat. Ik geloof niet, dat KIST'S pleidooi heeft kunnen aantonen, dat zijn indeling boven de meest gangbare te verkiezen is. Dit is trouwens alleen mogelijk, wanneer nieuwe feiten op tafel komen en zou blijken, dat de veronderstelde hybridisatie in de ontmoetingsgebieden niet of nauwelijks voorkomt. Wat de sub-specifieke plaatsing van de waargenomen geelpotige Zilvermeeuwen betreft, het is zeker niet uitgesloten, dat KIST hier gelijk heeft, maar verificatie van verzamelde exemplaren met goede vergelijkingsseries zal hiervan het bewijs moeten leveren. Zelfs met materiaal in de hand zal het nog moeilijk zijn de vogels thuis te brengen, te meer daar juist in het vermoedelijke broedgebied van deze vogels de situatie nog niet is opgehelderd. Overigens kan men slechts bewondering hebben voor de uiterst gedetailleerde veldwaarnemingen en KIST dankbaar zijn, dat hij deze zo uitvoerig vermeldt.

G. C. A. JUNGE

THE BEHAVIOUR OF THE BENGALESE FINCH IN THE NEST

by

ERICA EISNER

Dept. of Zoology, University of Edinburgh, Scotland.

Introduction

The Weaver-finches (Estrildidae) are a conspicuous and even economically important group of birds, distributed over Africa, Southern Asia and Australasia. None the less there is remarkably little field information available on their behaviour and breeding biology. The most compact source of general information on them is STEINBACHER & WOLTERS (1956) but regional avifaunas, especially BAKER (1926), BANNERMAN (1949) and CHAPIN (1954) are invaluable. Scraps of information can be

gathered from a variety of sources, but IMMELMANN (1960) provides the only extensive account of a species in the wild. There is, however, a rapidly increasing literature on estrildines kept in captivity (see HARRISON 1957; MORRIS 1958; IMMELMANN 1959; KUNKEL 1959). Much of this consists of studies of courtship behaviour, which can be obtained easily in most species in captivity. Although many species have been bred in captivity, only a few will do so predictably, making studies of parental behaviour more difficult. While the behaviour of adults towards fledglings can be observed simply, the fact that the nest characteristically is enclosed (loosely made of grass in the wild, and either globular or bottle-shaped with a side entrance) makes the recording of behaviour within the nest a much more difficult problem (c.f. KUNKEL 1959).

In order to meet this difficulty, I had built a set of cages (each 60 cm wide \times 30 cm deep \times 45 cm high) which were each provided with a nest box backed by a glass panel through which observations could be made from a darkened hide. Several species which are bred with sufficient ease to have seemed promising were tried in these cages. Magpie Mannikins (*Lonchura fringilloides*) and, more surprisingly, Zebra Finches (*Poephila guttata*) simply did not go to nest in these circumstances. Cutthroat Finches (*Amadina fasciata*) went to nest and hatched young in these cages but were so disturbed by any attempt at observation that serious study of them was out of the question, although they afforded me the opportunity of seeing that Cutthroat chicks have qualitatively different begging behaviour from that thought to be typical of estrildines (see report in KUNKEL 1959) and of seeing the quite extraordinary display given in the nest by the adult upon disturbance. Only the Bengalese Finch bred sufficiently reliably and was tolerant enough of disturbance at the nest to permit detailed study of its parental behaviour: the Bengalese is a domesticated form of *Lonchura striata* (see EISNER 1957).

The main part of the study consisted of a quantitative analysis of the behaviour after the young have hatched. This paper, however, will be concerned with a qualitative description of the behaviour seen in the nest, mainly during the period of care of the young. Further details of the management of the birds and quantitative data on their breeding biology have been published elsewhere (EISNER 1960a).

Incubation, hatching and brooding of the chicks.

Descriptions of the parental behaviour of estrildines in the wild are very scanty, the most useful sources being BOURKE (1941), VINCENT (1949), VAN SOMEREN (1956) and IMMELMANN (1960). It is obviously

quite general that male and female share nest-building, incubation and care of the young. In some species the shares of male and female seem to be about equal, although in others the female incubates most during the day-time; both birds sit on the nest at night (VAN SOMEREN 1956; IMMELMANN 1960). BOURKE (1941) noticed that Zebra Finch pairs were often on the nest together by day during the incubation period and when they had young, and IMMELMANN (1960) reports that during the time when their young are hatching Red-eared Firetails may stay in the nest together for up to thirty minutes.

Similarly, in the Bengalese Finch (as in wild *L. striata*: ALI 1953) male and female share the parental duties: the quantitative examination revealed no sex difference in the distribution of time spent on the nest after the chicks had hatched, and this probably is also the case during incubation. Especially during incubation and while the chicks are young, both birds are frequently on the nest together for long periods by day and both spend the night there.

A normally brooding bird appears very relaxed, the feathers are fluffed giving a rounded outline and the eyes are often half-closed or even fully closed. The flank feathers are always raised away from the ventral apertium. (Though the ventral skin is bare of feathers, there is no development of a true brood patch either in male or female: see EISNER 1960b.) After entering the nest and from time to time whilst brooding the adult settles in the way common to many species of birds: the flank feathers are raised and the position on the eggs or chicks is adjusted by side to side shuffling movements. Sometimes the adult rearranges the chicks or eggs by pushing them towards itself with the beak, occasionally it probes among them.

As the incubation period progresses the adults seem gradually to sit more and more closely; this is of course well known in many species of birds, and VAN SOMEREN (1956) records it of some wild estrildines. As the time of hatching approached many pairs became very difficult to flush from the nest when I wished to inspect it: they would display and would sometimes even attack my hand when I put it into the nest, and often I had to push them out by force. I did not do any systematic tests to assess how far this behaviour is characteristic of the end of the incubation period but 'natural experiments' showed that it does not depend upon the presence of newly hatched chicks or hatching eggs as it was fully shown by pairs whose eggs proved to be infertile. The display which may be shown when something is intruded into the nest is a backwards and forwards rocking which may develop

into quite powerful rapid forward lunges and pecks with the beak; the wings and tail are often spread, especially during the withdrawal phase (Fig. 1). This is very different from the display of the Cutthroat Finch, which is more complex and shows very much less obvious a relationship to overt attack. During the disturbance display, the Cutthroat has all the feathers very raised, except those of the head which are sleeked, the flank feathers being fluffed out over the wings. The beak is held open.

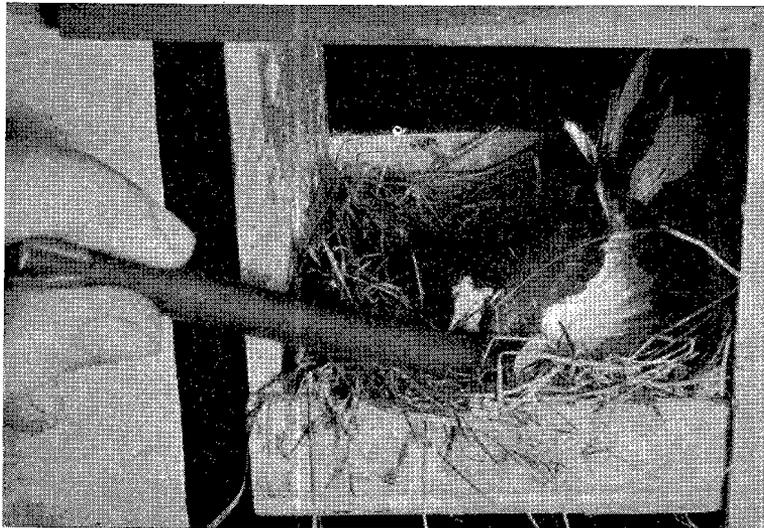


Fig. 1. Bengalese Finch displaying and attacking upon disturbance of the nest. Note that the wings and tail are spread, and that the beak is kept closed.

Meanwhile the bird moves with slow, rhythmic and sinuous side to side movements in an S-wave of chest, neck and head, the carpal joint sometimes being raised on the side opposite to the direction in which the head is turned at that moment (Fig. 2). This display aroused, to my surprise, an extremely strong subjective response in me and I found it very distressing to watch. It would be very interesting to know the response of other animals to such a display.

I have several times observed the nest of Bengalese Finches while a chick was hatching. The parents appear not to assist the process in any way, but just sit normally. Eventually one will poke down into the nest and pick up a piece of eggshell, and this is the only obvious sign that a chick has hatched. The shell is then rapidly eaten, large pieces being held in the beak and rotated while the edge is gradually



Fig. 2. Sketch of the nest-defence display of the Cutthroat Finch, *Amadina fasciata*.

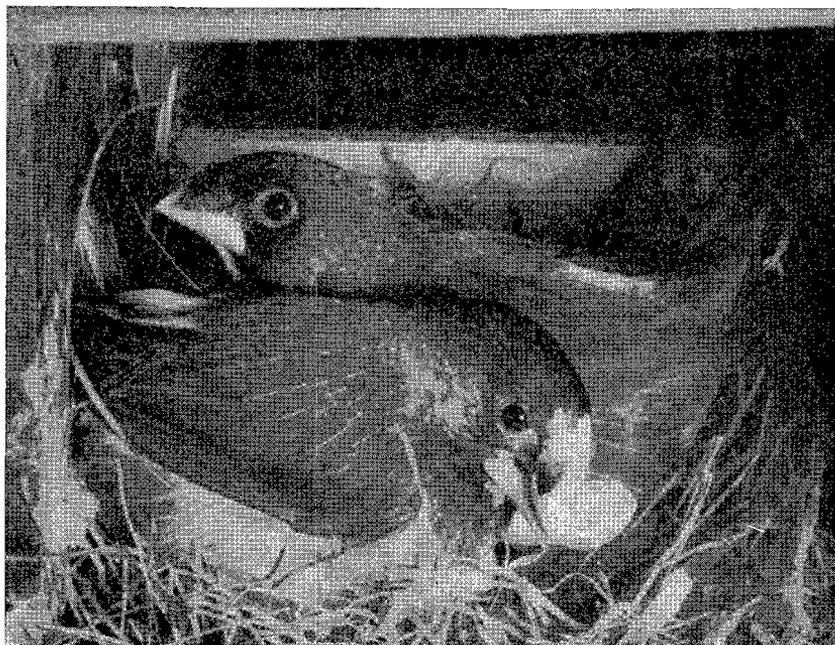


Fig. 3. Egg-shells are always eaten by the parents. During incubation and while the chicks are young the two adults are frequently on the nest together,

broken away and swallowed (Fig. 3) (c.f. NETHERSOLE-THOMPSON 1942). If both adults happen to be in the nest they often compete for the shell, each attempting to take it away from the other. Whole infertile eggs are simply left lying in the nest. The Red-eared Firetail carries the egg shells out of the nest and drops them at a distance (IMMELMANN 1960).

In the Bengalese Finch there are no nest-relief ceremonies. During incubation and the first days after hatching there is always at least one parent in the nest, and often both birds brood together for long periods. During this phase, a brooding adult never leaves the nest if its mate is not already there, unless it has been disturbed. Usually between the 8th and the 12th day after hatching the birds begin to leave the nest without the previous arrival of the mate, and gradually the chicks are left on their own for more and more of the time. Eventually the parents often stay only long enough to feed the young, although on occasional visits they will stay and brood even when the chicks are near fledging.

Note: The convention used in the following account is that the day of hatching is Day 0, the following day is Day 1, etc. Although normally all the chicks of the brood do not hatch on the same day, I found it necessary to interfere with the clutch in such a way as to have chicks of homogeneous age in most of the broods which I observed (see EISNER 1960a). As a result there is no discrepancy in this account between the age of the chicks and the number of days during which the parents have been tending young.

Feeding of the young and the begging response.

The chicks, if they beg, are most often fed immediately after a parent enters the nest. After a bird has been sitting in the nest for some time it seems to be less likely to respond to the begging of the young, even if it has not already fed them and probably still has food available. Begging by the chicks is released predominantly by tactile stimuli for about the first two weeks after hatching, while the chicks are blind. The calls of the parents or jarring of the nest are ineffective: the parent must touch the chicks before they will beg. The exact stimulus which is required varies, presumably according to the degree of hunger of the chicks. Sometimes any touch or movement by the parent may release begging, and chicks frequently beg when a brooding parent gets up or at the first, quite unspecific, touch of an incoming parent. If the chicks do not beg at the first touch, the incoming parent will usually settle on them, then a few moments later it will get up and the chicks may then be begging. If even after it has settled the chicks do not beg, the parent

may then 'offer' to them. This consists of gently poking them with the tip of the beak: if the chick's head is visible this will normally be touched preferentially, and often the touch is directed to the fairly conspicuous gape corners or 'Schnabelwulst'. Such touching of the head by the parents is usually quite effective in releasing begging, but I found that when I similarly touched chicks which had been taken out of the nest it was usually not effective except in very young chicks (about 0-2 days old). It is interesting to note that touching of the Schnabelwulst—even by the parent—does not appear to be more effective than touches elsewhere on the head, which is in line with WACKERNAGEL's (1954) finding that the Schnabelwulst is not especially well supplied with sensory structures.

Although the first chick must be stimulated to beg by touch, the other chicks may begin to beg without themselves having been touched by the parent. I believe this is because the calls given by a chick which is being fed are very effective in releasing begging in other chicks. It would be interesting to test this point by the use of tape recordings.

After the second week the chicks begin to beg at the sight of the parent, before the parent has touched them (this cannot be an auditory response, for the parent is normally silent as it enters). If, however, a parent has arrived without releasing begging visually, it will probably cause the chicks to beg by touching them as before. Tactile stimulation remains effective in older chicks but is often unnecessary.

Immediately after release, the begging display usually consists of holding the beak upwards with the gape open while the chick calls lightly. When the chicks are young, the tongue is held rigidly in the centre of the gape and is not flattened against the floor of the mouth. The neck is not stretched vertically, as it is in many passerine species of other families (e.g. ANDREW 1956) and also in the Cutthroat Finch (personal observation, and KUNKEL 1959). More intense begging is usually shown after feeding has begun. A chick which has just received food usually calls more loudly and shrilly, and it is this which appears to release or intensify begging in the other chicks; the chick also begins to rock its head rhythmically from side to side at a rate of about one oscillation per second; this rocking is rather less marked in chicks which are near fledging, when the beak is usually directed towards the parent. The head is always kept low during begging and, especially as the chicks get older, it is often turned to the side (see Fig. 4) in the way which is especially striking and characteristic amongst fledglings in certainly the majority of estrildine species (e.g. Photographs of fledgling Zebra Finches in

KUNKEL 1959). The degree to which the neck is turned appears to depend partly upon the intensity of begging and partly on the relative positions of parent and chick: the twisted position is not obligatory, although it is frequently shown, and only the lowness of the head is invariable. Of the many estrildine species bred in the Zoology Department at Oxford (M. F. HALL, in preparation) only young Cutthroat Finches and the closely related Red-headed Finches (*Amadina erythrocephala*) were exceptional: as young nestlings these stretch the neck straight upwards, and later they stretch straight towards the parent with no twisting of the neck at all. Young Bengalese may sometimes make balancing movements with the wings, but there is never any true wing vibration during begging.

A parent often shows a tendency to feed the chicks when it returns to the nest whether the chicks are begging or not. This is shown by the characteristic regurgitation movements, which consist of 'chewing' movements of the beak often accompanied by a side to side shaking of the head. VAN SOMEREN (1956) notes that several wild species of estrildine begin to regurgitate as soon as they land at the nest, before they enter and can have seen the chicks. Regurgitation movements may also be shown before or just after settling, and normally precede offering.

The feeding of very young chicks is a delicate procedure and may take a long time (up to 10 or 15 minutes), while older chicks are treated less delicately and are fed much more quickly (within a minute or two). Once begging has been released, the chicks usually continue to beg until the parent finishes feeding, although occasionally feeding ends because the chicks' begging has died down, presumably indicating satiation, while the parent is obviously still capable of giving more food. The parent then usually offers a few times but eventually gives up trying to feed unwilling chicks. In feeding, the parent places the tips of its beak into the corners of a chick's gape, and then slowly raises its head while the food drops (Fig. 4). The hold between a parent and a small chick seems to be tight, as the chick's head is often pulled up and very small chicks may sometimes be lifted completely clear of the nest while they are being fed. After the parent's beak is withdrawn the chick briefly shuts its gape and swallows, and then resumes begging. Meanwhile the parent may have regurgitated again and then it inserts its beak into the gape of either the same chick or another one. The several chicks appear to be fed at random. The number of insertions given in succession is large when the chicks are small, sometimes being a hundred or more, and feeding may take as long as 10 to 15 minutes during which the chicks beg all the while. As the chicks grow older the number of insertions given and the time

taken both decrease. Soon after the parent stops feeding the begging dies down, and I believe that this is controlled by the calls of the chicks. On being fed a chick calls especially strongly and this call, I believe, has the function not only of releasing begging but also of maintaining it in the other chicks. When the parent stops feeding there is no more of this 'rewarded calling' and begging then dies down.

Very young chicks (up to 2 or 3 days) seem to be fed on crushed seed, but during most of the nestling period the young are given seed which

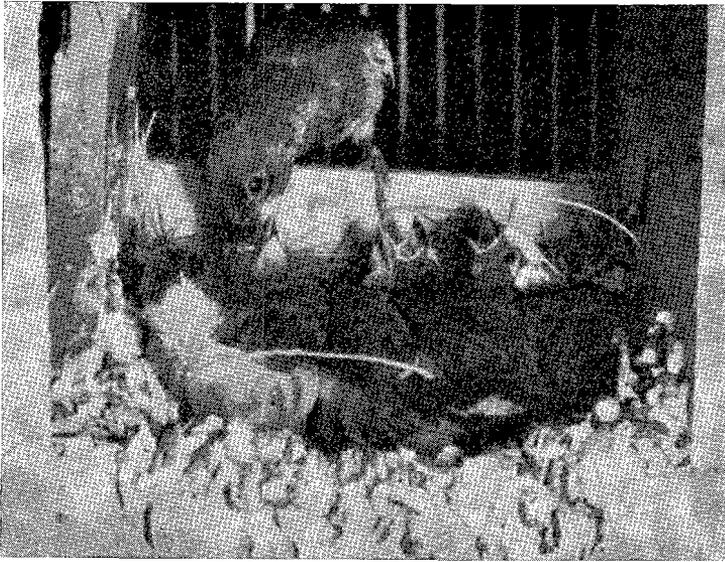


Fig. 4. Bengalese chicks being fed (day 23). The characteristic low position of the chicks' heads is well shown, and the way in which the head may be turned to the side can be seen in the centre and left-hand chicks.

is whole except that the husk has been removed. This food can be seen easily through the transparent walls of the chicks' crops. The crop, in both chicks and adults, is simply the very extensile oesophagus: there are no special diverticula such as are found in a few passerine species (MILLER 1941; FRENCH 1954).

Nest Sanitation.

In addition to warming and feeding the chicks, the other major function of the parents in most passerines is nest sanitation. Because estrildine nests are usually found to be fouled after the young have fledged, it was

thought that estrildines lacked this behaviour altogether (STEINER 1954; IMMELMANN 1959, 1960). In fact, the Bengalese Finch does take and eat the faeces of its young and keeps the nest immaculate for about the first ten days after hatching. During this time the chicks are being constantly brooded and therefore a parent is present whenever defaecation takes place; the faeces are normally picked up as soon as they are extruded and are promptly eaten (Fig. 5). If for some reason they are missed at the

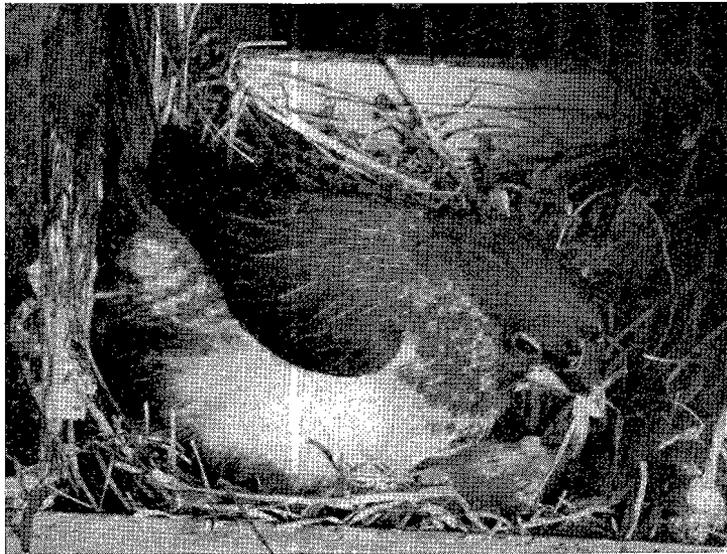


Fig. 5. Nest sanitation. A young chick defaecates: the parent picks up the faeces as they appear and then eats them (day 4).

time of defaecation, they are usually found and eaten later. Faeces are never carried out of the nest, and they are not encapsulated.

There is an important difference between the Bengalese and many other passerines, such as tits and thrushes. The young of the latter defaecate only immediately after they have been fed, but in the Bengalese the chicks may defaecate at any time and are not especially likely to defaecate just after being fed. The normal procedure is that the brooding parent rises as the chick stretches its vent outwards and upwards towards the wall of the nest. The movements of the chick are very characteristic and the parent always watches intently and then, when the faeces appear, rapidly picks them up. The parent does not usually touch the chick before it has defaecated, but if the chick takes longer than usual the parent

may peck its posterior gently. Occasionally a chick defaecates whilst the parent is feeding the brood: almost every time when I have seen this happen during the appropriate period the parent has promptly eaten the faeces and then resumed feeding the chicks (c.f. LAWRENCE 1953).

During the first day or two after hatching the chicks defaecate only very rarely in comparison to later days. For the first week, while the chicks are very small, the parents keep the nest clean. At the beginning of the second week brooding becomes irregular and at the same time faeces begin to accumulate in the nest; this is partly because the parents are often absent when defaecation takes place and also because they gradually cease to respond to the chicks' defaecation even when they are there. If there are many chicks the nest soon comes to consist largely of consolidated excrement.

BLAIR & TUCKER (1941) and TUCKER (1941) have reviewed nest sanitation over a wide range of species. They write that the parents (in passerine and near-passerine species) usually keep the nest clean during the early part of the nestling period, while the nestlings often cooperate in this at a later stage. A good illustration of this is provided by KLUIJVER's study (1933) of the Starling. At first the chicks defaecate only after being fed and the parents always wait for and remove the faeces, which are enclosed in a capsule. At about 9 or 10 days of age the chicks begin to defaecate at any time, and also the faeces cease to be encapsulated; this change is associated with a change in behaviour which normally results in the chicks defaecating out through the nest opening, after which the parents no longer effect nest sanitation. However it sometimes happens, for instance when the nest is too deep, that this system breaks down and the nest and the chicks themselves then become fouled: as the faeces are very wet this is usually disastrous and most such broods die.

This example provides a telling comparison with the Bengalese Finch. In my birds there is no change in the chicks' behaviour, but by the beginning of the second week the nestlings have grown so much that by pushing the posterior outwards and upwards, as they always have done, they can now place the faeces high on the walls of the nest (Fig. 6). At other times the chicks do not normally touch this part of the nest and, especially because the faeces are comparatively dry and soon dry out completely, the chicks themselves never become fouled. (The dryness of the faeces is probably primarily an adaptation to the dry habitats in which many estrildines live.) Thus, although the faeces

accumulate in the nest it is rather misleading to say that the nests become fouled, because the nests apparently remain perfectly sanitary: the same end is achieved as in other passerines, but by different means. VAN SOMEREN (1956) similarly reports that chicks of wild estrildine species remain perfectly clean although faeces are not removed from the nest, and attributes this to the dryness of the faeces ¹).



Fig. 6. Nest sanitation. Older chicks orient and stretch towards the wall of the nest, so that the faeces are placed well clear of the nest cup (day 15).

One curious activity occurs during the second half of the nestling period, after faeces have accumulated in the nest. As I have described, the faeces are placed in a ring around the walls of the nest; after they have dried they may get broken off and fall into the nest cup. In certain circumstances an adult will pick a piece of dry faeces out of the cup, chew it for a while and then usually push it back into the side of the nest: this occurs, quite specifically, only when there appears to be a frustrated tendency to feed the chicks. If a parent enters the nest, regurgitates and obviously is prepared to feed the chicks but they will not beg, dry faeces will probably be picked up; the bird will also do this after it has

¹) Although adults do not normally defaecate in nests containing eggs or young, they obviously do so in nests which are used solely for roosting as these may become thick with faeces. SKEAD (1947) reports similar behaviour in the Cape Weaver.

entered if the chicks beg but it apparently has no food to give them. In no other circumstances will this behaviour be shown. Thus, despite the association with a thwarted tendency, it does not seem justified to describe this as a displacement activity (see TINBERGEN 1951 & 1952; BASTOCK, MORRIS & MOYNIHAN 1954) because there is no evidence of a different autochthonous situation.

The development of the chicks.

At hatching the chicks are very diminutive and delicate. The skin is quite transparent and the liver, intestines, etc. can clearly be seen. Most chicks have a little down on the back, but the amount of down is variable

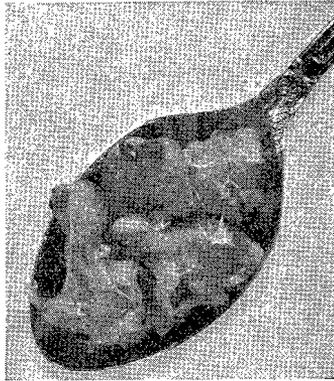


Fig. 7. Four newly-hatched chicks
in a coffee spoon.

and some chicks are hatched entirely naked. Thirteen chicks were weighed within three hours of hatching and the mean weight of chicks in this sample was 0.75 gm (range 0.65-0.93 gm). An impression of the size and appearance of newly hatched chicks can be obtained from Fig. 7.

For the first day or two after hatching the chicks seem to be silent but by about the third day a very gentle cheeping can be heard: these calls strengthen as the chicks age and, as has been described, provide an important part of the begging behaviour complex. During the first week of their life, the only conspicuous behaviour of the chicks is alimentary—patterns connected with begging and defaecation. In addition the chicks appear to sleep, and they make rather uncoordinated wriggling movements by which they may move over a considerable distance if put on a flat surface and by which they may right themselves if put on their backs.

This first week is a time of very rapid increase in weight without any marked changes in proportion. The hatching weight has usually been doubled by the third day, and the average weight at the end of the first week is about 4 gm (see Figure 8). On day 8 or 9 the flight feathers usually break through the skin of the wings, and with this begins the next phase of development. During the second week the wing feathers develop rapidly, and the legs and wings grow greatly relative to the body. Meanwhile the eyes open on about day 10 or 11.

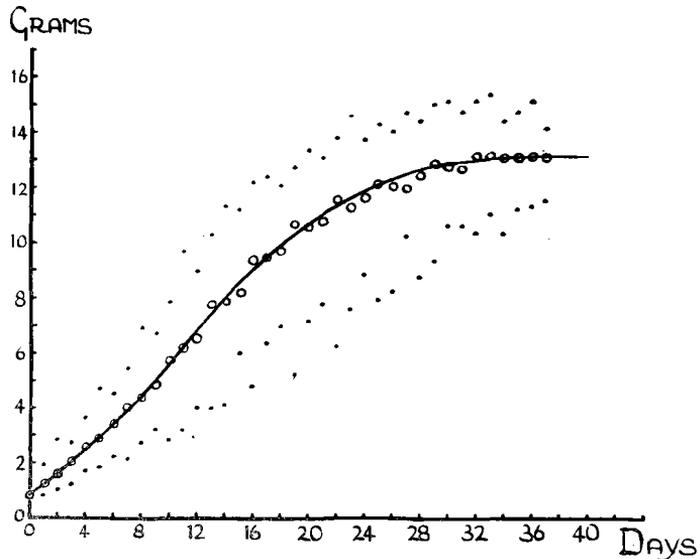


Fig. 8. The growth of the chicks.

This figure is derived from the records of 136 chicks all of which survived to fledging, the records of chicks which died being excluded. Each chick was normally weighed every three days. The circles represent the mean weight on each day while the dots, which represent the extreme values in each sample, indicate the range.

Day 0 is the day of hatching, fledging is usually on about day 24 or 25

The second week is not only a period of morphological change, but also one during which varied behaviour patterns are developed. Preening appears very soon after the flight feathers have emerged, often before the sheaths of these feathers have broken open. I have sometimes seen preening as early as day 9, but the 11th or 12th day is probably normal for the first preening. Wing-beating appears at much the same time as preening, while head-scratching and two types of stretching (both wings up together, and the wing and leg of the same side backwards

together) normally appear a day or two later. At the end of the second week the little birds appear alert and active.

By the beginning of the third week the nestlings are clearly able to see, as is best shown by the appearance of visual begging. Until this age begging is normally released by tactile stimuli but now it may be released by the sight of the parent. I have seen visual begging as early as day 14 but it probably usually appears about the 16th or 17th day. By this stage the flight feathers are well developed, and the main morphological change is in the development of the body feathers. The growth rate begins to slow down after a weight of about 10 gm has been reached: advanced chicks may reach this weight during the first half of the third week.

At about day 18 the first fear responses may be shown. The chicks begin to crouch at the alarm calls of adult birds. At this age they also crouched and appeared frightened when they were taken out of the nest (and also out of hearing of the adults) for weighing, whereas previously they had remained normally active. From about this time, if the nest is disturbed the chicks may scramble or flutter out of it. On about day 20 the chicks begin upon a series of actions which culminates, a few days later, in their fledging. Until this time they have always remained strictly within the nest cup, but now they begin to move about within the nest box and in particular they approach its front. At first they stand well away from the threshold and stretch their heads forward, lay their chins on the sill, and survey the world. The next day they venture further forward and stand immediately behind the threshold, looking out. A day later they will usually spend short periods actually standing on the sill: at first they are rather tense but by the following day they will stand on the sill and perform various activities such as preening and wing-whirring, holding on tightly with their feet the while. The wing-whirring which they do while standing on the sill differs from the wing-beating which occurs within the nest—in wing-beating the wings are fully extended, but when the chicks are on the sill the wing appears to be folded while it is vibrated rapidly, in a way resembling the behaviour of adults after bathing. Usually on the following day, day 24 or 25, the chicks fledge: they have been spending much time on the sill and somehow, probably often by over-balancing accidentally they lose their foothold and fly clumsily into the cage. I have seen no indication that the parents influence the fledging of the chicks in any way. The schedule which I have just given, whereby the behaviour progresses through daily stages, represents the average of the

many broods I have watched; of course the stages may sometimes be compressed or extended, but the sequence always remains the same.

In the Bengalese Finch, as is probably general amongst the estrildines, the young birds do not leave the nest finally at this time. At first they only spend short periods out, but gradually the periods away lengthen. Nests are normally used for roosting at night: this is also reported of wild *L. striata* (BAKER 1926; CALDWELL & CALDWELL 1931; ALI 1953; HENRY 1955). I have seen nothing corresponding with the behaviour described by IMMELMAN (1959) in the Zebra Finch and by KUNKEL (1959) in several species, whereby the parents lead the fledglings back to the nest, but this may well be a consequence of the smaller cages in which my birds were kept. Certainly the fledgling Bengalese frequently return to the nest but, in my experience, they do this on their own initiative. One situation in which they are likely to return to the nest is if another fledgling is being fed there, but this is only a particular example of a general tendency to approach when feeding is taking place.

The parents continue to feed the young for at least 10 days after fledging, sometimes for considerably longer. The fledglings begin to take food directly about a week after leaving the nest, and can safely be separated from their parents two weeks after leaving. Occasional feeding by the parents may continue longer than this unless a new clutch is begun meanwhile. The chicks usually weigh about 12 gm at the time of fledging, by which time the growth rate has slowed down considerably. When the chicks are becoming independent, about a week later, there is usually a slight loss of weight of up to half a gram, but this is soon made up again (this loss cannot be seen in Figure 2 as it does not occur on the same day for all chicks and is thus smoothed out by taking averages). Sexual maturation begins about two months from hatching (one month after independence) with the onset of moult into adult plumage and the gradual appearance of song and sexual behaviour. At about three months old the birds can be considered mature.

Acknowledgements.

This study of the Bengalese Finch was made in the Department of Zoology and Comparative Anatomy of Oxford University. I am most grateful to Professor Sir ALISTER HARDY and Dr. NIKO TINBERGEN for giving me the opportunity of doing this work and for their help to me during the time I was in Oxford. Amongst my colleagues in Oxford I must thank in particular Dr. FAE HALL and Dr. DESMOND MORRIS whose experience with estrildine finches was of great value to me. I wish very

much to thank the Principal and Fellows of Newnham College, Cambridge for research awards held during 1954-1957 and for granting me permission to take up these awards while in Oxford. I am also much indebted to the Ford Foundation for a personal grant received during 1957-1958, and to the Nuffield Foundation out of whose grant to Dr. TINBERGEN my birds and apparatus were purchased.

Summary.

This paper describes the behaviour in the nest of captive Bengalese Finches (domesticated *Lonchura striata*). As in the estrildine finches generally, male and female of this species share in all parental activities.

During the late incubation period and while the chicks are young, the adult birds may display upon disturbance of the nest, this display sometimes developing into definite attack. This display is described both in the Bengalese and in the Cutthroat Finch (*Amadina fasciata*) where it is more complex.

Bengalese Finches do not assist the hatching of their chicks, but they eat the eggshells shortly after hatching has taken place.

Chick feeding behaviour, including the begging of the chicks and the stimuli which evoke it, is described in detail.

Estrildine nests characteristically contain an accumulation of faeces after the young have fledged, and it was therefore thought that nest sanitation behaviour was lacking. However, in the Bengalese Finch the parents do eat the chicks' faeces for about the first ten days after hatching. After this the chicks deposit the faeces around the sides of the nest, keeping the nest cup and themselves clean. This system is possible, presumably, only because the faeces are dry.

An account of the morphological and behavioural changes in the chicks from hatching to fledging is given.

R e f e r e n c e s :

- Ali, S., 1953: The birds of Travancore and Cochin. Oxford University Press.
- Andrew, R. J., 1956: Begging responses of certain buntings. *Brit. Birds* 49, pp. 107-111.
- Baker, E. C. S., 1926: The fauna of British India: Birds, Vol. III. 2nd ed. Taylor & Francis, London.
- Bannerman D. A., 1949: The birds of tropical West Africa, Vol. 7. Crown Agents for the Colonies, London.
- Bastock, M., Morris, D., & Moynihan, M., 1954: Some comments on conflict and thwarting in animals. *Behaviour* 6, pp. 66-84.

- Blair, R. H. & Tucker, B. W., 1941: Nest sanitation. *Brit. Birds* 34, pp. 206-215, 226-235 & 250-255.
- Bourke, P. A., 1941: Notes on two finches. *Emu* 41, pp. 156-159.
- Caldwell, H. R. & Caldwell, J. C., 1931: South China birds. Hester May Vanderburgh, Shanghai.
- Chapin, J. P., 1954: The birds of the Belgian Congo. *Bull. Amer. Mus. Nat. Hist.* 75, part 4.
- Eisner, E., 1957: The Bengalese Finch. *Avicult. Mag.* 63, pp. 101-108.
- Eisner, E., 1960 a: The biology of the Bengalese Finch. *Auk* 77, pp. 271-287.
- Eisner, E., 1960 b: The relationship of hormones to the reproductive behaviour of birds, referring especially to parental behaviour. *Anim. Behav.* 8, pp. 155-179.
- French, N. R., 1954: Notes on breeding activities and on gular sacs in the pine grosbeak. *Condor* 56, pp. 83-85.
- Harrison, C. J. O., 1957: Notes on the dark fire-finch (*Lagonosticta rubricata*). *Avicult. Mag.* 63, pp. 128-131.
- Henry, G. M., 1955: A guide to the birds of Ceylon. Oxford University Press.
- Immelmann, K., 1959: Experimentelle Untersuchungen über die biologische Bedeutung artspezifischer Merkmale beim Zebrafinken (*Taeniopygia castanotis* Gould). *Zool. Jb. Syst.* 86, pp. 437-592.
- Immelmann, K., 1960: Contributions to the biology and ethology of the Red-eared Firetail (*Zonaeginthus oculus*). *West. Aust. Nat.* 7, pp. 142-160.
- Kluijver, H. N., 1933: Bijdrage tot de biologie en de ecologie van den spreeuw. *Versl. Plantenziekten. Dienst Wageningen* 69, pp. 1-146.
- Kunkel, P., 1959: Zum Verhalten einiger Prachtfinken (Estrildinae). *Z. Tierpsychol.* 16, pp. 302-350.
- Lawrence, L. de K., 1953: Nesting life and behaviour of the red-eyed vireo. *Canad. Field Nat.* 67, pp. 67-77.
- Miller, A. H., 1941: The buccal food-carrying pouch of the rosy finch. *Condor* 43, pp. 72-73.
- Morris, D. J., 1958: The comparative ethology of grassfinches (Erythrurae) and mannikins (Amadinae). *Proc. Zool. Soc. Lond.* 131, pp. 389-439.
- Nethersole-Thompson, C. & Nethersole-Thompson, D., 1942: Egg-shell disposal by birds. *Brit. Birds* 35, pp. 162-169, 190-200, 214-223, & 241-250.
- Skead, C. J., 1947: A study of the cape weaver (*Hyphantornis capensis olivaceus*). *Ostrich* 18, pp. 1-42.
- Steinbacher, J. & Wolters, H. E., 1956: Vögel in Käfig und Voliere. 1) Prachtfinken. Hans Limberg, Aachen.
- Steiner, H., 1954: Das Brutverhalten der Prachtfinken, als Ausdruck ihres selbständigen Familiencharakters. *Proc. XI Intern. Orn. Congr. Basel*, pp. 350-355.
- Tinbergen, N., 1951: The study of instinct. Oxford University Press.
- Tinbergen, N., 1952: 'Derived' activities, their causation, biological significance, origin and emancipation during evolution. *Quart. Rev. Biol.* 27, pp. 1-32.
- Tucker, B. W., 1941: Further data on nest-sanitation. *Brit. Birds* 35, pp. 66-72 & 90-97.

- van Someren, V. G. L., 1956: Days with birds: Studies of habits of some East African species. *Fieldiana, Zool.* 38, pp. 1-520.
- Vincent, A. W., 1949: On the breeding habits of some African birds. *Ibis* 91, pp. 660-673.
- Wackernagel, H., 1954: Der Schnabelwulst des Stars (*Sturnus vulgaris* L.) *Rev. Suisse Zool.* 61, pp. 9-82.

MICRO-GEOGRAPHICAL VARIATION
IN NETHERLANDS HERRING-GULLS,
LARUS ARGENTATUS

by

K. H. VOOUS

(Zoölogical Museum, Amsterdam)

Recently I have tried to show that the Herring-Gulls from western Europe are subject to gradual clinal variation with a distinct trend of growing larger and darker on the mantle from Britain to Fennoscandinavia (*Ardea* 47, 1959, p. 176-187). The gradual increase in size from southwest towards northeast is in agreement with the eco-geographical rule of BERGMANN, which more appropriately could be called the BERGMANN phenomenon. However, no correlation between climate and the colour of the mantle was found.

In order to learn whether the breeding in distinct colonies and the subsequent tendency of micro-geographical isolation between members of various colonies might induce micro-geographical variation of mantle colour I have examined as large a number of Herring-Gulls from Netherlands breeding colonies as I could assemble for this purpose. The number of 256 breeding birds examined for my previous paper has now been augmented to 604.

Netherlands Herring-Gulls from 6 breeding colonies have been arranged according to the scale of variation of the colour of the mantle referred to in my previous paper. Therefore each specimen has been directly compared to standard specimens representing the six colour classes chosen. The results are summarized in the tables 1 and 2 and figure 1.

It appears that the various colonies differ considerably from each other in the average mantle colour. Individual overlap, however, is large. Herring-Gulls from Schouwen (mean mantle colour 4.3) in the