INCUBATION AND FLEDGING PERIODS OF AFRICAN BIRDS

BY R. E. MOREAU, C.F.A.O.U., ETC., AND W. M. MOREAU

STUDIES of incubation periods have been made by Evans (1891, 1892); by Burns (1915), the uncritical nature of whose work has been severely commented upon; by Bergtold (1917), who is, however, "confident" that some of the records he includes are "grossly incorrect"; and by Heinroth (1922), whose approach to the subject is fully critical and scientific. Very few tropical species figure in these compilations and hardly any are African.

There is no doubt that the incubation period is, within narrow limits, specific, but as was noted by Evans (1891), even with intensive watching of a nest, it is not often possible to say exactly when incubation begins. In our experience in East Africa, as in the Temperate Zones, it appears that some birds, e. g. *Arizelocichla masukuensis,* begin to sit with normal assiduity as soon as the egg completing the clutch has been laid. Other species "play themselves in"; *Psalidoprocne holomelaena,* for example, has been observed to cover its egg for only 19% of the time on the first day although on subsequent days the percentage varied between about 45 and 60%. The fact that the eggs are laid at intervals introduces another element of uncertainty. Like Temperate Zone birds, most African birds in our experience lay an egg a day until the clutch is complete, but there are notable exceptions. The swift *Micropus caffer struebellii* lays it two eggs with an interval of two days, or more usually three, between them. Hornbills' eggs are laid at even longer intervals—five to seven days in *Lophoceros erythrorhynchus* (Moreau, 1937, and J. Laws *in litt.*). In the hornbills the eggs hatch at intervals nearly, but apparently not quite, as long as those between the egg-laying but this is evidently a direct consequence of the fact that as a rule the female remains in the nest-hole continuously from the time she begins to lay. In *Micropus caffer,* although both parents spend the 12-hour nights in the nest, which is a closed non-conducting one (at Amani it is always the mud ball of *Hirundo abyssinica,* taken over by the swift and lined with feathers), we have established by marking the eggs that the first laid is not necessarily the first hatched. For these reasons we take, as Heinroth has done, the time the last egg is laid as the beginning of the incubation period and the hatching of the young as its end. A clutch of two or three may, however, hatch practically together or, even in the same species, over a day or more. Unless the eggs have been marked this introduces an element of uncertainty in the length of the incubation period that needs to be recognized. It can satisfactorily be allowed for by using the device explained in a later paragraph. (To the above conception of the 'incubation period' there is, however, an obvious necessity to make an exception in such a case as the hornbills, where it is justifiable to take as the 'incubation period' that elapsing between the first laying and the first hatching.)

Fledging periods for tropical birds, like their incubation periods, are almost entirely unrecorded and moreover the subject as a whole has received less attention. There appears to be no compilation of Palaearctic or Nearctic data corresponding to Bergtold's or Heinroth's, and there has been no discussion nor generalization of them except in the illuminating paragraphs by Stresemann (1934: 304), which form an original contribution. Fledging periods may of course be accepted as specific, but the range of individual variation within the species is greater in fledging than in incubation period. This is to be expected because the young are exposed to a greater number of variable factors than the eggs are; and for this reason fledging data derived from captive birds are not acceptable, although in incubation Heinroth (1922) has shown that practically the same time is required for success by natural and by artificial means. Beebe (1917) has recorded that the fledging period was extended more than 30% beyond the normal in a brood of Gray-breasted Martins, *Progne chalybea,* whose nest was so situated that they could not exercise their wings.

Even apart from the case of nidifugous ground-nesters a difficulty in recording fledging periods arises from the uncertainty in deciding when the young bird is 'fledged.' The extreme of straightforwardness is represented by the young hornbill (e. g. *Bycanistes cristatus*), which flies as well as the adult from the moment it leaves its hole high up in a forest tree. An intermediate stage is represented by the Rock-martin, *Ptyonoprogne rufigula,* which at first usually flies only a few feet and returns repeatedly to the nest, or the swallow, *Hirundo abyssinica,* which, as we have established by intensive watching, may make one short flight and then return to its nest for another 36 hours. A case probably not peculiar is that of the *Pycnonotus* spp., which, although not well adapted for terrestrial life, drop from their nests to the ground some five days before they can raise themselves with their wings. The turacos (Musophagiformes), after preliminary expeditions, actually leave their nests permanently to scramble about in the branches some ten days before they can fly. In such conditions, which are probably more marked in the fauna with which we are dealing than with the more familiar birds of the Temperate Zone, it is misleading to take as a rule the day the young bird leaves the nest as the end of the fledging period; and it is preferable to take, so far as possible, the date on which the bird can raise itself in the air with its wings.

A minor element of uncertainty in recording fledging periods arises from the fact that the young may be frightened out of the nest or stolen from it prematurely, but at such a stage of development that, if the nest is not being watched intensively, their departure may be accepted as a natural one. For this reason, if for no other, it is desirable to replicate observations on each species. Where we have been able to do this fairly extensively with some of the Hirundinidae, we have been able to establish that although the smaller the number of young in the nest the greater the number of feeds each receives, the fledging period of the smaller brood is by no means always the shorter (Moreau, in press). In the list below the data are derived from broods of the full normal number except where otherwise stated.

It is necessary to emphasize that a single visit to a nest each day cannot fix a fledging or incubation period within practically two days (or more). For example, suppose that with daily visits all at 08.00 a first egg be found on December 1, the second (and last) egg on December 2, and both young birds on December 15. On these data the laying of the second egg (by definition the beginning of the incubation period) might have taken place just after 08.00 on December 1, or just before 08.00 on December 2; that egg might or might not have hatched second and in fact, apart from any indication obtainable from the state of the young when first seen, at any time between just after 08.00 on December 14 and just before 08.00 on December 15. Thus the periods December 1–15 or 2–14 are equally possible for the incubation; and the only impeccable way of recording a period derived from this set of observations is as 13 days ± 1. This is the method followed in our recording. (Where visits are made more often than daily, or not all at the same hour, the margin of error can best be given as ± so many hours.)

It follows that when the young birds are not all found hatched on the same day a wider margin of uncertainty needs to be allowed for. Suppose that in the foregoing example the young, instead of both being seen on December 15, were seen first on December 15 and 16, respectively. The longest and the shortest durations derived from these data are then December 1–16 and December 2–14; and the incubation period would therefore have to be stated as 13½ days ± 1½. A margin on the fledging period must be allowed for in the same way. If in the example above quoted the young were at the visit of December 31 both flown, the possible fledging periods range from December 14–31 to 16–30, and would have to be recorded as 15½ days ± 1½. If only one young bird had flown on December 31 and the second on the following day, the fledging period would have to be stated as 16 days ± 2. Strictly, it is justifiable to record a fledging and incubation period without margin only when the eggs hatch together, the young fly together and the date and time are known of (a) the last egg-laying, (b) the hatching, (c) the flying. Margins can of course be reduced by giving eggs and young distinctive marks.

Some of the difficulties inseparable from attempts to fix fledging and incubation periods have recently been discussed, with suggestions, by Bletchly (1938). Having seen the method of recording we propose in the present paper, he is inclined to prefer it.

December 2, the first young on December 15 and the second on December 16, all the visits being made at 08.00 o'clock, the only impeccable way of recording the incubation period is as 14 days ± 1; for the second egg might in fact have been laid a few minutes after the visit on December 15, it might or might not have hatched second, and it might have hatched at any time between 08.00 on December 15 and 08.00 on December 16. If visits are made more often, or not all at the same hour of the day, the margin of error can, and should best, be given as ± so many hours. This is the method followed in our recording; and a definite period without margin of error is only really acceptable for any one brood when the times and the dates are known of the last egg-laying, of the hatchings and of the flyings, and also when the members of the brood hatch, and fly, simultaneously.

In the following list incubation and/or fledging periods are given for about 45 African species. For a number of the records we have to thank other observers (as mentioned individually), who have generously passed their data to us. We have also included the few apparently reliable published records that exist. Our personal observations are indicated by our initials. It seems necessary to explain why, although we have paid special attention to collecting data on this subject for several seasons, the results are so meager. One reason is that in Amani, Tanganyika Territory, where we live, the environment is predominantly evergreen forest of a type in which nests are specially hard to find. The other reason is the very high mortality in the nest.

Except Hoesch's records from Damaraland all those in the list come from East Africa within 8° of the equator. An important general difference in the nest economy of such birds compared with those of higher latitudes is that their hours of daylight never reach 13, and for birds of the ground-stratum of evergreen forest, such as the *Sheppardia,* the "day" is still shorter. In general it may be said that all these very low-latitude birds have a working day more than 30% shorter than the average in the British nesting season.[1] On the other hand, practically without exception African broods run smaller in number than those of allied Temperate Zone birds.

FALCONIDAE

Cuncuma vocifer. C/1: Incubation 48 ± 1 days; Fledging 55 ± 1 days. C/2: Incubation 48 ± 1 days; Fledging 51 ± 1 days (both Myles North *in litt.*).

SCOPIDAE

Scopus umbretta bannermani. Incubation about 21 days; Fledging "7 weeks" (Cowles, 1930).

ANATIDAE

Dendrocygna viduata. C/4 under Muscovy Duck in Kenya: Incubation 32 days. Young "able to fly at the end of their third month" (Pitman *in litt.).*

Note.—Incubation period for *D. viduata* is given by Heinroth (1922) as only 26 days although previously (1908) he had given the period of *D. fulva* as 32 days.

COLUMBIDAE

Vinago spp. Incubation "14–16 days" (Van Someren, 1928).

Columba a. arquatrix. Incubation 16 days (Van Someren, 1927).

TURNICIDAE

Turnix sylvatica lepurana. Incubation 15 ± 1 days. Left nest on 8th day after hatching (W. P. Young *in litt.).*

CUCULIDAE

Centropus superciliosus. Fledging must take at least 30 days. After 14 days the quills are only just breaking sheath. From the size

[1] According to Hesse et al. (1937) "since the three or four hottest hours of midday are deducted from the 12-hour day, there remain only 8 or 9 hours for the search for food" by tropical birds. This deduction is, however, not generally appropriate: in the species at Amani for which long series of observations are available, mainly Hirundinidae and Micropodidae (Moreau, in press) there is no midday cessation of food-bringing.

and strength of the feet at this age it is most probable that the young coucals, like young turacos, scramble about in the bush before they acquire their always inefficient powers of flight (M. & M.).

MUSOPHAGIDAE

Turacus persa. Incubation about 20 days (Delacour).

Turacus spp. Fledging about 38 days.

Corythaixoides leucogaster. Fledging about 42 days.

Note.—All the young of this family begin to leave the nest as early as 10–12 days and permanently when they are about 28 days, well before they can fly (Moreau, 1938).

COLIIDAE

Colius striatus near *affinis.* Fledging 17½ ± ½ days. For several days before the young fly they leave the nest when it is approached and clamber away among the branches until the danger is past (M. & M.).

BUCEROTIDAE

Bucorvus cafer. Fledging 61 days (J. H. Rens *in litt.*).

Bycanistes cristatus. Incubation + Fledging 107 days, 108 days, 124 days (M. & M.).

From the second nest the eggshell was ejected on the 50th day, so that a fledging period of 58 days can safely be deduced. The incubation period may have been appreciably shorter than 50 days because of the lag in egg-laying that is characteristic of the hornbills (Moreau, 1937).

Lophoceros erythrorhynchus. Incubation 27–29 days; Fledging 43 days (Moreau, 1937).

Lophoceros deckeni. Incubation not exceeding 33–37 days—the date the female entered is known but not the date of oviposition. Fledging 46 days (Moreau, 1937).

MICROPODIDAE

Micropus caffer struebellii. Incubation 20 ± 1 days twice; 20½ ± ½; 21 ± 1, five times; 21½ ± ½; 22 ± 1, four times; 26 ± 1. Fledging, B/1: 40 ± 1 days; 46 ± 1. B/2: 34 ± 1 days, 35 ± 1, 38 ± 1, 39 ± 1, 40 ± 1 twice, 43 ± 1 twice, 46 ± 1 twice, 47 ± 1 twice, 47 days 10 hours ± 10 hours (M. & M.).

These may be summarized as: Incubation ca. 21 days; Fledging ca. 35–47 days. The extraordinarily wide spread in the recorded fledging periods is paralleled in the Common Swift of Europe, *Apus a. apus* (Witherby et al., 1938). The exceptional record of 26 ± 1 days incubation must be due to delay in the beginning of incubation after the clutch had been completed.

The numerous records available for this species provide data for layings in all months from September to March inclusive at Amani. September is one of the coolest months in the year, with daily mean temperatures, as recorded at the local meteorological station in 1938, varying between 16.6 and 20.0° C., the daily maxima between 19.8 and 24.8° C. In the months following September the temperature increases steadily, until in March, the hottest month in the year, the daily mean temperatures vary (1938) between 20.7 and 24.9° C., the maxima between 24.8 and 30.2° C. No correlation exists between these temperatures and the duration of either incubation or fledging period.

CAPITONIDAE

Tricholaema leucomelan. Incubation 14–15 days; Fledging five weeks (Hoesch, 1934). Fledging in the barbets is evidently slow: *Buccanodon o. olivaceum* is in the nest for more than 30 days (M. & M.).

TIMALIIDAE

Turdoides bicolor. Incubation 16 days (Hoesch, 1934).

PYCNONOTIDAE

Pycnonotus spp.:—

P. nigricans. Incubation 11–12 days; Fledging 13—"werden aber erst nach Ablauf von weiteren 5 bis 7 Tagen flugfähig" (Hoesch, 1934).

P. t. tricolor. Incubation 15 days. After 12 days "flew *down* from nest" (C. R. S. Pitman *in litt.*).

P. tricolor micrus. Incubation (i) 13 ± 1 days; (ii) 11 days 23 ± 2 hours.

On 14th day after hatching the surviving bird of (ii) flew *down* from nest into grass where it remained for at least three more days (M. & M.).

Note:—In the genus *Pycnonotus* it appears to be the rule for the young to leave the nest (which may be as much as twenty feet up) for the ground several days before they can raise themselves with their wings.

Eurillas virens. Fledging 13 days 14 ± 14 hours (M. & M.).

Phyllastrephus flavostriatus tenuirostris. Fledging 13 days 22 ± 20 hours (M. & M.).

Arizelocichla masukuensis roehli. Incubation at least 15 days; Fledging 14 days 4 ± 20 hours; 14 days ± 15 hours (M. & M.).

MUSCICAPIDAE

Trochocercus albonotatus. Incubation at least 14½ days; Fledging 15 ± 1 days; 14 days 18 ± 12 hours; 14 days 12 ± 12 hours (M. & M.).

Batis mixta. Fledging B/1: 15 ± 1 days (M. & M.).

Tchitrea viridis plumbeiceps. Incubation 13 days; left nest practically fully fledged in 10–12 days (Hoesch, 1938).

TURDIDAE

Sheppardia cyornithopsis bangsi. Incubation 16 ± ½ days (M. & M.).

SYLVIIDAE

Prinia mistacea immutabilis. Incubation at least 15 days (M. & M.).

Cisticola erythrops sylvia. Incubation 16 ± 1 days; Fledging (A) at least 13 days; (B) 14 ± 1 days (M. & M.).

Cisticola galactotes. Incubation 19 ± 1 days; Fledging 15 ± 1 days (N. R. Fuggles-Couchman).

HIRUNDINIDAE

Hirundo s. smithii. Incubation 14½ ± 1 days; Fledging (B/2): 19 days 8 ± 8 hours; 20 days 12 ± 12 hours; (B/1): 18 days 9 ± 9 hours (M. & M.).

Hirundo abyssinica unitatis. Incubation 16 days 7 ± 7 hours; 16 days 23 ± 23 hours; 15 ± 1 days. Fledging 18 days 12 ± 9 hours; 19 days 8 ± 8 hours; 17 days 15 ± 11 hours; 17½ ± ½ days — all B/3 (M. & M.).

This may be summarized as:—Incubation ca. 16 days; Fledging ca. 18 days.

Ptyonoprogne rufigula. Incubation 17 ± 1 days (four times); 16½ ± ½ days; 17½ ± 1 days; 18 ± 1 days. Fledging B/2: 25 ± 1 days; 29½ ± 1 days; 25 days 8 ± 16 hours; B/3: 24 ± 1 days (twice); 24 days 10 ± 8 hours; 25 ± 1 days (M. & M.).

This may be summarized as:—Incubation ca. 17 days; Fledging ca. 25 days, exceptionally at least 3 days longer. No correlation exists between temperature and length of period.

Psalidoprocne holomelaena massaica. Incubation 18 days 14 ± 10 hours; 18 ± 1 days. Fledging B/2: 25 days 9 ± 12 hours; 25 days 9 ± 9 hours; 24 days 9 ± 9 hours; 27 days 14 ± 10 hours; B/1: 25 days 13 ± 26 hours.

This may be summarized as:—Incubation ca. 18 days; Fledging ca. 25 days, exceptionally at least 2 days longer.

LANIIDAE

Lanius collaris humeralis. Fledging 20 ± 1 days (E. G. Rowe *in litt.*).

Tchagra senegala subsp. Incubation 15 ± 1 days (E. G. Rowe *in litt.*).

Tchagra australis littoralis. Incubation 15 ± 1 days; Fledging 13 ± 1 days twice (M. & M.).

DICRURIDAE

Dicrurus a. adsimilis. Fledging "2 weeks" (Hoesch, 1934).

STURNIDAE

Onychognathus w. walleri. Fledging 26 days 20 ± 13 hours (M. & M.).

NECTARINIIDAE

Cyanomitra olivacea near *changamwensis.* Incubation 15 ± 1 days; Fledging B/2: 13½ ± ½ days; 14 ± 1 days; 14½ ± ½ days; B/1: 14 ± 1 days (M. & M.).

The young of this species are especially likely to jump out of the nest when it is approached, when they are no more than eleven or twelve days old.

Anthreptes collaris ugandae. Fledging 16 ± 1 days (E. G. Rowe *in litt.*).

Anthreptes collaris elachior. Fledging 15 ± 1 days (M. & M.).

PLOCEIDAE

Uraeginthus granatina. Incubation 12–13 days; Fledging 16 days, "noch wenig fluggewandten" (Hoesch, 1934).

Estrilda astrild minor. Incubation 12½ ± ½ days, 13 ± 1 days; Fledging 13 days 14 ± 14 hours; 15 ± 1 days; 16 ± 1 days (M. & M.).

Coccopygia melanotis kilimensis. Incubation 12 ± 1 days twice, 15 ± 1 days twice; Fledging 15 ± 1 days four times (M. & M.).

There is no explanation of the disagreement between the incubation periods.

Spermestes scutatus cucullatus. Eight eggs were laid at the rate of one a day, the last being found on April 19. Two young had been hatched by the morning of April 30, but the last was not hatched until between May 1 and 2. All the young flew between 08.00 and 16.00 on May 23 (R. C. Jerrard *in litt.*). These data give:—Incubation probably 12 days; Fledging 22½ ± 1½ days.

These figures are authenticated but probably abnormal. The clutch was larger than the usual four to six; the nest was so exposed that sun heat might have started germination in the earlier eggs before the later ones; personal observations for a period on April 16 gave us the impression that the parents were less diligent than would be expected.

Euplectes nigroventris. Incubation 18 ± 1 days, 19 ± 1 days, 20 ± 1 days (N. R. Fuggles-Couchman *in litt.*).

Euplectes hordeacea. Incubation 18 ± 1 days (N. R. Fuggles-Couchman *in litt.*).

Poliospiza gularis reichardi. Incubation 14 ± 1 days; Fledging 13 ± 1 days (W. P. Young *in litt.*).

DISCUSSION

Although the number of African records available is still so small, some comparisons are possible.

Incubation periods.—Many of the African species recorded have incubation periods corresponding closely to, and certainly no longer than, those of their Nearctic and Palaearctic relatives as given by Bergtold (1917), by Heinroth (1922) and by Witherby et al. (1938). This is true of the Columbidae, *Micropus* sp., Muscicapidae, and *Tchagra* spp., while the Pycnonotidae agree with the temperate Turdidae and the smallest Ploceidae (Spermestinae) with the *Passer-Fringilla* group. On the other hand, the *Euplectes* spp., more comparable in size with the latter, take nearly 50% longer to hatch, while the African Hirundinidae and three of the Sylviidae also take slightly, but definitely, longer than their Temperate Zone relatives.

It might be expected that the shortness of the warm season of higher latitudes would put a high premium on shorter incubation, and hence that tropical incubation periods would more markedly exceed those of Temperate birds than appears to be the fact. A modifying influence is doubtless that the breeding seasons in Tropical Africa are by no means unlimited; apart from the sharply determining effects of drought in many areas, even in the equable conditions of evergreen forest a species' breeding is often concentrated into five months of the year (Moreau, 1936).

Fledging periods.—Stresemann's main generalizations are that: (1) small passerine (nidicolous) birds as a rule take about as long to fledge as they do to hatch, but (2) bigger passerines, (3) specially protected nestlings (e.g. hole-dwellers) and (4) exceptionally long-winged birds (e.g. swifts) take much longer to fledge than to hatch. Of the few African species for which we have both fledging and incubation periods it can be said that the Muscicapidae, Pycnonotidae, Sylviidae, *Cyanomitra* sp. and Ploceidae show some conformity with Stresemann's generalization (1), but with notable irregularity and with a frequent tendency for the fledging period to be shorter than the incubation; moreover the Musophagiformes, *Colius* sp. and *Pycnonotus* spp. resemble ground-nesters (e.g. *Turnix*) in leaving their nests before they can fly. Stresemann's generalization (3) holds good for the *Micropus, Ptyonoprogne, Psalidoprocne* and *Hirundo smithii,* but *H. abyssinica* is an unaccountable exception. The hole-dwelling Bucerotidae conform with generalization (2), but not perhaps in such marked degree as might have been expected, or as appears to be true of the Capitonidae and of *Onychognathus walleri.* Also *Cuncuma vocifer,* with nearly equal fledging and incubation periods, does not resemble the Palaearctic *Aquila chrysaëtos.*

Comparing African with Palaearctic birds, we find close agreement in *Micropus-Apus,* and in the Muscicapidae. The *Turdoides,* the Pycnonotidae, the *Sheppardia,* the Sylviidae, the Nectariniidae and the spermestine Ploceidae take a little longer than allied and comparable Palaearctic birds. This is the tendency to be expected from the shorter 'day' near the equator, but the difference is not nearly in (inverse) proportion to the great difference in the 'day,' which is presumably offset by the smaller average number in the brood. It is noteworthy also that both *Hirundo abyssinica* and *H. smithii* fledge more quickly than *H. rustica;* on the other hand the two African hole-dwelling birds on our list that have closely comparable Palaearctic species, *Psalidoprocne holomelaena* and *Onychognathus walleri,*[1] are much slower in fledging than *Riparia riparia* and *Sturnus v. vulgaris*[1] respectively. The interesting difference of 50% between the fledging periods of *Tchagra australis* and *Lanius collaris* finds a close parallel in the difference between those of *L. c. collurio* on the one hand and *L. excubitor* and *L. s. senator* on the other.

SUMMARY

Difficulties and necessary precautions in recording fledging and incubation periods are reviewed. Data are given, mostly for the first time, for about forty-five Tropical African species, some with many replications. None of the birds have incubation periods shorter than those of comparable Temperate Zone birds and some have slightly longer. As with Temperate Zone birds there is a tendency for fledging and incubation periods to be more or less equal in the same species, but hole-dwelling and long-winged birds take longer to fledge than to hatch. On the whole the African birds take longer

[1] Both parents are known to feed the young.

to fledge than do comparable Temperate Zone birds, but not in (inverse) proportion to the shorter daylight.

Temperature, at least within the seasonal variation at Amani (ca. 4° C.), does not affect length of individual incubation or fledging period.

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