A CONTRIBUTION TO THE BREEDING BIOLOGY OF THE PALM-SWIFT, *CYPSELUS PARVUS*.

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These small grey swifts occur throughout Tropical Africa wherever there are palm-trees, and the outlines of their nesting habits have been known for more than eighty years. The first observations, made on *C.p. parvus* in the Sudan by von Heuglin and by Brehm independently (cit. Reichenow, 1900), are good. The chief additional notes have been those of Lynes (1925) on the same sub-species; of Chapin (1939) on *C.p. brachypterus* (Rchw.); and of Loveridge (Coward, 1917) and Moreau (Sclater and Moreau, 1933) on *C.p. myochrous* (Rchw.) in East Africa. Most of the available information relates to the nest-site, shape and materials, in which there appears, as will be shown below, to be local, and perhaps sub-specific, variation.

At Amani there have lately been favourable opportunities for close observation of breeding behaviour. As for previous studies of this nature, closely supervised African observers were used to make long series of records of birds' activities at nests containing eggs and young. The expenses were for the most part defrayed from a Royal Society grant. At one nest continuous dawn-to-dusk records were obtained for fourteen consecutive days. Nearly six hundred more hours of observations in continuous spells of six hours and upwards have been made at fifteen other nests. Special attention was paid to the extent to which the eggs were brooded and to the frequency with which food was brought to the young in the latter half of the fledging period. The observers worked at ranges of five to fifteen yards, for the palm-swifts took no notice of them, though some were liable to fly off when something passed just under their nest. The birds are fully active throughout the daylight hours though most obvious, because tending to fly lowest, about sunset.

At Amani, with its evergreen environment (Moreau, 1936), it appears probable that breeding does not cease entirely at any time in the year, but there seems to be a minimum of activity in the coolest period, late June to August, and what may be called the full nesting season lasts from late September to at least February.

THE SITE AND CONSTRUCTION OF THE NEST.

It appears that throughout its extensive range this species builds almost exclusively on palm fronds. Those which are pinnate, like coconut- and oil-palms, can give only poor overhead cover; borassus and dom-palms (*Hyphaene*) can, however, give a solid roof. The only recorded exceptions to the use of palms appear to be the occasional nests in hut-thatch in the Congo (Chapin) and those in a tree Dracaena, *D. papahu* Agavaceae (formerly known as *Pleomele papahu*, Liliaceae), which has a simple leaf like an aspidistra up to three feet long and five inches wide (Sclater and Moreau). (The reference by Loveridge, quoted by Coward, to nesting in " banana-palms " is a slip of the pen for " coconut-palms."—Loveridge, M.S.). The birds build on both green and withered leaves; with the *Dracaena* this unselectiveness is certainly a source of avoidable mortality, for the withered leaves do not pack down against the stem as in many palms, and are readily torn off by the wind.

Although they are so sociable in the air palm-swifts are not, I think, necessarily colonial in nesting. At Amani there is every grade of density from a single nest on a palm to several dozens. One *Livistonia* palm (an introduced species with a fan-frond like a borassus, very favourable for a nesting-site) had a mass of dead fronds some seven feet in diameter enclosing the trunk firmly about thirty feet above the ground. In fact they were so closely packed by their own weight that a strong breeze did not move them in the least and they formed a sort of cone traversed by a great number of vertical culs-de-sac opening downwards. Scores of palm-swifts were about this tree at all hours of the day, the ground below was speckled with their dung and a patch of grass withered by it. A man sent up to cut the dead fronds had of necessity to attack the innermost first. In these there were no " live " nor recently used nests, though there were many remnants. As soon, however, as he began to get away from the trunk many newish nests appeared, and when half-a-dozen containing eggs or young had been produced work was stopped to allow the nesting to finish. In the sixty fronds cut there were about fifteen nests judged to be of the season; in the whole tree there were probably nearly one hundred.

The disturbance of this big nesting-site, where individual pairs could not be watched, led to birds establishing themselves on four small *Livistonia* palms where their nests were all between six and fifteen feet of the ground and hence most favourably placed for observation. On these palms between the beginning of September and early December 1, 2, 7, and 29 nests respectively were built, nearly all of which were used.

They were put on the upper side (not on the mid-ribs) of fronds so bent that their surface was vertical; and on outside fronds the incubating birds, perched with body vertical, were often exposed to direct sun and weather. If nests were built on the underside they would be efficiently roofed.

There is so far no evidence that a nest is ever occupied more than once. A factor may be the swarming mites that infest the nests soon after incubation has begun. In other respects a used nest is quite clean.

At Amani the main nesting material is feathers, stuck to the leaf and to each other at all angles, but there is usually some admixture of vegetable floss, which may form nearly half the total. Through the kindness of Mr. P. J. Greenway it has been possible to identify four kinds of floss, namely, *Funtumia elastica, Bombax rhodognaphalon* (which is reddish brown), kapok (*Ceiba pentandra,* which is grown locally) and seed-heads of a *Vernonia* sp. (Compositae). The feathers used are nearly all between 10 and 30 mm. long (say ½ to 1¼ inches), predominantly grey and very soft.

In a series of nests recently examined it appears that downy-based breast-feathers of doves are favourite material; *Tympanistria, Streptopelia semitorquata,* and *Turtur kilimensis* are probably all represented and a number of Green Pigeon feathers (*Vinago wakefieldii* is the local species) are certainly identifiable in every nest. At least one strongly yellow feather appears in practically all nests and we have been able to match individual specimens with the breast plumage of a local bunting (*Emberiza cabanisi orientalis*), oriole (*O. chlorocephalus*), and weaver (*Symplectes kersteni*). A few white feathers seem to be fowls'. Out of eight nests examined carefully two contained a few glossy black feathers, apparently from a drongo (*Dicrurus adsimilis*) and a starling (*Lamprocolius corruscus*). Feathers of other colours were very uncommon: two minute chestnut feathers cannot be matched; three barred ones proved to be from the wings-coverts, rump and flank of a coucal (*Centropus superciliosus*).

It is noteworthy that Amani palm-swifts' nests built at all seasons of the year contain much the same high proportion of feathers, although a much larger proportion of the total local bird-population is in moult December-June than in the other six months of the year. It would be very difficult to establish whether there is any seasonal variation in the specific composition of the feathers used. In fact at Amani it is unlikely that all that large proportion of the avifauna which is confined to the lower strata of the evergreen forests can contribute to the palm-swifts' nests at any season because their dropped feathers

cannot get carried into the upper air, where the swifts do their collecting. Reviewing the list of species given above in the light of this limitation I think it likely that the Amani palm-swifts select for size and texture but not for colour. Chapin has, however, noted that the feathers used by *C.p. brachypterus* are " most often those of *Vinago calva* " and Bates thought feathers must be definitely selected by the palm-swift in the Cameroons because " in several nests examined at different times the feathers were always those of the Green Pigeon although other feathers could easily have been found ".

West African *C.p. brachypterus nests* and Tanganyika nests of *C.p. myochrous* seem to have less vegetable down in their make-up than nests of *C.p. parvus* and *C.p. gracilis;* for Lynes describes Sudan nests as " made of vegetable down ", and both Heuglin and Brehm indicate that cotton fibres formed the bulk of the nests they examined there; while Rand mentions only plant down in Madagascar nests. (Jackson's description of Kenya nests of *C.p. myochrous* as formed of " agglutinated saliva " with a " fine fibre or cobweb lining " must surely be uncritical. Nests often glisten as if dabbed with isinglass but in none I have ever seen is the saliva more than an adhesive.) Occasionally during incubation, and even when young are in the nest, a parent coming to brood adds a feather. Often no effort seems to be necessary to make it stick; the bird places it on the vertical pad and there it remains. But at other times the bird makes regurgitating movements and saliva can actually be seen coming from the bill.

At Amani a pad of material is stuck flat on the supporting leaf and at its lower edge a loop is built that is a mere curved flange with a comparatively firm edge well bound with saliva. The shape of the pad varies; four nests in use measured recently were 4½ cm. high x 5 cm. wide, 7 x 5½ cm., 9 x 5 cm. and 12 x 4½ cm. One reason for such variation is that some birds add to the nest-pad (though not to the flange) in a desultory fashion during the incubation-period. In all four nests the internal width of the flange was about 15 mm., some 4 mm. less than the long axis of egg, which, without being stuck to the nest, could never remain " in " it for a moment. Actually the eggs are arranged to stand on their narrow ends, which are stuck to the nest-flange and often the side of the egg is also stuck to the back of the nest. The texture of the nest is so loose and fluffy, at any rate on the surface, that the egg is not held at all rigidly. For example, the egg in Plate 19 has tilted sideways. Nests of *C.p. brachypterus,* " tiny hammock-shaped structures 9 cm. x 5.5 " (Chapin), seem to be similar to those of Amani *C.p. myochrous,* but those of *C.p. parvus* are apparently different. Heuglin gives

this impression when he says that in the Sudan the " nest hollow is not very deep and not a well-rounded bowl form ": Lynes leaves no doubt of it, for he remarks that the nests are " in profile fish-hook-shaped . . . most, if not all, the eggs are stuck by their bottoms to the nest, but I should have thought . . . this . . . little more necessary to prevent them getting rolled out in a breeze . . . than in many orioles, doves and reed-warblers ". The nests of *C.p. gracilis* of Madagascar must also be comparatively ample, for Rand describes five nests as " shallow saucers " 30 x 18 mm. deep internally. In this connection it is very noteworthy that the usual clutch of palm-swifts is two everywhere on the continent, but three in Madagascar.

NEST HISTORIES AND NESTING SUCCESS.

Using the method of assessing fledging and incubation periods advocated by Moreau (1940) the following data have been obtained:—

(a) Incubation periods: 19 days 4 hours ± 1 day; 19 days ± 1 day; 19 days 14 hours ± 16 hours; 20 days ± 1 day (twice); 20 days 3 hours ± 23 hours; 20 days 17 hours ± 8 hours; 21 days ± 1 day (twice); 22 days 13 hours ± 12 hours. From these data the average incubation period can safely be taken as twenty days. The time taken for the last-cited clutch was clearly abnormal and one of the two chicks died after chipping the shell.

(b) Fledging periods:—
Solitary young birds: 29 days 10 hours ± 12 hours, 29 days 3 hours ± 20 hours; at least 31 days; 31 days 8 hours ± 12 hours; 33 days 11 hours ± 8 hours.
Broods of two: 32 days 16 hours ± 11 hours; 32 days 20 hours ± 2 days. In this last nest the second young bird made its first flight fully two days after the other.

It is of great interest to compare these results with the incubation and fledging periods of the bigger swift, *Micropus caffer struebellii*, also at Amani (Moreau, 1940). Its average incubation period, twenty-one days (based on fourteen records), is only 5% longer than the palm-swift's, while its average fledging period, forty-two days (based on fifteen records), is fully 30% longer. The fledging periods of the only other swifts for which data appears to be on record, *M. apus apus* and *M. melba*, also approximate to forty-two days. The much shorter period of the palm-swift may be adaptive; it is unquestionably of advantage to young birds whose survival depends on their ability to support themselves day after day by grip.

PLATE 19.

Much more extensive fledging period data would have been obtained from the Amani palm-swifts but for the high mortality in the nest. The fate of sixteen clutches of two and of three single eggs is definitely known. Of these thirty-five eggs only twenty-three hatched, for two pairs were smashed and sucked, another pair fell out of the nest, two (in different nests) were addled, one pair and one single egg were deserted and another was lost through the fall of the whole palm front. The mortality in the young was even heavier: out of the twenty-three chicks that hatched thirteen disappeared from the nest at ages ranging from three hours to twenty-two days; one died at three days old; one died because the leaf shut up so that its parents could not visit it; two were deserted apparently without cause at the age of about six days.

Thus thirty-five eggs of which twenty-three hatched produced only six fledged young. Such a high mortality in the nest may not be abnormal. The loss of the four smashed eggs and the thirteen young that disappeared was almost certainly due to Fiscal Shrikes (*Lanius collaris humeralis*), which on two occasions were actually seen at work.* In East Africa this predator is practically confined to country above 3,000 feet, while the main stronghold of the palm-swift is below that altitude, especially along the coast and in northern Uganda. But there it is likely that the crows, which are absent from Amani, may do great destruction, as Winterbottom observed in West Africa.

PRE-INCUBATION BEHAVIOUR.

Nest building is leisurely; feathers are brought at long intervals, apparently by both members of the pair. In each of two nests the beginnings of which were observed the first egg was laid ten days later. From the earliest stages each pair of birds slept at its nest-pad.

*Their responsibility has since been virtually proved. From the beginning of November all Fiscals seen anywhere near the nest trees have been shot (six up to 15th December). Of eight young palm-swifts in the nest on 1st November three disappeared by 9th, the other five have flown; of ten hatched 1st to 15th November, seven have flown, one disappeared, two were deserted; of six hatched 16th to 30th November all still survived on 15th December. A striking contrast to the mortality before the Fiscals were controlled. These observations accord far better with the reputation given by Roberts (*The Birds of South Africa*, 1940), to the species there than with the view taken by Jackson and Sclater (1938) of the Kenya bird.

Male and female may often be seen together at a partially built nest and frequently they are in the closest possible contact. At nest 19, for example, three days before the first egg was laid the birds visited the nest together repeatedly, usually for only about five minutes but twice for over an hour. As a rule one of the birds would on arrival take up the vertical brooding-position on the pad, and shortly its mate would change places with it. Most of the time they were touching each other, the outside bird with a wing thrown over the " sitting " bird, an attention that was offered by whichever member of the pair was not " sitting." Alternatively the mate would perch vertically above the nest, covering the " sitter's " head with its body. Frequently also the " sitter " had its mate clinging to its back, but without copulation.

There is no evidence that these swifts copulate in the air, but they do so repeatedly on the nest before egg-laying is complete. The male has been seen to perch just above the " sitter " and lower himself over her body until he completely covered it. At a very early stage of one nest copulation, lasting about twenty seconds, was seen to take place three times in a visit of twenty-one minutes. At another nest copulation took place two hours before the second (and last egg) was laid.

Where the clutch is two eggs, as it is nine times out of ten at Amani (and never three eggs), the intervals between the egg-layings have always been about forty-eight hours, and all those eggs of which the time of deposition is known were laid before three hours after sunrise. It is common for an egg to be laid during the roosting period and for a time it seemed that we should not succeed in observing how the egg was attached to the nest-pad. Eventually Charles Abdallah, using binoculars at a range of about ten yards, was able to make notes of which the following is a translation:—

> 09.10. A bird settled on the nest [in the usual vertical position]. 09.14. It bent its neck to one side and its tail strongly inwards. Then keeping its body very firmly pressed against the nest it moved downwards till I could see the egg against its upper breast. Then it made vomiting motions, put its head down and I could see it putting saliva on the nest alongside the egg. It moved up again [until it was in the usual brooding position], then it worked its body from side to side, still pressing firmly.

This would have the effect of sticking the egg on to the moistened patch; and not content with one application the bird on this occasion repeated the whole performance, spreading more saliva and a second time working the egg into it. Al-

though, as already noted, the surface of the nest pad is loose enough to allow the egg some play it cannot be " turned ", a departure from the normal procedure in birds generally that has been verified by observations on marked eggs at Amani.

THE INCUBATION PERIOD.

(*a*) *Result of One Week's Dawn-to-Dusk Observations at Nest 1.*

When the nest was uncovered a bird coming to incubate usually settled a few inches away, making an audible tap on the extended palm-leaf, and then sidled onto the eggs. The incubating posture, with feet gripping the back of the nest, was a strained one, the body vertical and rigid, head stiffly upwards at an unnatural angle, back and rump slightly convex and the wings held a little open as in Fig 1. The abdomen was pressed on the eggs, firmly enough in fact for the young to hatch safely, an operation that without this safeguard must in such a nest have been impossible. What actually happened was that on 21st February a bird settled on the two eggs at 09.10 and when it flew off at 10.22 one young bird was clinging (also in a vertical position) to the nest pad. Shortly afterwards nothing was visible of the empty egg-shell, although the old birds were not seen to carry it away. (This would in fact have been difficult, because they would have had to unstick it from the nest material.) The next morning the second young bird was hatched between 08.14 and 09.55. This time the bird was, as the observer noted, pressing itself tightly against the nest pad and moving its body restlessly; it was evidently breaking up the egg-shell, for tiny scraps could be seen falling to the ground. Certainly the egg-shells did not remain intact at all after the young were hatched and they could not have served as refuges for the young to " lower themselves into " as Loveridge observed (Coward).*

Both the parent birds incubated by day (cf. Loveridge's statement), frequently changing over, and apparently either may incubate at night (Chapin). Certainly on six of the seven days under observation both birds slept at the nest, one incubating and the other also on the nest-pad or very close alongside. They rarely came to roost together, but, as with their departure in the morning, one was usually a few minutes (up to 9) after the other. Their period of wakefulness lasted about 12½ hours, from approximately 06.00 to 18.30 local time.

During the day the parent birds were often to be seen together at the nest (as noted by Winterbottom (Bannerman) for

* At other Amani nests the egg-shells have always disappeared within a short time of the young being hatched.

C.p. brachypterus), as a rule in connection with a change-over on the eggs, which was however usually quite leisurely. The new arrival (A) might settle on the nest-pad alongside the incubating bird (B) and nudge it. (B) might then move to one side, (A) settle on the eggs and after a minute or two (B) fly away. At other times the new arrival would settle on a level with its mate's head and, after the eggs had been left uncovered, lower itself onto them. Both birds seemed eager to sit. Thus on 17th February one (A) began to sit at 08.40. At 09.18 (B) hung up alongside and remained there until two minutes after (A) had vacated the nest, which was not till 09.41. Meanwhile (A) sat close by and did not depart till 09.45. Again, the next day a bird (A) began to sit at 06.47; its mate (B) arrived at 06.50, settled alongside, nudged it without rousing it off the eggs and flew away at 06.55, leaving (A) still on. At 07.00 (B) returned and hung up by the sitter until 08.29, when it was allowed to take over.

During the last seven days of incubation, when the daily maximum temperatures were 26.2, 26.8, 29.0, 28.2, 28.8, 29.2 and 28.0°C. (between 79 and 84°F.), the eggs were covered for an average of 70% of the hours of day-light, the daily figures being 81, 73, 71, 78, 70, 63, 60%. This downward trend as hatching approached is not what would have been expected, but it has been recorded in another species sitting for only about 54% of daylight, *Hirundo smithii* (Moreau, 1939) that there is no increase in assiduity as hatching approaches.

The duration of individual spells on eggs showed a remarkably wide diversity, which could hardly have been affected by the weather, for this was uniformly rainless and sunny during the week under observation. Of the 65 complete recorded spells (not terminated by human disturbance) about half (32) lasted less than 20 minutes, with the favourite duration about 10 minutes; 10 more spells (16%) lasted from 20 to 40 minutes; and 20 (about 30%) for an hour or more, the longest being 102, 103, 104, 105, 138 and 213 minutes.

On nearly half the occasions when the sitting bird left the eggs they were covered again by the mate after practically no interval. There remain 37 intervals when the eggs were uncovered for more than one minute. Half of these lasted less than 15 minutes and most of the rest 20-40 minutes. Yet four days each had one long interval, of 105, 123, 154 and 220 minutes, when for no apparent reason the parents were not seen near the nest at all.

(b) *Observations at Other Nests.*

As a rule brooding does not begin directly the last egg has been laid, nor for some hours afterwards, though frequent visits

THE INCUBATING PALM-SWIFT.

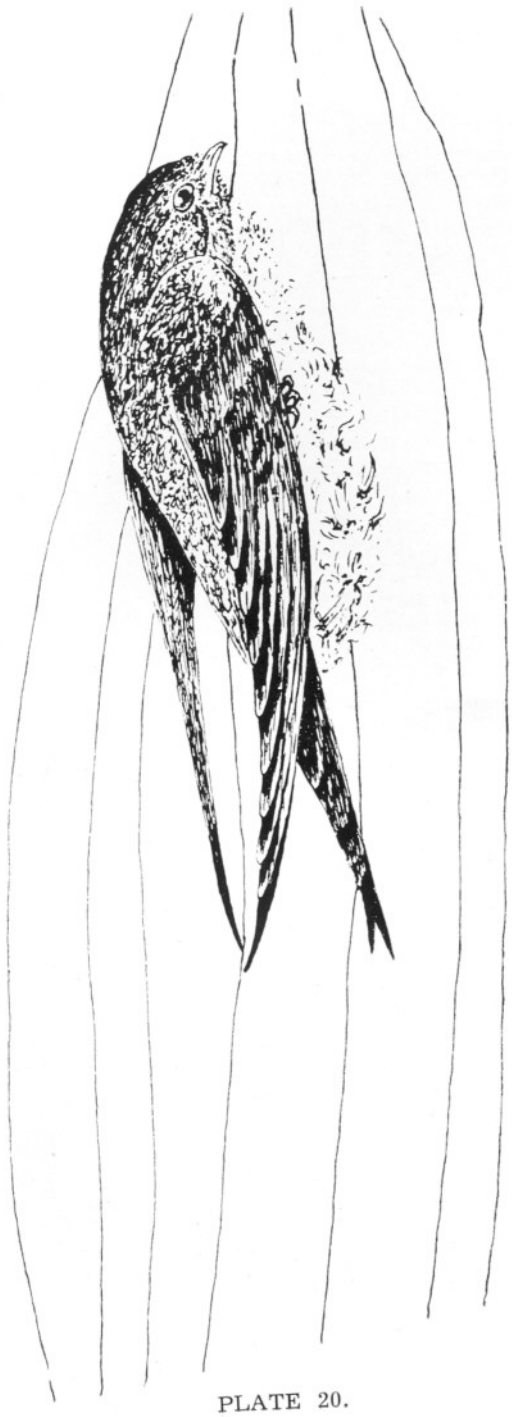

PLATE 20.

of less than five minutes may be paid on that day. Incubating birds always adopt the rigid-looking posture described under nest 1 but are often in movement, wriggling and preening. Their large eyes, which might seem adapted to crepuscular habits, are open, even in the strongest light. One bird brooding on a nest, the " back " of which was particularly ample, picked feathers from the top and added them to the lower part of the pad.

The percentages of time the eggs are incubated are subject to almost the greatest variation possible as the following records for 6-hour spells on successive days indicate:—

Nest 4: 54, 46, 80, 4, 82%
,, 5: 78, 88, 56, 7, 98%
,, 9: 70, 68, 60, 55, 100%
,, 18: 69, 87, 98, 91, 84, 89%
,, 23: 26, 60, 69, 96, 100%
,, 26: 49, 42, 70, 50, 60%
,, 27: 33, 60, 38, 76, 98, 34%

The very high percentages were achieved by close collaboration of the parents, the sitting bird not leaving until it was pushed off by its mate. The very low percentages are quite inexplicable. They were not due to disturbance by human agency. It seems surprising that embryos could survive the occasional extremes of neglect in Nests 4, 5 and 23, when in the first half of a day the eggs were incubated altogether for less than half an hour, for half an hour and for 1½ hours respectively. Actually both eggs hatched in Nests 4 and 5, and one in Nest 23, the other being addled.

The variation in percentage of time brooded is made the more inexplicable by its lack of relation to temperature (as measured in the screen). For example on the days when 38, 76 and 98% were recorded at nest 27 the minima were 16.3 14.5 and 17.8°C. and the maxima 20.4, 24.0 and 24.3°C. The day when nests 4 and 5 had such unreasonably low brooding records was comparatively warm though misty and wet (min. 17.0°C., max. 25.2°C., mean 21.1), but the preceding three days, when the birds brooded altogether more consistently, had mean temperatures very little different—21.2, 21.0, 20.3°C.

Brooding assiduity also has no relation to rainfall. As it happens, most of the observation periods cited above were of continuous sunny weather, but enough observations have been made on wet days to establish that palm-swifts do not, like some other birds, for example, the rock-martin (*Ptyonoprogne*), regularly cover their eggs when rain falls.

In duration of individual spells on eggs the birds at all the seven nests quoted above differed from those at nest 1 in having a much smaller proportion of spells under 20 minutes, altogether only 26% instead of nearly 50%. Spells of 20-40 minutes accounted for another 26%, 50-60 for 19%, the remaining 29% being long spells of over an hour. Five spells lasted over two hours, and two of these were over three hours.

In most pairs watched the eagerness to sit is striking. As in nest 1 the bird alongside the nest-pad often jostles the sitter and the latter is often reluctant to give place. A change-over without uncovering the eggs is a feature of behaviour at all nests, though only at nests 9 and 18 was the percentage of such change-overs so high as in nest 1. It is most difficult to reconcile such evidence of eagerness to sit with the very long periods when the eggs are left uncovered; for at every nest, even those showing the highest brooding assiduity, a lapse of 1½ hours or more occurs on the average once every other day. Intervals of over three hours are not rare and over five hours has actually been recorded twice. Such long periods of neglect are liable to occur at all times; as many of them begin in the chilly morning hours soon after sunrise as later in the day, especially because it is the rule for both parents to fly off soon after sunrise and more or less together. An instance, at nest 18, where one went off at 05.58 and the other not till 06.55 is very unusual. At night also they come to roost practically together.

The foregoing data of periods " on " and " off " relate only to occasions when the bird was not for any reason scared off its eggs. Some data have been accumulated incidentally on behaviour in such circumstances. It might be supposed that a bird scared off, especially when it had been brooding for only a short time, might quickly attempt to return or the collaboration between the members of the pair might be such that its mate would. On the contrary there is no evidence that such a thing happens; when a bird is scared off there are the same chances that the eggs will be uncovered for 20 minutes or for 100 or for only 5 as there are when the bird goes off normally.

DEVELOPMENT OF THE YOUNG.

At hatching the young are entirely naked and dusky reddish brown in colour, which darkens slowly to sooty on the upper parts, while the under-parts remain reddish longer. It is remarkable however that in one nest the first hatched was redder from the start than the other and a difference was still perceptible at the age of seven and eight days (when they were deserted).

There is no doubt that the newly-hatched birds are not stuck to the nest-pad by the parent as the eggs are. The young

have to cling on, whenever they are not actually being brooded, for the thirty days until they fly; and since on the day of their birth they may be left alone for a couple of hours, considerable muscular effort is demanded of them from the start. In their hanging on they are favoured by being hatched with claws that are unusually well developed, sharp, curved, and fully as long as the toes, and by the texture of the nest, which gives the best possible holding surface. In fact a young palm-swift about three days old that died of neglect remained dangling by one foot for thirty-six hours.

From within a few hours of birth the muscular activity of young swifts is remarkable. Some are constantly in motion, rubbing their necks and sightless heads together, jerking their rumps and wagging their wing-stumps. Often they fling their heads sideways or backwards, even right onto their shoulders. These movements have nothing to do with the arrival of food and may be caused in part by the irritation from the nest parasites. However, one pair when only two and three days old respectively were not quiescent even when being brooded; they occasionally poked a head out from under the parental wing and actually changed places on the nest-pad. At four days old this pair were already to some extent independent of the support of the flange, for one would move up the vertical pad until his body was on a level with the other's head. Older fledglings may be seen crawling up their leaf right off the nest. One got as far as another nest a couple of feet away, where it went into a huddle with the two fledglings belonging there. The reactions of their parents were not seen, but later the wanderer got back to its own nest.

At three days old the palm-swifts are still blind and perfectly naked. Their bill and gape, which is not much enlarged along its edge, are horn pink, with a paler raised spot round each nostril. A minute white egg-tooth is sometimes still present. They are now capable of uttering a very tiny piping noise, inaudible at a distance of much more than one yard. They spend most of their time, as they have from birth, in a vertical position, jammed together flank to flank, and with their heads stretched up flat against the back of the nest, in fact, in the same posture as the brooding adult's. This attitude leaves their anus projecting constantly over the edge of the nest-flange, so that they always, from birth, can drop their faeces to the ground and the parents, unlike most birds, never have any nest-cleaning to do. It is noteworthy that within two hours of hatching one young bird was seen to pass a minute pellet of faeces. In one pair it was observed that the size of the faecal pellets increased rather suddenly to about 4 min. in diameter on the 4th day.

At about five days old white points of quills begin to show on the upper parts. By the 6th day some young birds are just beginning to open their eyes. Whitish down now breaks out very rapidly all over the upper parts so that the young bird is soon a mass of it. Clinging in a vertical position to the nest it harmonizes pretty well with the nest material, loses all semblance of a bird and so long as it is still would pass for a clot of lichen on the palm frond. By the 15th day much of the whitish down has gone and feathers, of which mainly the brown tips are apparent, clothe the forehead, shoulders and sides of the belly. Some down is still left by the 20th day.

The growth of the remiges is interesting. The quills all start about level but the outer primaries soon grow much more quickly than the others. At 15 days old the longest primary is about 8 mm. longer than the shortest; but by 22 days the difference is nearly twice as great (in one wing measured, 43 mm. against 29). At about 28 days the disparity has increased to 64 mm. against 32.

Owing to the position of many of the young birds, in a constricted fold of a withered frond, they can exercise their wings hardly at all. One young bird under close observation was never seen to move its wings except when it was being fed: then it rattled them audibly against the dry frond. However, each of the five young birds whose actual first departure from the nest has been witnessed flew well, following a parent who had fed it and apparently without coaxing or compulsion. On our evidence it is unusual for a young swift to return to its nest except to roost; some families return with their parents for the first night or two, others do not.

PARENTAL CARE AFTER HATCHING.

(*a*) *Brooding.*

For about the first week after the hatching of the young the general behaviour of the parents is much what it was before. The young are brooded with the same curious admixture of assiduity and neglect as the eggs.

At nest 1 the day after the first egg hatched, a parent was " on " for two long spells, of 95 and 101 minutes, in the early morning, and during the latter (08.14—09.55) the second egg hatched. The same evening, when the second fledgling was only eight hours old and still of course perfectly naked, there was an astonishing period of 108 minutes, from 10.12 till 12.00, when no adult came near the nest. On the next day there were three periods of over an hour each—61, 117 and 143 minutes —when no parent appeared. The maximum air (" screen ") temperature reached that day was 29°C. In subsequent days

the young were brooded 40, 30, 21, 42 and 52% of the hours of daylight. Thus the general level of brooding was rather lower than during incubation. The main reason was a shortening of individual spells (while visits remained as irregular as ever); and almost as soon as feeding began the parents began to make a proportion of their visits for that sole purpose, without brooding.

The young in nest 1 disappeared while brooding was still at a fairly high level. Observations at other nests make it clear that brooding ceases to be of significant extent by about the 9th day (when the young are partially covered with down): at nest 10 the young were brooded 67% of the time on the 7th day but only 13% on the 9th and not at all thereafter; at nest 18 the percentages were 69, 74 and 8 on the 5th, 7th and 9th days.

(b) *Feeding.*

Owing to their situation in the shadow of the leaf, it is at some nests difficult, even in broad daylight, to be sure whether a visiting parent actually feeds its young or not. However, on the strength of observations on especially well-placed nests I have concluded that each recorded visit may without risk of serious error be taken, for purposes of the following discussion, as meaning a feed for one young bird. Visits without giving food are uncommon and the giving of food to two young at a single visit rare.

As a rule the first meal of the day is brought some time between 10 and 60 minutes after the parents' first departure from their roost. A delay of 1½ hours is very unusual. At this early hour, as later in the day, the parents may arrive more or less together, which proves that they share the duty of feeding, or the first feed of the day by a single parent may be followed by an interval of anything up to 90 minutes. There is certainly no rush to feed the young, which have been without food for about 12 hours, and the feeding frequency in the early morning is no greater than at any other time of the day. On the other hand it is a definite rule that feeding speeds up at the end of the day. Excluding the occasions when the two parents come to roost (always too much in the dusk to see whether they bring food then), they usually make about four visits in the last hour of daylight, which, as will be shown below, is much more frequent that during the rest of the day. For example, at nest 1 on days following the hatching the total visits numbered 17, 16, 16, 27, 24, of which four on each day were in the last hour before coming to roost. The corresponding figures at nest 12 for the last hour on the 6th, 5th, and 4th days before the young flew were 4, 4 and 5.

On most days at most nests, whether they contain one young or two, there is at least one period of 1½ hours or more during which no parent brings food, but on the whole the attentions of the parents are not quite so irregular as when they have eggs. Excluding the last hour of daylight, when the intervals average only 15 minutes, about two-thirds of all the intervals between feeds do not exceed 45 minutes, and within that range the intervals are fairly evenly distributed.

Actually the general feeding rate is too slow for one hour to be a satisfactory unit and it is preferable to use the unit of 200 minutes that I have adopted in other specific studies. Calculated on continuous watching spells of six hours and upwards (but excluding the last hour of daylight) we have the following feeding rates (per 200 minutes) all in fine weather:—

For a solitary young one:—

Nest 10: 3.0, 3.3, 3.8, 3.3; average 3.3.
,, 13: 3.3, 4.1, 3.8, 4.4; average 3.9.
,, 23: 4.7, 2.5, 3.3, 3.3, 3.3, 4.1, 4.7; average 4.3.
,, 25: (later) 1.8, 4.0, 4.0; average 3.3.

For each of two young in nest:—

Nest 9: 2.6, 2.5, 4.1, 4.2, 2.6; average 3.2.
,, 18: 3.3, 2.6, 3.0, 2.3, 3.0, 2.9; average 2.8.
,, 25 (at first). 1.8, 2.5, 1.5; average 1.9.

It is clear from these data that the solitary young palm-swift in a nest tends to get more food than when it is one of a pair, an observation paralleled in other species of birds (Moreau, 1939).

The rates compare with about 7.5 for each young Rough-wing Bank-martin (*Psalidoprocne holomelaena*) and about 40 for each young *Hirundo smithii* (Moreau, 1939), so that it seems probable that the mechanism of feeding by the swift may be different from at least that of *H. smithii*. With this latter bird it can practically always be seen that the conveyance of food is instantaneous, as if a single morsel were given each time. In the parent swift convulsive movements of the head can sometime be seen, as if it were regurgitating food, after it has alighted and before it has fed its offspring—by thrusting its bill well inside theirs. Probably the feeding mechanism is the same as in the Common European Swift, *Apus* (*Micropus*) *a. apus*, regarding which there is a certain amount of evidence that they regurgitate packets of insects (Ingram, 1920; Kirkman, 1910; Jourdain, 1938).

SUMMARY AND REFERENCES.

The subspecies of *Cypselus parvus* show differences in nest-shape, nest-material and clutch size. At Amani nests of *C.p. myochrous* are mainly of feathers, with plant floss of several species, all stuck together with saliva. Among the feathers those from the breast of species of the pigeon family are prominent but a number of other birds have been identified as contributing. At Amani the eggs are always stuck to the nest directly they are laid (process described), a safety device entirely necessary because the nest is a vertical pad with a mere flange, narrower than the egg-length, at its lower edge.

Data are available from about 700 hours of observations on behaviour at several Amani nests. Copulation takes place on the nest-pad. The parents share incubation (in a vertical position), spend much time on the nest together and often change over on the eggs without uncovering them. Seventy-five per cent of individual spells " on " last over 20 minutes, nearly 30% of all spells over one hour. This assiduity alternates with astonishing periods of neglect, up to 3 hours (not rare) and even 5. One result is very great variation in the percentage of daytime for which eggs are brooded in successive days; and the percentage has no relation to weather or to temperature.

Incubation averages 20 days. The young are hatched while the abdomen of the brooding parent presses them against the nest-pad. Unlike the eggs they are not stuck on; they cling; and in this they are aided by being born with unusually long sharp claws and with great muscular power, though naked and blind. Possibly their relatively short fledging period of 31 days may be an adaptive feature. For while their incubation period is about the same as that of the bigger *Micropus* (*Apus*) species, which live in nests of normal shape, their fledging period is 30% shorter. The young *Cypselus*, whose development is described, often have no opportunity of exercizing their wings yet fly well at their first launching.

The parents brood them for about the first eight days, but with long periods of neglect (up to 108 minutes) even on the day of hatching. The first feed of the day may not be brought till an hour or more after sunrise but feeding is accelerated in the last hour of daylight. For the rest of the 12-hour period of activity on the average only about one meal per hour is brought to each young bird when alone and less when there are two in a nest.

Of 35 eggs laid in 19 nests only 23 hatched and only six survived to fly. Over half the losses appear to have been due to a shrike, *Lanius collaris*.

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