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 EDWARD GREY INSTITUTE  
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 OXFORD

THE BREEDING BEHAVIOUR OF THE SWIFT.

BY

DAVID AND ELIZABETH LACK.  
 (Edward Grey Institute, Oxford).



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## (1) INTRODUCTION.

We started to study the breeding biology of the Swift (*Apus apus*) in the summer of 1946, thinking that little was known of this remarkable bird. In Switzerland, however, Weitman (1947) had a long-term study of the species in preparation, and a shorter paper by Cutcliffe (1951) has now appeared in this country. Our first observations were made on pairs nesting in holes in thatched roofs in villages near Oxford. Stimulated by a visit to Weitman in the autumn of 1946, we decided to try to induce the birds to breed in nest-boxes. Swifts have nested for many years in the ventilators of the tower of the University Museum in Oxford (hereafter referred to as "the Tower"). In 1948, helped by a grant from Mrs. J. B. Priestley, we had platforms erected inside the Tower, and the ventilators were replaced by nest-boxes, to which glass backs were fitted in 1949. The observer can now sit in semi-darkness a few inches from the birds, watching them against the light from their entrance holes without causing them any disturbance. In this paper we describe the behaviour of the birds in their holes. Aerial behaviour is not considered except where necessary for interpreting behaviour at the nest, and the numerical aspects of breeding biology have been treated elsewhere (Lack and Lack, 1951). We are greatly indebted to R. E. Moreau for his extensive criticisms of this paper in manuscript.



The Tower has a steeply sloping roof with 10 ventilators on each of its four sides. Buildings lower than the Tower adjoin it on three sides, the east being clearer than the north or south, while the west side is open. Swifts seem to prefer a clear "run-in" to the nests, and this is probably why the west is used more than the other sides. Of our breeding records during four years, 27 have been on the west, 20 on the east, 15 on the south and 13 on the north side of the Tower.

Most adult Swifts show little fear in their boxes, presumably owing to lack of natural enemies at the nest. There is, however, great individual variation. Some were extremely tame from the start and were not at all disturbed when, in our weighing experiments, we removed and later replaced their eggs or young under them. Others at first left the box if a hand was inserted, but became tame through repeated handling. Some fiercely attacked an inserted hand with their claws, and displayed (see later) if they heard us outside the box or saw an object near the glass. A few birds, on the other hand, always left when a hand was placed in the box, and later became shyer, not tamer, leaving if they merely heard a slight noise near the box.

Some of the Tower adults became so used to being handled that, near the end of the 1948 breeding season, we were able to place rings on their legs in the boxes without causing them any appreciable disturbance. When, however, we took a few of the adults out of the boxes for ringing, several of them deserted their nests. This came as a great surprise, both in view of their previous tameness, and because we did not think that we had caused any desertions in 1946 and 1947, when we caught the adults on nests in thatched roofs by inserting a hand from outside. (Actually a few had deserted, but we had not realised that we were the cause.) Acting on a suggestion from Weithauer, we later caught some of the Tower birds and, instead of replacing them in their boxes, released them from a window. Fewer deserted, but some still did so. We therefore gave up catching and ringing adult Swifts, and would urge other ringers to do the same. We may add that, in Sweden, Magnusson and Svärdsön (1948) found that a rather high proportion of the breeding Swifts deserted when caught at their nests from outside for ringing.

## (2) OCCUPATION OF BOXES.

In 1948, 16 pairs of Swifts laid eggs in the Tower boxes; the non-breeders were not counted. In 1949, 19 pairs laid eggs and 7 more boxes were occupied for at least part of the season by birds which did not lay eggs, the largest number of adults present on one day being 45. In both 1950 and 1951, 20 pairs laid eggs

and about 45 adults were present in all. The latter total cannot be given exactly, as some of the non-breeders occupied boxes for only a few days or weeks, and some possibly changed from one box to another in the Tower. Most of the non-breeders were doubtless one-year-old birds. The latter were found by Weithauer (1947) to occupy nest-sites and to form pairs, but not normally to breed, though one first-year male bred with an older female. Likewise Arn (1945) found that most Alpine Swifts (*Apus melba*) did not breed until their second year, though two individuals did so in their first year.

Weithauer (1947) found that Common Swifts tended to return to the same nest-sites in successive years and that, probably for this reason, the same pairs tended to breed together in successive years. As we gave up catching the adult Swifts, we cannot assess the extent to which they were faithful to their nest-sites or to each other. Some individuals returned to the same nest-site and the same mate, but others changed, perhaps due to our disturbing them.

## (3) ARRIVAL IN SPRING.

The arrival of the adults in spring was recorded by inspecting the boxes each evening when the birds came in for the night. In 1949, the first two adults appeared on May 5th and most came May 11th-27th. In 1950, the first appeared on May 1st and most came May 4th-17th, decidedly earlier than in 1949. In both years the colony assembled gradually, there being 2 to 5 newcomers each day. The biggest arrivals were of 10 on May 10th, 1949, and of 7 on May 4th, 1950. In 1951, the pattern of arrival was rather different. The first two came on May 1st and 13 others had arrived by May 6th. The next newcomer did not appear until May 15th, and the rest came between then and June 8th, between 2 and 5 arriving each day. There was thus a gap of 9 days with no arrivals, presumably due to a hold-up on the migration route; H. G. Hurrell (*in litt.*) found a similar hold-up in arrivals on the coast in 1951.

In several cases, particularly in 1951, a nest-box was frequented by one bird or a pair during the day, but was not used for roosting at night until several days later. It is not known where such birds roosted meanwhile. In several boxes, also, roosting was rather intermittent at first, a bird appearing one night, not the next, and so on, but this occurred chiefly with single birds, before the mate arrived.

In about a quarter of the observed pairs, the two members arrived on the same day. This happened with 7 out of 19 pairs in 1949, 2 out of 20 in 1950 and 5 out of 20 in 1951. In the



rest, one bird arrived 1 to 10 days after its mate, while in the exceptional hold-up of 1951, one arrived 20 days and another 21 days after its mate. In view of these facts, it seems most unlikely that the pair stay together in their winter quarters and migrate north together in spring. Re-matings are presumably due to a tendency for both birds to return to the nest-site occupied in the previous year. Non-breeders, i.e. those pairs which did not lay eggs, arrived concurrently with the pairs that later bred.

#### (4) ROOSTING.

Except occasionally in the first few days after their arrival, each pair roosted in its box regularly each night throughout the breeding season. Very rarely, a bird returned so late in the evening that it failed to enter its nest-hole in the dusk, and we do not know where such individuals eventually spent the night. Once or twice a non-breeding bird, or a pair, disturbed and put out of their box at roosting time, returned to roost in another box, but we did not find this in the breeding pairs. In August, 1951, also, one non-breeding bird alternated irregularly, both for roosting and on its daytime visits, between two adjacent boxes, one of which was empty and the other regularly occupied by another individual. On only one occasion, in August, 1951, have we found three individuals roosting in the same box, the strange bird presumably being a passing migrant. The trio was not disturbed and only two birds were roosting there on subsequent nights. In May, 1951, one bird, presumably a stranger, came to roost at dusk clinging outside the Tower near one of the nest-holes, but we do not know whether it stayed the night.

The roosting pair sit with their heads facing inwards, often side by side, but particularly in cold weather with one on top of the other. We agree with Weinbauer (1947) that Swifts do not enter or leave the nest-holes during the night. The famous dusk ascents, which Weinbauer has shown are carried out by the first-year birds, are not considered in this paper. We saw them in various parts of Oxford. When one occurred on June 8th, 1949, about a mile from the Tower, none of the Tower birds, breeders or non-breeders, took part.

The Swift is a late riser by avian standards, and it comes out much later and retires much earlier in bad than good weather. In early May, 1951, when 8 individuals had arrived in the upper part of the Tower, it was found that the order in which they came in to roost was nearly, though not quite, the same on each of nine consecutive evenings. Certain individuals were always among the first and others always among the last to arrive. One

bird regularly came in, stayed for a few minutes, and then went out again for a few minutes, before finally coming in for the night. In August, 1951, those parents feeding chicks stayed out much later than those without young. Rising and roosting times have recently been studied quantitatively by v. Hartman (1949) and Scheer (1949).

#### (5) BEHAVIOUR IN BOXES BY DAY.

The Swift usually enters its hole by a straight flight with a short rise at the end, alighting on the rim of the hole and immediately running in. With a wind force of 3 or more, or in fading light at dusk, a bird sometimes appears to miss the entrance hole; it then drops off and tries again. On a dark evening one individual actually made 20 consecutive attempts to enter its hole and then gave it up. During the day, several individuals often arrive almost simultaneously at their boxes. This is particularly common when they are feeding young, and suggests that they travel and feed in small groups.

Both the breeding and non-breeding adults visit the boxes regularly during the daytime in fine weather, the most favoured times being around 0730 and 1800 hours, and the least popular between 1200 and 1600 hours. On these visits they often stay inside for less than five minutes but sometimes for periods of an hour or more. (When eggs or young are present, the frequency of visits of course increases greatly.)

In rain, the Swifts often take shelter in the boxes, and in continuous heavy rain they may stay in for much of the day. During a watch from 0800 to 1800 hours on June 26th, 1951, when the weather was cold, windy and almost continuously wet, the two members of a non-breeding pair spent respectively only 6 and 12 (out of 600) minutes outside. The pairs with young, however, spent part of the day seeking food.

In August, 1951, on the Berkshire Downs, we saw several Swifts flying in front of and away from an approaching heavy thunderstorm. Swifts regularly dodge local storms in this way, and we have seen parents coming in to feed their young a few minutes after a heavy rainstorm had passed, but with their feathers quite dry. We have also seen Swifts flying through heavy rain, and arriving in their boxes very wet. During a watch in the Tower on July 17th, 1950, a sudden severe rain-squall brought seven adults into the Tower at once, presumably because they were feeding close by. The many other adults did not come in at that time.



In very cold weather, the pair sit close together or on top of each other in the box, with hunched bodies and ruffled feathers. At 1500 hours on May 8th, 1950, in cold rainy weather, we found three birds huddled together in a box. The third bird remained at least an hour, but had gone by roosting time. There was scarcely any excitement, low clucks and occasional low screams, and a little subdued preening, though on every other occasion (except the roosting incident already mentioned) three birds in a box meant severe fighting. In really cold weather, Swifts have a remarkable habit of congregating in clusters on walls (see Lack, 1951), and the above was possibly an incipient case of this kind.

#### (6) "BANGERS".

In an aerial display, here called "banging", Swifts fly up to the nest-holes of other individuals and brush or bang against them, apparently with the wings, and then fly on. Sometimes a lone bird flies up in this way to several different nest-holes in succession, or to the same hole repeatedly, and sometimes a small party follow each other up to the same hole, then passing on to another hole. We have also had a banger follow up a parent returning to its nest. The bangers are usually silent and their flight is rather leisurely. Usually the banger just touches the hole and immediately flies on, sometimes it comes up to the hole and turns away without touching it at all, and occasionally it alights at the entrance hole and looks in. Still more occasionally, the stranger may actually enter a hole, as described later. "Banging" is quite distinct from the missed attempts at entrance by the parent birds described in the previous paragraph, though it may sound similar when heard inside the Tower. Banging occurs throughout the breeding season, and at any time of day, being especially common around 0800 hours and infrequent in the afternoon. It is restricted to good weather with little or no wind, and is particularly noticeable on the first fine day after a spell of bad weather. The significance of this behaviour is unknown. Possibly it is initiated by non-breeders seeking nest-sites. One of us has seen similar display, with follow-my-leader up to the nest-holes, in the shearwater *Puffinus lherminieri subalaris* in the late afternoons along the cliffs in the Galapagos Islands.

When a banger or a banging party is going the rounds, the breeding adults often return and enter their boxes. They then sit looking out of the entrance holes, which makes their white throats prominent, and scream violently as the bangers pass by. If both parents have returned, they scream in duet, one giving a higher note than the other. If a single parent is present and sitting on the eggs or young, it sometimes ignores the banging, but more often it screams, sometimes without leaving the eggs, while at other times it leaves the nest and walks to the entrance

hole, perhaps with incipient threat display. One bird, disturbed by a banger while building, advanced still carrying a leaf in its beak, but returned after a minute to continue building. The owners of the boxes react to the bangers as if they were intruders.

Banging is a quite different type of behaviour from the screaming parties which dash rapidly round the Tower, particularly on fine evenings. Birds in the boxes often answer the screams of those outside, and sometimes come out and join in. Screaming parties are a communal display in which a whole colony may join, and perhaps members of other colonies also, as more individuals have sometimes circled the Tower than could be accounted for by the residents. Screaming parties occur throughout the breeding season, but only in fine weather, and they are rare at the start and end of the season when few birds are present.

#### (7) THREAT DISPLAY AND GREETING OF MATE.

A Swift entering an occupied box is usually greeted by incipient threat display. The occupant screams, rises up on its feet (instead of sitting with its body on the floor of the box) and advances with wings held partly out and raised. Alternatively, it raises only the wing nearest the newcomer, tipping its body sideways and exposing the feet, which is probably significant as the feet play the chief part in fighting.

So far, the display is the same whether the newcomer is the bird's own mate or a stranger, but the next stage differs. If it is the bird's own mate, both may now scream and advance, and the mate may also show incipient threat display, but they then quickly come together, sometimes almost bowing at each other, and start vigorous mutual preening. A similar sequence of behaviour is sometimes seen when the pair enter their box one immediately after the other, and occasionally when both are already sitting in the box.

We have twice, on May 9th and 11th, 1950, seen a definite scuffle between a presumptive pair. In each case the box had until then been occupied by a single bird, so we perhaps witnessed the first meeting between the pair that year. The bird in the box greeted the newcomer with much threat display, the newcomer responded similarly, and a short scuffle developed, though the birds did not actually grip each other with their claws. One pair quickly settled down together for the night. In the other case, one of the birds dropped out of the box, but was back two minutes later, after which there was a second scuffle, and the pair then settled down together for the night.

The extent of the threat display between the pair varies greatly. There is a tendency for it to diminish in intensity as the season progresses, but sometimes it is extremely reduced even early in



the season, while occasionally it is strong late in the season. Sometimes it is omitted entirely and often it is reduced to a short scream with no posturing, but often there is a little posturing. The behaviour is usually so unlike fighting that we at first called it a "greeting ceremony", but its origin from threat display is now evident.

If the newcomer to the box is a stranger, the threat display of the owner becomes exaggerated. The newcomer may then leave at once, but occasionally it responds. Both birds then prance round each other on raised legs, then pause with the near-side wing tipped up. They then come to grips and a fight commences.

#### (8) FIGHTING.

A strange Swift entering a box usually acts very nervously, sometimes staying quietly in the entrance before proceeding further in, then exploring tentatively, sometimes flicking its wings or walking high on its feet. Even if the owners of the box are absent, it often leaves after a minute or two, and it does not respond to begging chicks. If one of the owners is present and displays at it, it often leaves immediately. Early in the season, however, an intruder sometimes persists and a fight follows. Out of 16 observed fights, 15 occurred before there were eggs in the box concerned. Five were seen in 1949, 8 in 1950, but only 3 in 1951. Nearly all occurred in May, a few in early June and 1 on July 13th. Six started in the morning, 1 at midday, 3 about 1700 hours, 1 at 2000 hours and 5 were first noticed on our routine visit at dusk.

Although there have always been unoccupied boxes available in the Tower, the fights are probably for ownership of a box rather than of a mate. A fight often developed between an intruder and one of the owning pair when its mate was absent, and one of the pair (? the male) always does much more of the fighting than the other. Omitting brief scuffles, due to the ejection of a bird which perhaps entered by mistake, the shortest fight lasted for 20 minutes, the longest for 343 minutes. In another case, two birds were found already fighting and continued for a further 333 minutes. Fights of 2 to 5 hours seem not uncommon. In one box there were fights on two consecutive days, in another case a second fight took place three days after the first.

Nearly all the fights started when an intruder entered an already occupied box. On one occasion, however, a bird entered a temporarily empty box with an angry scream, and when we next looked in five minutes later, two birds were fighting at the entrance hole with a third behind them on the nest. Likewise, Weitrauer (1947) has recorded three birds entering a hole in quick succession and then fighting. This suggests that a fight may occasionally start in the air.

After a few seconds of excited screaming and posturing, the birds rush together, gripping each others' legs with their claws and struggling furiously. They remain thus gripped together for the rest of the fight. The claws are sharp and their grip is extremely strong, but as the birds usually grip their opponent's legs, little if any damage results. The birds also peck repeatedly with their beaks at whatever part of their opponent's body comes within range, usually the wing or body feathers. The pecks are vigorous but harmless, as we tested by inserting a finger during a fight and allowing a bird to strike it. The birds struggle with their wings, sometimes shifting their positions. Periods of great activity alternate with pauses when the birds lie motionless and silent, apparently exhausted, with nictitating membranes over the eyes.

After a time, one of the fighters will be found to be lying on its back below the other. Surprisingly, it is usually the under bird which is winning. It gradually shifts the other towards the entrance hole, the other resisting, and though it is hard to be sure of what is happening, as the birds are closely interlocked, it seems that the under bird is trying to throw the other out of the hole. At this stage the upper bird sometimes tries to escape on its own, but it cannot do so, as the victor does not relax its grip. Eventually the fight carries on over the hole itself, with one bird partly outside, and then both birds usually tumble out, though occasionally one has managed to remain in. One fight continued with one bird partly out of the hole, flapping violently, for as long as 12 minutes.

During their struggles, the birds scream violently, and during the later stages the bird that is getting the worst of it utters a plaintive piping call, not heard in any other circumstances. The loser often appears to be in great agony, alternately piping and lying back breathing faintly. On one occasion, after a fight had lasted 4½ hours, we accidentally disturbed the birds. The apparent victor ran to the entrance hole, while the other lay back and seemed utterly exhausted. After about four minutes, the victor returned, sat beside the other and pecked it. There was no response, so it got onto it and started dragging the unresisting body to the entrance hole, but it was then again frightened, and left the box. A moment later, the apparent corpse rose and left the box, evidently quite uninjured, though it had looked dead for several minutes. After other fierce fights also, we have found no trace of a dead or injured bird beneath the nest hole, nor was any bird visibly damaged. Hence the apparent ferocity of the fights is misleading. On May 20th, 1948, however, we found a freshly dead adult male, perhaps killed in a fight, in a box with a pair.

On one occasion when an intruding Swift looked into a box, one of the owning pair at the back of the box rushed past its mate and attacked, while its mate, who had been nearer to the enemy, retired to the nest. In every other fight, also, one member



of the owing pair ( ? the male) took a much more active part than the other. The more retiring sex sometimes took part for a short while at the start, screaming and attacking the intruder, but after a few minutes it usually retired to the nest and took no more notice. Sometimes it left the box altogether; while one such bird built calmly at the nest, another quietly entered and left several times, and yet another preened one of the fighters repeatedly!

In one fight, four individuals, presumably two pairs, were involved. Two were fighting hard, with a third joining in occasionally, when a fourth bird entered. The third bird immediately left the other two and attacked the newcomer, and after five minutes it was driven from the box. The third bird then joined the original fight. After 20 minutes one of the three was pushed out of the box, but the other two continued fighting for some time.

In a long fight the presumed female usually left well before the end, but she sometimes remained throughout a brief fight, after which the mated pair sometimes scuffled mildly with each other for a few moments, as also recorded in the Robin (*Erithacus rubecula*) following ejection of a rival (Lack, 1943). In one case on May 17th, a third Swift entered a nest-box a little before dusk. It was ejected after a brief scuffle, and the owing pair had a slight dispute before settling down. A few minutes later the third bird entered again, it was again ejected and there was again a scuffle between the owing pair, which then settled down for the night at opposite sides of the nest-box, instead of side by side as is usual.

An exceptional fight occurred on July 13th, 1950, in a box with a 25-day-old chick. An adult fed the chick at 1115 hours and remained in the box. At 1121 another adult, its throat-pouch full of food, entered. The parent usually pays little attention to its mate entering with food for the young, but this bird was immediately attacked. A confused fight followed over the hole; after 9 minutes one bird was half out of the hole, and after it had clung there for a further 6 minutes, both fighters fell out. Six minutes later an adult returned, possibly fed the chick, but then quickly settled by the hole preening, and remained preening for 29 minutes, which is very unusual at this stage, and suggests that it had been engaged in the fight. This is the only fight that we have seen with young in the nest, and it was presumably due to an adult entering the wrong box by mistake. The record is of interest in showing that the parent appeared to recognise immediately that the other adult was a stranger, even though it was carrying food for the young.

Some of the Swifts had an aggressive display at us. This was quite distinct from the threat display against other Swifts. The bird would suddenly lunge forwards, flicking the wings partly

open and making a sharp noise on the box. A few adults violently attacked a hand inserted in the box, gripping strongly with their claws, and sometimes drawing blood. The aggressive display with flicked wings was also given by some of the young, normally those whose parents behaved similarly.

#### (9) COURSHIP.

The pair is probably formed when the second bird arrives in the box at the beginning of the season. As already mentioned, the first display between the pair resembles threat, but this subsides. The most characteristic display between the pair is mutual preening, especially of those parts of the body which the bird cannot preen for itself, the throat, nape, and other parts of the head. Mutual preening occurs throughout the breeding season, but is particularly vigorous before the eggs are laid, when it may almost look like pecking. Sometimes it is accompanied by vibration of the wings, and occasionally in the courtship period the birds sit close together in a rather humped position with the feathers fluffed out, excitedly preening and calling. Occasionally one bird has then tried to mount the other, but as the usual behaviour prior to copulation is different, we think that mutual preening is not linked with sexual display in the narrow sense. It is perhaps comparable with the courtship-feeding of the Robin, which likewise continues through much of the breeding season, is quite separate from the pre-copulatory display and perhaps has a 'bond-forming' function (Lack, 1943).

A gentle "clucking" note, lower pitched and much softer than the usual scream, is characteristic of the courtship period. It is not heard from unpaired individuals, but starts as soon as a mate has been obtained and ceases when the eggs are laid. It is uttered by only one of the pair ( ? the female), usually when both are together in the box, but occasionally when one is alone. We have heard this call resumed in midsummer after pairs had lost their eggs, and also in August just after the young had fledged, while in the non-breeders (presumed first-year birds) it is heard throughout the breeding season. It is often heard independently of any particular display, but also accompanies mutual preening, though not copulation.

The duet screaming, already mentioned, is another mutual activity of the pair, a joint threat display at other Swifts flying past. The two birds scream in rapid alternation so that there is no pause between the sounds. This is probably the "sweetee" call mentioned in *The Handbook*, where its double origin was apparently not recognised. We have not determined whether the duetting is always started by the same member of the pair, nor whether the one which screams at a lower pitch than the other is the same as the bird which clucks.



We not infrequently saw copulation in the boxes, but only between 0630 and 0730 and between 1630 and 1830 hours, these being the times of day when Swifts seem most excited, both in their boxes and round the Tower. A characteristic subdued call, between a scream and a cluck, usually but not invariably preceded copulation. The female sat in the normal resting position on the floor of the box. The male than mounted, gripping the female's back with his claws and her nape with his beak. The female elevated the tail and the male twisted round, on one occasion almost lying on his back in the effort. Usually the male mounted three or four times in succession, but sometimes only once. Afterwards, there was usually mutual preening, but clucking was not heard. Copulation was observed only just prior to, and during, the egg-laying period. We, like other observers, have seen what we took to be copulation on the wing, but there has been much dispute as to whether this is effective or not. When we analysed the published records in *Beitrag zur Fortpflanzungsbiologie der Vögel*, where most have appeared, we found that they were seen around either 0700 or 1800 hours, the same times of day at which we observed copulation in the Tower. This coincidence supports the view that Swifts copulate both on the wing and in the nest-hole. Certainly, we did not see copulation in the boxes as often as we should have expected if it happened only there. Moreau (1942) thought that copulation occurred both in the nest-hole and in the air in the White-rumped Swift (*Apus cafer*) of Africa.

Some unexplained behaviour was seen between a pair in the first three weeks of June, 1949. One bird often pursued the other round the box, almost treading on its tail. Twice it mounted, but the under bird then slipped out of the nest-hole, leaving the other within. On several occasions vigorous mutual preening led to display, a chase and then a short fight, after which both birds went out. Twice, a third bird was involved for a time. The birds built a large untidy nest, and the box was later abandoned after a long fight on June 21st. We do not know enough to interpret this behaviour.

#### (10) NEST-BUILDING.

All the nests have been placed at the back of the box, as far from the entrance hole as possible. Knowing this, we at the start placed a little hollow ring of straw at the back of each box, and many pairs lined this ring for their nest, while others built to one side of it. The same nest is used and added to year after year.

Building often starts on the day that the second member of the pair arrives, but sometimes there was a delay of several days. Occasionally, we saw nest material in a box before the birds spent the night there. Both sexes bring material and build it into the nest; their behaviour is indistinguishable. They work quite independently of each other. Thus, if one is on the nest when

the other arrives with material, the sitter does not assist the newcomer. On two occasions when both adults arrived together with material, there was some display and even a brief scuffle before each built it in. The material is normally brought in the beak, but sometimes inside the mouth.

The nest material is caught in the air, hence building is erratic, being most frequent when there is sufficient wind to carry up suitable material into the air. The time between successive visits with material varies greatly. One bird returned with an elm seed only two minutes after leaving the box. Dead grass, hay, straw, dead and green leaves, flower petals, winged seeds, seed fluff, bud sheaths, cocoons, feathers and scraps of paper, including a bus ticket, have been found in the Tower nests. On several occasions, birds have brought fresh poppy petals, which made a vivid splash of colour in the nest. All the birds collected hay in large quantities when a field near by was cut. Just after the local pigeons had had a scrap on the roof, a Swift entered with a pigeon's feather. Another bird brought in a Cabbage White Butterfly (*Pieris brassicae*), making no attempt to eat it, but trying to stick it down to the nest, in which it had great difficulty as the butterfly started a reflex jerking of its wings.

The material is stuck to the nest with saliva, which is used from the start of building, and has even been seen in a box before the birds had collected any material. When secreting saliva, the bird sometimes continues to hold the nest material in its beak and at other times lays it down. It crouches with the head held rather low, sometimes nodding the head or vibrating the whole body, the wings being held partly out. Bill and throat can be seen moving, and saliva appears in sticky threads. The bird usually builds for three to four minutes after bringing material into the box, with pauses of up to half a minute to rest, when the head is often laid on the side of the nest. One bird which was disturbed when building raised its head and swallowed hard. The nest is shaped by the bird turning round in it and scrabbling with its feet.

Building does not cease with the laying of the eggs, but continues right through incubation. As a result, the nest is larger and much neater at the end than at the start of incubation. An adult relieving its mate on the eggs often returns with nest material in its bill, and the incubating bird spends much time pecking round the outside of the nest and sticking down odd pieces of material. The pecking looks rather aimless, and the material seems to be found by touch, not sight. This may be because many natural nest-sites are darker than the Tower boxes, for the latter would seem light enough for the birds to have used their eyes. Heinroth (1911) has suggested that the Swift is long-sighted, and cannot focus on near objects. This may be so, but in that case it is surprising how accurately it feeds its tiny young.



Building stops completely when the young hatch, though we once saw a parent (with chicks three weeks old) playing with a feather in the box. The non-breeders continue building throughout the summer, but spend much less time than the incubating birds in sticking the material down. Because of this, the nests acquire more material but are much less tidy than those of incubating birds. Parents which have lost their eggs also continue building until late into the season.

On July 26th, 1950, a bird was caught with nest material in a box where building had occurred intermittently through the summer. This bird, which we ringed, we supposed was a first-year non-breeder, but two days later it was caught feeding its 21-day-old chicks in another box! On June 4th, the original female of this latter box had been found dead, and the newly laid clutch was thrown out. We guess that the male of the pair then mated up with the presumed first-year bird, which then laid a clutch of eggs and raised a family, but at the same time retained some of its first-year behaviour with reference to the box which it originally occupied. This interpretation may be thought far-fetched, but it is difficult to see why otherwise a bird should build in one box and raise young in another. Further, Weinauer (1947) has recorded a first-year male which paired up with an older female and raised young, but which retained its first-year behaviour in relation to night ascents, then deserting its young for a time.

#### (11) Egg-laying.

The first egg was laid between 7 and 29 days after the start of building. In seven cases, we know that the egg was laid between 0740 and 1115 hours, and in one case between 1715 and 2045 hours, the last being the only occasion on which we have any reason to think that an egg was laid after noon. Breeding seasons and clutch-size are treated elsewhere (Lack, 1951).

On the morning when the egg is laid, we have sometimes found faeces in the box. The adults do not normally defecate in the boxes, and this suggests that the laying female may not leave the box between waking and producing the egg. We have seen her go up to the entrance hole when Swifts were flying round outside, but, if she had not yet laid her egg, she returned quickly to the nest. The male is sometimes present in the box while the female is laying the egg, and in one case he kept trying to sit on the first egg, but the female each time managed to insert herself under him, and he left at 1015 hours. The female then sat quietly, and at 1043 humped her back and looked under her wings, which were held low. She then resumed a normal position, and when she preened at 1100 hours, the second egg could be seen under her. At 1104, she moved the eggs a little with her beak, and seven minutes later she went slowly to the hole and flew out. We

recorded similar behaviour by the laying female on other occasions, including the humped attitude, her turning of the eggs a few minutes after laying, and her departure soon afterwards.

If the clutch is destroyed or ejected, Swifts sometimes, though not usually, lay again. In two cases in which the clutch was lost during incubation, the repeat clutch was started respectively 10 and 17 days later, while another pair that deserted on the day that the first egg hatched laid again 12 days later. In addition, we have three records of pairs which laid one or two eggs but did not incubate them, and later laid again, the new clutch following respectively 6, 24 and 29 days after the previous laying. There was also a remarkable pair which in 1950 laid four eggs in succession at two-day intervals, throwing out the first two but incubating the last two. In the same box in 1951, a pair (? the same) actually laid five eggs in succession, on June 6th, 7th, 9th, 10th and 13th or 14th respectively. Some of these eggs were ejected, but we replaced them in the nest, so that the bird incubated all five eggs, but the only ones to hatch were the last two laid. It is most unusual for a Swift to lay a clutch of more than three, or to lay eggs at a shorter interval than two days, but we saw only two adults in this box, and have no reason to think that two females were involved.

Weinauer (1947) states that Swifts will not accept extra eggs added to their completed clutch, a point that he tested on five occasions. We have in three cases added a third egg to a clutch of two, in two cases on the day that the second egg was laid, and in the third case after six days of incubation, and in each case it was accepted.

#### (12) Ejection of eggs.

Swifts not infrequently ejected one of their eggs, or even the whole clutch. This might happen at any stage between laying and hatching. Usually the ejected egg was left for a while in the box just outside the nest, but later it often disappeared, presumably being dropped out of the entrance hole.

Any cracked egg was normally ejected, and if we replaced it, it was usually ejected again within a day. An infertile egg was sometimes ejected, but it was sometimes retained throughout incubation and for several days after the other egg or eggs had hatched. A fertile egg was also ejected not infrequently. Except on one occasion when a parent disturbed by us accidentally carried an egg between its legs and body on to the floor of the box, we do not know why fertile eggs were ejected. Perhaps the parents are rather careless, in addition to which they seem to have no instinct to bring misplaced eggs back into the nest. When we replaced an ejected egg in the nest, the parents often hatched it successfully, though sometimes they again ejected it. In 1951, a pair threw out one of their eggs seven times during incubation, in five cases



the first egg and in two cases the second egg of their clutch. Each time we replaced the ejected egg, and eventually both hatched. In another case when we replaced an ejected egg several times, the parents deserted.

Swifts sometimes threw out their complete clutch, possibly in one or more cases due to disturbance by us, but usually for no apparent reason. Weitnauer (1947) claims that single eggs and complete clutches may be ejected in abnormally cold weather, and Cutcliffe (1951) also states that eggs tend to be thrown out in bad weather. Our evidence on this point is inconclusive. If the correlation with cold weather is genuine, it might mean either that abnormal cold deranges the reproductive behaviour of the parents, or that cold weather addles the eggs, which are then ejected. There is, however, no evidence for the latter suggestion at present. As mentioned later, the parent Swifts sometimes leave their eggs uncovered for several hours of the day, including in cold weather, but the eggs seem unusually resistant to cooling, and they often hatch out after such treatment. The whole problem of egg ejection, and of the degree to which the eggs can withstand cooling, requires further study.

We have twice seen an egg ejected. A sitting bird was fidgeting in the nest with head down, when an egg suddenly popped out from its flank, but so quickly that we could not see how it was ejected. (Egg-shells are ejected by the foot, and the foot may well have been used in this case also.) In another box, both parents were sitting in a box with a freshly laid but cracked egg on the rim of the nest. One of the birds suddenly picked up the egg in its mouth, and holding it with the long axis at right angles to the beak, ran up with it to the entrance hole, and dropped it near, but not out of, the hole. The egg rolled back towards the nest, but the parents paid no more attention to it at that time, though it vanished later in the day. Moreau (1942) has seen the African *Apus caffer* carrying an egg in its mouth to the nest entrance and dropping it out.

### (13) INCUBATION.

The birds usually start incubating by day when the second egg is laid, but in a clutch of two the first egg often hatches a day before the second, presumably because it receives some incubation on the night before the second egg is laid (see full discussion in Lack, 1951). In May, 1948, several clutches were completed during unusually cold and stormy weather, the parents left their eggs uncovered for much of the day, and the interval between the completion of the clutch and the hatching of the young was 4-5 days longer than usual.

The incubating bird normally sits with its back to the entrance hole. It is continually fidgeting, preening, scratching, vibrating the body, shuffling the eggs or turning them with its bill or feet,

ratting its bill on the side of the box, picking up loose nest material or building it into the nest. If a banger is heard outside, the sitter may turn temporarily to face the entrance hole, and sometimes it even leaves the eggs and looks out of the hole, but usually it returns to the eggs after a few minutes. One bird stood up over its eggs each time that it heard the loud clapping from the Parks near by as successive New Zealand wickets fell to a triumphant University. In very hot weather, the parent sometimes sits in the box without covering the eggs. When the eggs are turned, they can often be heard rattling on the floor of the box, but they seem to come to no harm.

The two parents take turn and turn about on the eggs. The sitter often greets the arrival of its mate with a scream or with very mild threat display as it moves slowly off the eggs. Sometimes it is reluctant to leave, and the newcomer then prods it gently or gradually insinuates its body under that of the sitter. On one occasion when the newcomer was kept waiting, it picked up some grass lying in the box, presumably a displacement reaction. The bird which has been relieved usually sits by the entrance hole for two or three minutes and then flies out. Very occasionally it has not flown out, but has returned and taken its place again on the eggs, relieving the bird which had only just come in. If the newcomer has entered with nest material, it may build it into the nest immediately, or it may settle on the eggs and build later, while incubating. Sometimes, and particularly when the sitter has not been relieved for a long time, it leaves the eggs, and after a pause flies out. The eggs may then be uncovered for an interval varying from one minute to at least 6½ hours. When both parents stay in the box, as in the early morning or in continuous rain, one sits on the eggs while the other often sits close alongside it. We do not know whether they periodically change places on the eggs under these circumstances, nor whether they relieve each other at night.

In 1949, we carried out 4 dawn-to-dusk watches on the incubating birds, relieving each other about as frequently as the parent Swifts. We were able to observe the 11 upper nests in the Tower simultaneously, helped by the fact that the returning parent makes a slight bang as it alights at the hole. In 1950, we carried out 4 watches from 0800 to 1800 hours on one incubating pair, and in 1951, 5 ten-hour watches on up to 10 different nests. We found a ten-hour watch far less tiring than one from dawn to dusk. Altogether, we obtained in this way 58 ten-hour records of incubation, the total being smaller than the previous figures might suggest because not all of the nests mentioned contained eggs on every visit.

The length of time for which each parent sits on the eggs depends primarily on the relieving bird, i.e. the sitting bird normally departs as soon as it is relieved, however short or long



the interval, though occasionally it leaves before being relieved. Under the latter circumstances, the next bird to return is sometimes the one that has been out longest, but occasionally one bird has returned in less than five minutes and the other a few minutes later, suggesting that the sitter left for a few minutes, had a short look round and then returned without feeding. Likewise when both parents have stayed in the box in rainy weather, one of them has sometimes gone out for from 1 to 10 minutes and then returned, presumably without having fed.

For our 58 ten-hour records, the average number of reliefs occurring between 0800 and 1800 hours was 5.2, which means that the average interval for which the parent was away was 115 minutes. The maximum number of reliefs at one nest in the ten hours was 12, the minimum 2, and the interval between successive reliefs (i.e. the length of a sit) varied between 2 and 345 minutes. There were often big differences in the length of individual sits at the same nest on the same day. On the average, the two members of the pair bore an equal share, as found by Weitauer (1947), though Cutcliffe (1951) thought that the female bore the major share. Some pairs consistently relieved each other at more frequent intervals than others. As shown in Table 1, of five pairs watched on three different days in 1949, pair A had consistently the shortest average sit, pair E consistently the longest, and B's average was always shorter than C's. Pair D were more erratic, as were pair F (see footnote).

TABLE 1. AVERAGE LENGTH OF EACH SIT BY 5 PAIRS ON 3 DAYS IN 1949.

PAIR	JUNE 15	JUNE 21	JUNE 25
A	72 mins.	55 mins.	65 mins.
B	79 "	67 "	120 "
C	90 "	74 "	120 "
D	120 "	63 "	93 "
E	149 "	99 "	183 "

NOTES: (i) The averages for pair F were 103 minutes on June 15th and 106 minutes on June 21st, but by June 25th the eggs had hatched.

(ii) Watch from dawn to dusk on June 15th and 25th, but starting only at 0645 on June 21st.

The average length of sit is longer before than after midday, as was particularly clear in the 1949 watches started at dawn. The birds relieve each other at particularly long intervals early in the morning.

In 38 of our 58 ten-hour watches, the eggs were covered by one or other parent throughout the ten hours, and they were left uncovered for only one minute in another case, but in the remaining 19 the eggs were left uncovered for a total varying from 4 to 392 minutes out of the 600. There was much individual variation. Thus on one day, when the eggs in one nest were left uncovered for 172 minutes, another pair brooded continuously. The longest period for which the eggs were uncovered, just over

6½ hours, occurred in cold and squally weather on the day before the eggs hatched; the same pair had brooded continuously throughout an earlier watch. The parents rarely left their eggs uncovered before 1100 hours. Thus considering all our watches, and scoring 1 for each hour in which each nest was left uncovered for at least part of the time, 44 out of 52 records occurred between 1100 and 1700 hours, being very evenly divided over this part of the day, while only 4 occurred between 0800 and 1100 hours and 4 between 1700 and 1800 hours.

Incubation was sometimes intermittent for a day or two after the clutch was completed, but, apart from this, the extent to which the eggs were left uncovered did not seem influenced by the stage of incubation. Indeed, it is difficult to know what causes the observed variations. Surprisingly, weather had no clear influence, possibly because the weather has several rather different effects. One might guess that a brooding parent would be more likely to depart leaving the eggs uncovered, either during very cold weather through becoming hungry before its mate returned, or in very hot weather when the eggs would scarcely require brooding. We might also be thought that the time for which the relieving parent stays out feeding would be shorter in good than bad weather, as feeding is easier in good weather, but our data do not support this view. Great irregularity in the incubation rhythm, and a similar difficulty in relating it to weather or other factors, was found by Moreau (1942) in the African *Apus caffer*.

#### (14) BROODING OF YOUNG.

The eggs usually hatch on consecutive days, as discussed elsewhere (Lack, 1951). The eggshell is sometimes left in or beside the nest, where it gradually disintegrates, but at other times it disappears, presumably being removed from the box by the parents. On one occasion, shortly after a chick had hatched, the brooding adult ejected the eggshell backwards from the nest with a quick movement of one leg.

The parents quickly respond to the presence of a newly hatched chick by bringing food, but the change from incubating to feeding behaviour is gradual, as for the first week of their life the young are brooded almost continuously, each adult still regularly relieving the other on the nest when it returns with food. The time for which each parent broods the young is primarily determined by the incoming bird, and seems to be basically a problem of feeding frequency, which we analysed in our earlier paper, showing the marked influence of the weather (Lack, 1951). After it has been relieved, the brooding parent usually waits for a minute or two by the nest-entrance before flying out. On one occasion when the brooding parent was pushed off the chicks by the relieving bird,



the displaced bird pecked vigorously at nest material, and this also happened once when we removed the chicks for weighing. These were displacement reactions.

In 17 ten-hour watches on broods under a week old, the young were covered for 98 per cent. of the time, and in 11 similar watches on broods in their second week for 52 per cent. of the time, while young more than a fortnight old were covered for 7 per cent. of the time or less. Very wet days were excluded from the above summary, because then the adults sometimes stay in their boxes, and it becomes difficult to tell whether they are really brooding the young or are merely sitting beside or over them. The effect of rain is illustrated by our records from 0800 to 1800 hours on July 20th, 23rd and 25th, 1951. Considering 8 broods over a fortnight old, a parent was in the box with the young for an average of 9 per cent. of the time on July 20th and 2 per cent. on July 25th, both days being fine, but for an average of 78 per cent. of the time on July 23rd, which was very wet. Further, both parents were together in the box for a negligible amount of the time on July 20th and 25th, but for 34 per cent. of the time on July 23rd. It is chiefly in continuous heavy rain that the parents shelter in the boxes in this way. In cold and windy, but dry, weather, when food may also be very scarce, the parents with older young usually stay out hunting.

#### (15) FEEDING OF YOUNG.

The parent returning to the box with food for its young has an enormous bulge just below the beak, due to the mass of insects packed into the throat and stuck together with saliva. There is usually a definite food-ball, though at times the insects adhere together only loosely. On coming to the nest, the adult holds its head low with throat moving and then produces the insects. When the chicks are very small, the adult passes over the food in several successive portions; sometimes one mouthful to each chick, and the feed may last for three or four minutes, as the adult sometimes takes the food back into its own mouth and then produces it again, presumably because the original meal was too large for the chick. When the chicks are older, the food is always passed quickly in one large ball to one of the chicks only.

We on two occasions thought it possible that food passed between a returning adult and its mate brooding the young chicks, but we could not be sure. If it occurred, it may have been by accident, the mouth of the brooding parent getting in the way at the critical moment. We never saw one adult feed the other during incubation, and we wonder whether Wetmayer (1947) is correct in saying that this is occasional, as the billing in mutual preening sometimes looks rather like feeding.

The adults normally bring food for the young every time that they return to the nest, including on the last visit when they come in for the night. If, however, a banger is going the rounds, the parent birds often return to their boxes without bringing food, and then sit in the entrance holes screaming as the intruder flies past. The ready return of these adults, and their similar return in numbers in a sudden shower, suggest that they often hunt for food near their nests.

The chicks are normally fed on the nest itself. This is true even in the later stages, when between feeds the chicks wander about the box and often sit looking out of the entrance hole. On the return of a parent, they dash back to the nest and beg for food. In thatched roofs, we have sometimes found the young wandering for some distance from the original nest, and their habit of returning for the feed perhaps helps to prevent them from straying too far. Very occasionally when the young were exceedingly hungry, they appeared to be fed at the entrance hole by the returning parent, which immediately left again.

The chicks call repeatedly, a plaintive note much weaker than the adult's scream. One was heard before it was out of the egg, the sound being clearly audible six feet from the closed box. Another youngster, found with a damaged wing about a mile from the Tower the day after it had fledged, still gave the typical nestling call when handled. The young beg for food by squeaking and waving the open bill. When they are older, they also pursue the adult round the box with excited flapping of the wings, repeatedly trying to grab its beak in theirs. The begging becomes much more violent when the young are hungry, as during a spell of poor weather, and particularly with broods of three young. The young start to beg as soon as they hear the adult alight at the nest entrance, and when particularly hungry they also react to any other similar noise, such as a sharp gust of wind outside, or a backfire from a car in the road, or a sneeze by the observer, and they then continue the reaction by begging from each other. When excited, also, they often beg from the brooding parent as its mate arrives, and they usually beg when the brooding adult moves off them even though no other adult has entered the box. (The brooding adult of course has no food for them.) After about the first week, the young keep up a quiet high-pitched murmuring throughout the time that the parents stay with them, but not usually when both parents are out.

Very occasionally, presumably because temporarily satisfied, the young did not beg from an incoming parent. With very young chicks, the parent then prodded gently, the young then begged and were fed. We have only four records of an older chick failing to beg. In two cases the adult merely waited for several minutes, after which the chick took the food. In the third case the adult waited for three minutes and then left the box,



still carrying the food. In the fourth case the adult, retaining the food in its throat, preened the chick's throat. It then made some small swallowing movements. The second parent now entered with food. The first parent promptly displayed at it with lifted wing, a most unusual occurrence at this stage of the breeding cycle, and presumably a displacement reaction. The second parent fed one of the chicks while the first parent went to the entrance hole, made more swallowing movements, picked up some faeces, and left.

After it has been fed, the chick sometimes turns away from the adult, calling and shivering its wings, and sometimes it plays with the adult's beak, but there is usually no special behaviour after the feed.

#### (16) RECOGNITION OF NESTLINGS.

Swifts appear unable to recognise their own young individually, or even to be aware of the correct number in their brood. When weighing broods of only one young, we usually placed a member of another brood in the box so that the adult would not return to an empty nest. On several such occasions the returning parent has fed the strange youngster, though in one case it was ten days younger than its own chick and was much less well feathered. We have also added an extra nestling to a brood of one, and in another case to a brood of two, and in both cases the parents successfully raised the foundling with their own family without any apparent disturbance.

More remarkably, after the last chick of a brood of two had fledged at 0720 hours on July 30th, 1950, and while both parents were still out, we inserted a 26-day-old chick in the box. This chick had been deserted by its parents and had been starving for 40 hours. Being only partly feathered, it looked very different from the departed fledgling and it was so feeble that it failed to beg when one of the adults returned to the box a minute after it had been inserted. Indeed, the returning adult failed to notice the chick, and sat by the entrance hole. The adult later screamed at a passing Swift, which roused the chick to beg feebly, and the adult then turned and looked at it. After 50 minutes, the adult moved from the entrance hole to the nest, where it allowed the chick to preen it, and 20 minutes later it left the box. The chick was not visited by either parent until 1850, when one adult entered, but so quietly that we did not see whether it fed it. On the following day, both parents fed the chick normally, and they continued to do so till it fledged 15 days later. The parents had previously fed their own brood for 40 days, and as they normally migrate a few days after the young have fledged, the addition of the strange chick not only prolonged their nest-care by 15 days, but probably postponed their departure on migration by at least as long.

On one occasion, as already mentioned, an adult bringing food into a box with young was attacked and expelled by another adult in the box, presumably because the newcomer had mistaken this box for its own. One wonders whether, had the rightful parent been absent, the stranger would have fed the young. If so, we may well have failed to notice similar cases of mistaken entry elsewhere. We have also four records of an adult Swift bringing food into a box containing no young. One of these birds we caught and ringed (but did not see again), the other three we watched. Each bird came to the back of the box, investigated the nest, poking about in it, then went to the entrance hole and looked out, then returned to the nest. Two of the birds left after 5 minutes, the other after 28 minutes. Each left with its throat still bulging with food, though one had made some small swallowing movements. After one of these departures, the young in the next-door box were fed within half a minute, suggesting that this parent had been the intruder. Such mistakes are probably more frequent at the Tower, with its symmetrical entrance holes, than in natural nesting sites.

#### (17) NEST SANITATION.

We have not seen an adult Swift defecate in the box, and have found fresh droppings from the adults only on the morning when an egg was laid, and occasionally on the first arrival of the birds in May. When the chicks are very young, they defecate over the rim of the nest, but after they are three to four weeks old they often, though not always, go up to the entrance hole, turn round with the cloaca over the hole, and defecate outside. Swifts' nests can be located late in the season by the white splashes outside.

In the early stages, the adults appear to swallow the faeces of the young, but later to carry them away in the throat; it is, however, difficult to be sure. The adults seek for faeces particularly just after they have fed the young, and they peck around the box in the same vague manner as an incubating bird seeking nest material. It seems as though they find the faeces by touch, not sight, and faeces are normally removed only when damp. If in their search the adults touch dry faeces they often ignore them. Although the adults continue to remove some of the faeces up to the time when the young fledge, many faeces get left in the box, which becomes extremely dirty. One bird picked up some faeces to which a feather had stuck, and took the whole lot into its mouth.

#### (18) EXERCISING OF YOUNG.

From the day of hatching, the young can both flap their wings and grip strongly with their claws. Care must be taken in lifting them out of the nest, as they grip so tightly that a claw may be left behind. Very occasionally, a youngster has got pushed out over the edge of the nest on to the floor of the box, and if it is



less than about ten days old, it cannot climb back in again. Surprisingly, the adults do not then feed it, even though it may be only just over the edge of the nest and may beg hard for food; hence it usually dies. We have seen 10-12-day-old nestlings climb back into the nest when pushed out.

At an age of two or three weeks, the young start shuffling round the floor of the box. They take exercise by flapping violently with the wings and jumping up and down, resting every few seconds. Sometimes, the body is tipped forward, the tail spread and the wings vibrated. At other times, the body is pressed against the vertical side of the box, with tail spread and pressed against the floor. Starting when they are about four weeks old, the young do a form of 'press-up', the wings being partly extended and pressed down on the floor, taking the weight, while the body is raised until both it and the feet leave the floor altogether. At first the bird cannot sustain this position, and merely hops up and down, but after a few days it can hold its body clear of the ground for a second or two, and the time gradually increases until, just before fledging, the chicks have held this position for 10 seconds or more.

The chicks take exercise particularly in fine weather and when well fed. In July, 1950, after bad weather and poor feeding, they exercised much less. When badly undernourished, the chicks become torpid and clammy, losing temperature control, as we first noticed in the bad summer of 1946, and they may remain in this state for several days. At first, we thought that such chicks were dying, but they recovered amazingly quickly if supplied with food.

The chicks were first seen to make preening movements when about three weeks old, and thereafter the amount of preening increased. A chick will preen itself, other chicks in the nest and its own parents, who sometimes preen the chicks. The mutual preening of the parents in courtship is perhaps linked with this juvenile behaviour.

#### (19) FLEDGING.

At Oxford most young Swifts left the nest between the third week of July and the third week of August, the latest on September 7th. The young left equally in good and bad weather, departing very gradually, one on one day and one on another, most of them over a period of 3-4 weeks. At least in the years 1948-51, there was no case of a temporary hold-up due to bad weather. Hence the departure of the young was in marked contrast to that of the adults in 1951, described later.

The young Swift leaves the nest fully able to take care of itself, and independent of its parents. This is unusual in birds, particularly in an Order placed close to the Passeriformes. We suppose that the young migrate on the day that they leave the nest. No young Swift has returned to our boxes after fledging, and this was

also the experience of Weinbauer (1947), though Cutcliffe (1951) states that some of the young returned to his nests on the evening after fledging. There are two possible explanations for Cutcliffe's finding. At the nests in thatched roofs near Oxford, we found that the older young sometimes wandered off for several feet under the roofs and might be absent from their nests for a few hours at a time. Possibly Cutcliffe mistook such temporary absences for true departures. Alternatively, Weinbauer's and the Oxford Swifts were breeding in nest-boxes, each entered by one small hole, whereas Cutcliffe's birds bred in a church tower to which there was much easier access all round the tower, so that the young might find their way into the tower to roost and, once in, might recognise where they were. In the African White-rumped Swift (*Apus caffer*) the young do not return to the nests once they have flown (Moreau, 1942), but in the Alpine Swift (*Apus melba*), the young regularly return to roost in the colony after they have fledged, staying for several weeks before migrating (Arn, 1945).

The young normally left the nest in the morning, often before 0800, as also found by Moreau (1942) in African Swifts. We have only one record of a Swift leaving after midday, between 1330 and 1930 hours, but another fledgling capable of flight fell from the nest at 1245, probably by accident during excited movements of the brood. Omitting this last case, we observed five actual departures. As already mentioned, the older young spend much of the day looking out of the nest-hole, and in the last few days before they fledge, they spend most of the day there. In one case, the parent left the box at 0825 hours. The chick sat looking out of the entrance hole. It spread its wings and tail, and tipped forward with its head out of the hole, but then turned back into the box. This performance it repeated. Finally, at 0835, it inserted its right wing out of the hole and gently tipped itself out. Another bird behaved very similarly. At 0810, it was found sitting with its head out of the hole and its wings and tail partly spread. It then stretched its wings and preened them, moved back from the hole, and went up to it again. The body feathers were alternately fluffed out and flattened, giving the appearance of deep breathing, and the tail was moved up and down. The youngster then stretched its wings above its back, and tipped forward half out of the hole, but hesitated to make the final effort, and scrambled awkwardly back into the box, supporting itself on its wings. After sitting by the entrance hole for about a minute, it slipped out.

In several other cases we saw similar behaviour prior to fledging, but as the preliminary hesitations occasionally last for several hours, or even for more than a day, we have not always stayed to watch the final departure. In another case, a fledgling launched



itself quietly from the hole without our having seen any preliminary movements. Twice, we saw a fledgling leave, possibly by accident during the excitement, when bangers were going round the Tower.

When another nesting is present in the box, it seems unaffected by the departure of its companion. It sometimes leaves on the same morning, but often not until from one to several days later. All the young referred to above fledged when both parents were out of the box, and this is probably normal. Hence the parent Swift is unaware that the young bird has gone, and on its next visit it returns as usual with food to the now empty box. We have several times watched its subsequent behaviour. The adult moved on to and then off the nest several times, walking rather high on its feet as in threat display, then stretched the wings, yawned repeatedly, poked the nest with its beak and displayed at it with one wing raised; presumably a series of displacement reactions. After this, the bird usually sat about half way up the box, facing towards the entrance. Two of the birds then made violent swallowing movements, involving great effort, with the eyes partly closed, but a third left the box still carrying an intact food pouch. Four of the adults left the box after 8-10 minutes, another after 15 minutes, but we could not always see what they did with the food ball.

If in the later stages a nesting is deserted by its parents, it usually stays in the nest for several days, but eventually it jumps out, even though its wings are not fully grown. It may be able to fly a short distance, but it then comes to earth and cannot rise again. The widespread belief that a Swift cannot take off from the ground is presumably due to people finding these premature fledglings, which look fully feathered, though the wings are not full grown. An adult Swift can easily rise from a flat surface, as we have tested several times.

#### (20) DEPARTURE OF ADULTS.

The departure of the adult Swifts was studied only in 1951, by a regular roosting check each evening from July 30th to August 18th inclusive. In this period, we recorded the day of departure for 25 parents which raised young and for 8 other adults which had no young. A few other individuals were excluded, either because we could not see clearly into their boxes, or because their departure might have been due to our disturbing them.

At least in 1951, the adult Swifts, unlike the fledglings, tended to depart in waves. Thus 30 out of the 33 recorded departures took place on only 6 of the 20 days of the watch: 5 on August 3rd and 5 on the 4th, then 7 on the 8th and 4 on the 9th, and finally 7 on the 17th and 2 on the 18th. The other 3 individuals left singly on intervening days. The gap of seven days between August 9th and 17th, during which only two individuals left, was probably caused by the weather. The first five days were very

bad, the next two were very fine and were presumably used by the Swifts to feed up prior to leaving. The early morning of August 17th was overcast and rain started at 0745 hours, lasting the rest of the morning. A flock of over a hundred Swifts gradually collected over Oxford and at about 0800 hours, after circling and apparently feeding, most of them set off between S.W. and S.S.W., rising as they went. Some returned and joined another party of about 50, which then left in the same direction. That evening, it was found that 7 out of the 9 'free' adults remaining in the Tower had departed, the other two going next day, leaving only the parents still feeding young.

We had rather expected that the non-breeders would leave earlier than parents which had raised young, but this did not happen during the main period of departures. Thus parents and non-breeders were included in similar proportions in both the first exodus on August 3rd-4th and the last on August 17th. When the main departures were completed on August 18th, however, the only birds which remained were two pairs feeding late broods, and these stayed for 2½ weeks longer, leaving immediately after their young fledged in the first week of September.

In 4 out of 17 pairs both individuals left on the same day, while in the rest one of the pair left 1 to 5 days after its mate. The parents normally left a few days after the last of their young, the commonest interval being 5 days, the longest 7, 9, 13 and 16 days. 170 adults left on the same day as the last of their young. In 4 cases one, but never both, of the parents left 1 or 2 days before the last of the brood departed, but in these cases only one of the young was still left. In a brood of one, one of the parents left 5 days before the nesting. The average interval between the departure of the last nesting in each brood and of its parents was 3 days for the first and 5 days for the second parent (reckoning as minus those parents which left before their young).

Weinauer (1947) states that the parent Swifts usually left on the same day as their young, though a few stayed for another night or two, and that one parent often left several days before the young fledged, as also reported by other workers (references in Koskimies, 1950). This was contrary to our experience in 1951. Further, Swifts on autumn migration tend to weigh much more than breeding adults, suggesting that they have had time to put on weight before departure (Lack, 1951). The extent to which the parents leave their young before they are fledged evidently needs further study. It would be highly remarkable if the parents frequently desert their broods before the end of the normal breeding season, and then migrate before putting on fat; though we can understand how one of the two parents might leave a single chick before the end, as in good weather one chick needs only one parent to feed it. We found that parent Swifts readily



desert through disturbance in the final stages, and we wonder whether many of the reported cases of Swifts abandoning their young may not have been caused inadvertently by the observer.

(21) WORK BY OTHERS.

The literature on the breeding of the Common Swift has been surveyed by Koskimies (1950) and we ourselves gave many references in our earlier paper (Lack, 1951). Hence in the present paper, we have not thought it necessary to refer to the work of others on *Apus apus* except where we seriously differ. We ought, therefore, to record that, except for the few points discussed in the text, we are in full agreement with the conclusions reached by Weirner (1947) in his long and important paper, and also with Cutcliffe (1951). The review of breeding habits by Koskimies (1950) is another matter, as the author seems to us to have been uncritical in both his acceptance and his interpretation of the work of others. In addition to various minor errors in emphasis, he includes the following statements which we consider erroneous (the page references are to Koskimies' paper): there is an afternoon rest (p. 14); there is probably no feed on the last return to the nest at roosting time (p. 21); building lasts 8 days (p. 55); incubation starts only after the second egg is laid (p. 60); most of the young fledge at about the same date in any one year (pp. 65, 75); the fledging period is longer in broods of larger size (p. 66, apparently based on two broods in different years studied by v. Boxberger, though Koskimies quotes the quantitative evidence of Moreau to the contrary); the young depart on migration in waves (p. 75); the whole colony tends to leave together (p. 76). The above statements are mainly derived from others, but as the author's aim was a critical review, it is unfortunate that he should have accepted all of them and based arguments on them.

SUMMARY.

- (1) A colony of Swifts was induced to breed in nest-boxes with glass backs.
- (2) Each year about 20 pairs laid eggs and several non-breeding pairs (? in their first year) occupied other boxes.
- (3) The adults arrived in spring and departed in autumn over about three weeks. There was sometimes a hold-up during part of this time. The two members of each pair usually arrived and departed separately.
- (4) Each pair normally roosted in their box throughout the summer.
- (5) The adults visit the boxes at any hour of the day, but especially around 0730 and 1800 hours. They sometimes shelter in the boxes in rain.
- (6) In fine weather single individuals or small parties, the "bangers", may fly up to and brush against the boxes. They are treated as strangers by the owing birds.

(7) When another Swift enters a box, it is often greeted with incipient threat display. If it is the bird's own mate, this quickly gives place to mutual preening. If it is a stranger, a fight may follow.

(8) Violent fights were seen, the birds remaining grappled for up to five hours, but no serious harm usually resulted.

(9) Copulation occurs in the boxes, with little preliminary display.

(10) Nest-building starts on the day that the pair is formed and continues until the end of incubation. Non-breeders build throughout the summer. The material is stuck down with saliva.

(11) Egg-laying is described. If a clutch is lost, a repeat clutch sometimes follows.

(12) Swifts sometimes eject part or the whole of their clutch. The ejected eggs are sometimes fertile, and the reasons for the habit are obscure.

(13) The parents take an equal share in incubation. The time of each sit varied from 2 to 345 minutes. The eggs were sometimes left uncovered during the day for periods of up to 6½ hours. The influence of weather on the incubation rhythm is obscure.

(14) The parents brood the young by day nearly continuously in the first week and for about half the time in the second week, but very little thereafter.

(15) The feeding parent brings a mass of insects stuck together with saliva. This is normally passed as a single food-ball to one nestling, but with very small nestlings it is divided.

(16) Parent Swifts readily adopt a strange nestling added to, or in place of, their own.

(17) The parents remove some of the faeces, but many others are left in the box. The older nestlings sometimes defecate from the hole.

(18) The older nestlings exercise their wings vigorously, and have a curious form of "press-up".

(19) Fledging is described. Nearly all the departures were in the morning, and no fledgling returned to its box.

(20) At least in 1951, most of the parent Swifts stayed for several days after the departure of their young.

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