THE NEST AS A DORMITORY

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In most parts of the world, the great majority of birds roost with no better protection from the elements than foliage can give them, or even, as in sea fowl which gather to rest on barren isles, under the open sky. Some birds sleep on ponds and lakes, and even on the sea. A few birds, however, retire at nightfall into nests, which they have made for themselves or perhaps taken from some other species. When one contemplates a tropical wren sleeping in the nest that it has built, or a woodpecker lodging in a chamber that it has carved in a dead tree, it appears so much more comfortable, so much better protected from the weather and prowling animals, that one asks why this manner of sleeping is exceptional among birds as a whole, why it has not been more widely adopted by them. By what steps did the habit of sleeping in dormitories arise? What environmental factors favour their use and what conditions discourage it? What disadvantages might dormitories have to weigh against certain obvious advantages?

I first became interested in this problem years ago, in high tropical mountains where nights were so piercingly cold that I surmised that birds would seek whatever protection they could find. Later I discovered that even in tropical lowlands many birds use dormitories—apparently a larger proportion of the total number of species than in extra-tropical regions. A long residence in the tropics has favoured investigation of the sleeping habits of birds; for the relatively brief period of morning and evening twilight shortens the attentive watches that one must make to see the birds leave or enter their sleeping places. Moreover, at low latitudes this study does not demand such early rising, or staying out so late in the evening, as it does in summer in the temperate or arctic zones, nor yet such exposure to inclement weather as it does in winter in these regions.

In the present paper we shall understand by the word " nest " either a structure or enclosed space actually used by a bird for breeding or one which resembles its breeding nest, even if it is simpler or more carelessly made. Thus if a bird rears its young in an open, cup-like nest but in inclement weather seeks protection in an enclosed space, its sleeping habits are beyond the scope of our present study, for its dormitory bears no resemblance to its breeding nest. Even with this limitation, the subject is so large that only a general survey is here possible. For details, the reader must be referred to published accounts of the species treated.

TYPES OF SLEEPING ARRANGEMENTS

Were one writing a book on this subject, one would probably present the data in taxonomic sequence, then try to trace the evolution of the various types of sleeping arrangements. In a short paper, the material must be arranged in accordance with a theory or interpretation that is the result of its analysis. Hence at the outset we must try to decide what are the probable stages by which the habit of using nests as dormitories arose in birds, then attempt to support this theory by the citation of examples.

When we recall that only a small proportion of the birds which prepare nests for their eggs use them or similar structures for sleeping, we must conclude that the primary purpose of nests is for hatching eggs and rearing young, and that some species later discovered that these structures have advantages as lodgings. For this secondary use, only roofed or covered nests are, in general, attractive to birds. Open nests protect

the eggs and young because the brooding parent itself serves as a roof above them. The parent is no less exposed to rain than when it roosts amid the foliage; indeed, in wet weather it may stay drier on a perch than with sodden nest material around it. If birds roost in open nests, it must be because they require protection from below rather than from above. The chief users of open nests for sleeping are the rails, coots, and gallinules, who find it convenient to rest on a platform above the wet ground or water where many members of the Rallidae live. Another bird which constructs an open dormitory inhabits dry rather than wet areas. The Curved-billed Thrasher *Toxostoma curvirostre* of the deserts of Mexico and adjacent parts of the United States sleeps on an open nest in a cholla cactus; the sharp thorns protect the thrasher from prowling quadrupeds and the platform of twigs and weed stems protects it from the thorns (Bent 1948 : 396–397). Aside from these, almost the only arboreal birds that I have found, or read about, using open nests as dormitories are certain Southern House Wrens *Troglodytes musculus* who slept in old, cup-like nests made by other birds, apparently because they could not find suitable nooks or crannies such as they prefer.

Most birds breed in open nests but, except in special circumstances, they do not sleep in such nests at times when they neither incubate nor brood. Of the birds which rear their families in roofed or closed nests, a substantial proportion use these structures as dormitories. Although it seems obvious that the primary use of nests is as receptacles for eggs, and a few of them have secondarily come to serve as dormitories, might it not be that the refinement of covering over the nest was first adopted by birds which needed a dry place for sleeping, and that later these birds constructed nests on the improved model for rearing their families? If this were true, we would expect to find in some groups of birds, especially those that had recently acquired the dormitory habit, species that sleep in nests that are better enclosed than those in which they breed. Since I am am aware of no species in which such a condition prevails, but of a number which build covered nests that are not used as dormitories, I must conclude that the more or less elaborate structures in which some birds sleep were first built to contain their eggs and were later adopted as dormitories. Or perhaps the use of a somewhat adequately roofed nest for sleeping as well as for breeding gave impetus to its further elaboration.

From this point of departure, we may trace successive stages in the development of the dormitory habit, as follows:

1. Only the breeding nest is used as a dormitory and for only part of the year.
   - A. By the female only.
   - B. By both parents, sometimes also by their helpers.
   - C. By fledged young, alone or with one or both parents and sometimes also with helpers.
2. Nests or enclosed spaces similar to those in which the bird breeds are made or acquired for use as dormitories throughout the year.
   - A. By self-supporting birds singly.
   - B. By self-supporting birds in pairs.
   - C. By parents and dependent young.
   - D. By parents and self-supporting young.
   - E. By larger groups.

The first point to be noticed is that only in the species included in the second group (2 A-E) is the dormitory habit fully developed. Birds which use their breeding nests for sleeping, but do not at least occasionally build or acquire similar structures for this special purpose, cannot always sleep in snug shelters throughout the year; for nests built of vegetable materials in trees or bushes decay in wet weather, trees which contain cavities often fall, burrows in banks may collapse, and shelters of all these classes may be taken from the original occupants by a more powerful bird or mammal.

I am not aware of any family of birds which exemplifies all the stages from 1A to 2D or 2E; but numerous examples of each of these classes are available, and some families, such as the woodpeckers and wrens, illustrate segments of this developmental sequence.

1*A*. *The female uses the breeding nest as a domitory.* Sometimes we find a bird, usually the female, passing the night in a newly completed nest before the first egg is laid, or even in an unfinished nest, and this appears to be more frequent in covered than in open structures. Such behaviour has been reported for the Great Tit *Parus major* (Kluijver 1950 : 102), the Black-capped Chickadee *P. atricapillus* (Odum 1942 : 527), the Violet-green Swallow *Tachycineta thalassina* (Combellack 1954 : 437), the Eastern Phoebe *Sayornis phoebe* (Sherman 1952 : 97), and other birds. A Sulphur-rumped Myiobius *Myiobius sulphureipygius* slept in her well-enclosed pensile nest four or more nights before she laid her first egg.

In another American flycatcher, the Sulphury Flat-bill *Tolmomyias sulphurescens*, the female uses her nest as a dormitory for a far longer period than I have known the myiobius to do. This flat-bill builds a retort-shaped structure which is usually composed of tough, blackish fibres and hangs from the extremity of a slender, drooping twig or vine, from about 6 to 20 feet above the ground, at the woodland's edge or in a shady pasture or plantation. The rounded chamber which occupies the body of the retort is reached through the downwardly directed spout, which the flycatcher enters by means of an upward dart. Working without help from her mate, the female takes two or three weeks to construct this remarkable nest, and as it approaches completion she sleeps in it. By the time she lays her first egg, she has already passed from seven to ten nights in her nest. She continues to sleep in the nest throughout the period of laying, the 17 or 18 days of the incubation period, and the 22 to 24 days of the nestling period. After the fledglings take wing, they do not return to roost in the nest, but their mother continues to do so. I have known a Sulphury Flat-bill to lodge in her nest for nearly four months after the departure of the single brood that she rears here in the valley of El General; but under almost daily rains most nests become dilapidated sooner than this, or else some other small bird takes them to rear its brood.

I am fairly certain that after her old nest becomes untenable the flat-bill does not build herself another dormitory, for until the approach of the following breeding season no new structures appear among the trees near our house, where the old misshapen ones still hang conspicuously. Female Sulphury Flat-bills apparently roost amid the foliage from August or September, if not earlier, until the new breeding nests near completion the following March or April. In the wettest and coolest months, they lack dormitories; and the males seem to be without them at all seasons. This American flycatcher, then, exemplifies an early stage in the evolution of the dormitory habit: lodging in the breeding nest as long as it holds its shape, without the construction of special nests for sleeping. As we shall see, the Eye-ringed Flat-bill *Rhynchocyclus brevirostris*, which builds a similar nest, has advanced a step farther in the use of dormitories (Skutch 1956 b, 1960).

1*B*. *Both parents sleep in the breeding nest, sometimes with their helpers.* Sometimes both parents pass the night in the breeding nest while it contains eggs, and they do this even more frequently after the nestlings hatch. Since it is improbable that more than one parent is needed for incubating or brooding, the second is evidently using the nest as a lodging. Moreover, in a number of species, the mated pair sleep in the same nest not only while they are rearing a family, but throughout the year. And those which use only the breeding nest as a dormitory are likely to begin lodging in it before the first egg is laid. It is this last class which interests us at present.

In the Black-eared Bushtit *Psaltriparus melanotis* of the Guatemalan highlands, in the dry season the male and female together build an exquisite pensile pouch, which is composed of soft downy materials and encrusted over the outside with foliaceous lichens. The entrance is a sideward-facing round hole in the hooded top of the pouch. As the

nest nears completion, both sexes take advantage of it to protect themselves from the frosty night air. Throughout the incubation period they continue to sleep with the four white eggs. In this diminutive tit, males are far more numerous than females, and after the nestlings hatch, some of those which remain unmated help the parents to attend the nestlings. At nightfall, these helpers often join the parents in the nest. For a while, one pouch sheltered four nestlings, two parents, and two male assistants. After the young take wing, the nests remain deserted, and all the bushtits roost amid foliage through the cold and often rainy nights of the wet season. The downy pouches now become sodden and would be unhealthful dormitories. No new ones are built until the following breeding season approaches (Skutch 1935, 1960).

A similar situation is found in the Common Bushtit *Psaltriparus minimus* of the western United States and the Long-tailed Tit *Aegithalos caudatus* of Europe. In the former, four adults have been found sleeping with the eggs, but after the breeding season these bushtits roost in trees (Bent 1946 : 449). In the Long-tailed Tit, male and female sleep in the oval, feather-lined breeding nest, beginning before it is finished and continuing until the young fly (Owen 1945). But in winter these tiny birds, instead of providing snug nests for themselves, usually roost in compact rows or balls in trees and thickets (Lack & Lack 1958 : 2).

The Common Swift *Apus apus* of Europe begins, before the eggs are laid, to roost in its nest space, a cleft in a precipice, a cranny in a building, or a nest box; and both parents continue to sleep there till their nestlings fly. They also enter their nests to escape rain. After the young swifts leave, the parents may lodge in the nest for a few additional nights, but not the young. Little is known about the way the Common Swifts sleep after they leave their breeding areas, but there is growing evidence that they may, at least on occasions, spend the whole night high in the air (Lack 1956 a, b).

In Tanganyika, the White-rumped Swift *Micropus caffer* often breeds in the closed, mud-walled nests which Abyssinian Swallows *Hirundo abyssinicus* attach to the sides of buildings, in the shelter of the eaves. The swifts line the lower half of the nest's inner wall with feathers and plant down, which they glue in place with their saliva. At night both the male and the female swifts sleep in the remodelled swallow's nest and continue to do so till the end of the nestling period. On quitting the nest, the young promptly fly out of sight and appear not to return to the nest again. The parents, however, continue to sleep in it throughout the breeding season that occupies more than half the year, and in which three broods may be reared (Moreau 1942 a). In another African swift, *Colletoptera affinis*, both parents also sleep in the nest and the fledged young fail to return to it (Moreau 1942 b). Later we shall notice some swifts in which the young do return to sleep with their parents.

In the Brown-headed Nuthatch *Sitta pusilla* of the southeastern United States, both parents may roost in the nest cavity, beginning before the eggs are laid and continuing until the young are nearly fledged. After the young emerge from the hole, they and their parents roost amid vegetation rather than in a cavity. On a cold December night, however, four were found sleeping in a nest box (Norris 1958). This species adumbrates the more consistent use of dormitories that we shall find in the Pygmy Nuthatch *Sitta pygmaea*. (For additional instances, see the Appendix.)

1*C*. *The young return to sleep in the nest which they have just left.* Most of my examples of the return of fully fledged young birds to sleep in the nest in which they were hatched and reared are of species which build dormitories, hence they come later in our classification. It seems that birds which use only the breeding nest, or the space that held it, as a lodging rarely lead their fledglings to a closed sleeping place; but in a number of instances in which it is stated that the young return to sleep in their nest, we lack information about their roosting habits later in the year. Among these is the Firewood-gatherer *Anumbius acuticaudatus* of southern South America, of which the young remain

with their parents for three or four months, the whole family sleeping in the old nest, a very bulky structure of interlaced sticks that is entered through a narrow passageway (Hudson 1920, 1 : 224). Possibly the Firewood-gatherer sleeps in nests throughout the year and so should be placed later in our classification, but I have found no definite statement on this point.

In the Chimney Swift *Chaetura pelagica* of North America, the male and female sleep on the bracket-like nest attached to the inner wall of a chimney or in some similar situation, and frequently a helper or two rest close by them (Kendeigh 1952 : 98; Dexter 1952 : 135). After the young have taken their first flights, the whole family returns to roost in the chimney for about a fortnight. Then for another week or ten days only two individuals, evidently the parents, enter the chimney for the night (Sherman 1952 : 50). While migrating, hundreds or thousands of Chimney Swifts may pass the night in a disused factory chimney or a hollow tree. In the African Palm Swift *Cypselus parvus*, the two parents sleep clinging upright side by side on their narrow bracket, which is glued to the surface of a drooping dead palm frond. After their first flights, some young birds return to roost on the nest with their parents for a night or two, but other individuals do not come back (Moreau 1941).

In numerous swallows, both parents sleep in the breeding nest if it is a closed structure; or if it is cup-shaped and placed in a burrow or some sheltered nook in a building or cliff, one parent sleeps on the eggs or young while the other rests on the rim, sometimes with its breast above its mate. Among swallows which sleep together in this fashion are the Barn Swallow *Hirundo rustica* (Bent 1942 : 448), Wire-tailed Swallow *H. smithii* (Moreau 1939 : 122), Purple Martin *Progne subis* (Allen & Nice 1952 : 632), Cliff Swallow *Petrochelidon pyrrhonota* (Mayhew 1958 : 23), Dusky Sand Martin *Riparia paludicola* (Van Someren 1956 : 378), House Martin *Delichon urbica* (Witherby *et al.* 1938, 2 : 235–238), Blue-and-white Swallow *Pygochelidon cyanoleuca* (Skutch 1952). In the Black-capped Swallow *Notiochelidon pileata*, the second parent slept in the burrow, at least after the eggs hatched (Skutch 1960).

In a number of swallows, the fledglings return to sleep in their nest for at least a few nights. These include the Barn Swallow (Bent 1942 : 449; Hosking & Newberry 1946 : 41, etc.), Cliff Swallow (Mayhew 1958 : 25), Purple Martin (Bent 1942 : 495 ; Cater 1944 : 16), and Grey-breasted Martin *Progne chalybea* (Beebe, Hartley & Howes 1917 : 332, and my observations). In the House Martin, fledged young of two earlier broods may sleep with the nestlings of the third brood (Witherby *et al.* 1938, 2 : 235–238). In the Tree Swallow *Iridoprocne bicolor* and the Violet-green Swallow *Tachycineta thalassina* the behaviour of the nestlings is variable; some return to sleep in their nests and others do not (Bent 1942 : 390; Edson 1943 : 400). In the Bank Swallow or Sand Martin *Riparia riparia*, the fledglings are as likely to enter a neighbouring burrow as that in which they were reared, and those of two or three broods may sleep in the same tunnel (Stoner 1942). Most of these swallows are migratory, and soon after the young can fly they and their parents gather to roost in trees or marsh vegetation before they leave for warmer regions. Some of those which are permanent residents will receive more attention under another heading.

The fledglings of some hole-nesting thrushes may also return to sleep in their nests. A young Red-breasted Chat *Oenanthe heuglini* retired at dusk into the underground hole where it was reared (Macgregor 1950). Juvenile Wheatears *O. oenanthe* may enter burrows near that in which they hatched (Conder 1956).

In the Grey-headed Waxbill *Coccopygia melanotis* of East Africa, the parents and fledglings return to roost in the nest for a few nights, although afterward they take shelter in a dense bush or small tree. The same appears to be true of the Crimson-cheeked Blue Waxbill *Uraeginthus bengalus* (Van Someren 1956 : 490, 500–501).

In numerous other birds, the return of the young to sleep in the nest seems to be related not to the dormitory habit, but to the gradual manner in which they sever connection with their nursery. In a number of raptors, herons, ibises, and other large birds that breed in open structures in trees, on cliffs, or on the ground, the young may hop or flit beyond their nest for distances which increase daily as they grow in strength, after each excursion returning to rest or sleep in it, until they are strong enough to fly for considerable distances. Exceptionally, a fledgling dove, humming-bird, American flycatcher, jay, or finch will return to pass another night or two in its open nest, and it is more likely to do this if another member of its brood remains there.

2*A*. *Self-supporting birds sleep singly in dormitories throughout the year.* The Eye-ringed Flat-bill of Central America appears to represent the next step in the developmental sequence. Although it is probably not closely related to the Sulphury Flat-bill, like the latter it attaches a pensile, retort-shaped nest to a slender, drooping shoot. But the Eye-ringed Flat-bill's nest is bulkier, for it contains dead leaves and other coarse pieces of vegetation in addition to fibres. At all seasons, I have found these solitary flycatchers sleeping singly in these hanging structures, some of which have scarcely any entrance tube, while the chamber is so shallow that an egg would probably roll out, so that they could not be used for breeding. Unfortunately, the sexes of the Eye-ringed Flat-bill are indistinguishable by appearance and voice, and I do not know whether both build and use these dormitories. A female slept for a few nights in a nest which her young had just vacated, but they failed to return to it. The Olivaceous Flat-bill *Rhynchocyclus olivaceus* of Panama and South America sleeps singly in bulky nests which closely resemble those of the northern species (Skutch 1960).

One of the best-known representatives of this class is the Bananaquit *Coereba flaveola*, which has been carefully studied in three widely separated parts of its vast range (Skutch 1954, Biaggi 1955, Gross 1958). This tiny yellow-breasted honeycreeper builds of grass blades and similar materials a small, roughly globular nest with a round doorway that faces obliquely downward. Some nests, especially those which will be used for breeding, are built by both sexes, whereas others are made by a single individual. Throughout the year, adults sleep singly in these nests, which they replace with new structures when the old ones become dilapidated. If one member of a pair tries to join its mate in the nest, a struggle ensues and one is ousted. After the departure of the young, the female may continue to sleep in the breeding nest, leaving the fledglings outside. Here they roost until they can find an abandoned nest of a Bananaquit or a wren; or until, while still in dull juvenal plumage, each can make a dormitory for itself. If a juvenal bird builds in the territory of an adult of its kind, the latter may evict the youngster and occupy the nest itself.

A similar situation appears to exist in the Chinchirigüí Wren *Thryothorus modestus* of Central America. Although in the Bananaquit there is no constant, pronounced difference between nests used for breeding and those built solely as dormitories, in this wren the sleeping nests, flimsy horizontal pockets with an opening at one end, are too shallow to hold eggs and are readily distinguished from the deeper, more substantial breeding nests. Adults sleep singly at all seasons. As far as I can learn, the parents do not lead their fledglings to a dormitory; and I once found a young Chinchirigüí lodging alone in an abandoned nest of a Bananaquit. But because this wren inhabits exceedingly dense second-growth thickets, I am not so certain that the parents neglect to install their fledglings in a dormitory, as I am in the case of the Bananaquit (Skutch 1940, 1960).

There is no doubt, however, that many woodpeckers of both the Old World and the New are solitary sleepers and fail to provide a shelter for their fledglings. Here belong the Red-crowned Woodpecker *Centurus rubricapillus*, Hairy Woodpecker *Dendrocopus*

villosus, Lineated Woodpecker *Dryocopus lineatus* (Skutch 1943), Golden-olive Woodpecker *Piculus rubiginosus* (Skutch 1956 a), Ivory-billed Woodpecker *Campephilus principalis* (Tanner 1941), Northern Flicker *Colaptes auratus* (Sherman 1952), Black Woodpecker *Dryocopus martius* (Sielmann 1958), and apparently numerous other species. In the non-breeding season, the male woodpecker carves new holes for himself more frequently than his mate, who is often content to use the cavity that he had abandoned, and whose lodging is often very dilapidated. Since the male frequently has the sounder hole, it is not surprising that the female often lays her eggs in it in preference to her own; although if need be they join forces to excavate a new breeding nest. With rare exceptions, the male alone stays with the eggs and nestlings through the night, although by day both sexes incubate and brood by turns. If a fledgling Red-crowned Woodpecker tries to join either of its parents in the adult's dormitory, it is sternly repulsed; and if a parent coming to its hole finds a young bird already within, it evicts the youngster. Hence the fledglings must sleep clinging to the outside of a trunk until each can find an old hole no longer in use, or until it can carve one for itself. Even in the cold highlands, I have watched young Hairy Woodpeckers settle down in the open on wet evenings, while their parents retired into their shelters (Skutch 1955). Certain other woodpeckers, however, carefully lead their fledglings to their dormitory (see below, under 2D).

In this class belong also the woodcreepers or woodhewers of tropical America, slender brown birds that hunt over trees much in the manner of the Certhiidae, which they superficially resemble, although most of them are larger. The best-known representatives of this family are the Streaked-headed Woodcreeper *Lepidocolaptes souleyetii* and the Allied or Spotted-crowned Woodcreeper *L. affinis* (Skutch 1945 a). Adults sleep singly at all seasons, sometimes in old woodpeckers' holes but more often in a less conspicuous cranny resulting from decay, high in a tree. Woodcreepers go to rest after the light has grown so dim that their brown bodies are almost indistinguishable from the trunks up which they climb, and they dart forth in the dim light of daybreak. The fledglings are not led back to the hole in which they were reared, and as far as I can discover they sleep in the open until they find crannies to shelter them. The sleeping habits of the Plain Xenops *Xenops minutus*, a diminutive brown ovenbird widespread in tropical America, are similar to those of the woodcreepers. As in the latter, when one tries to enter a cavity in a tree with another, apparently its mate, it is vigorously repulsed.

In a number of weavers, including the Golden-crowned Weaver *Othyphantes reichenowi*, Spectacled Weaver *Hyphanturgus ocularis*, Masked Red Weaver *Anaplectes melanotis*, and Cardinal Weaver Finch *Quelea cardinalis*, the male sleeps alone in an unlined nest while his mate incubates (Van Someren 1956 : 454–462). Possibly these East African birds should be placed in this class, but without information on their roosting habits throughout the year, and on the way the fledglings sleep, they cannot be definitely allocated.

2*B*. *Self-supporting birds sleep in pairs* (*without fledged young*) *throughout the year.* The motmots are a lowland family most abundant in hot, arid regions of nothern Central America and southern Mexico; but the Blue-throated Green Motmot *Aspatha gularis* is resident in the highlands of Guatemala and adjacent countries up to about 10,000 feet. This retiring motmot, which lacks the racquet-like central tail-feathers of most of its relatives, finds protection from the frigid night air of the mountains by sleeping throughout the year in long and often very crooked burrows that the male and female together dig in roadside banks and other vertical exposures of earth. These tunnels are excavated around the end of June, about a month after the single annual brood has taken wing, but they do not shelter the young from the cold nocturnal rains that are frequent at this season. The parents retire into these new burrows in the evening twilight; the young appear to roost in the open until they can provide lodgings for themselves.

The mated pair of motmots continue to sleep together in the same burrow through the remainder of the wet season and through the frosty nights of the dry season, which begins in October. They slumber pressed so closely together that they form a single mass of fluffy green plumage. Rarely, in the non-breeding season, one sleeps alone or three individuals sleep together, probably in consequence of the disruption of a pair by death. Early in the following April, the female lays three eggs in the burrow which has already served as a dormitory for about nine months. The pair continue to sleep in it while they incubate their eggs and rear their young. After the latter are about three weeks old, one or both parents may cease to pass the night with them, but in other pairs both parents continue to lodge in the burrow. After the young emerge at the age of about a month, the parents continue to sleep in the burrow; or if they have been roosting elsewhere for the last week or so, they may now resume their old habit. But the burrow has been fouled by the nestlings' droppings, for motmots give no attention to sanitation. Hence, at their earliest opportunity, the parents dig new tunnels for themselves (Skutch 1945 b).

Since in this motmot the eggs are laid in a burrow which has long served as a lodging, it appears that the dormitory has become the breeding nest, rather than the reverse. But, at lower altitudes, another species, the Blue-diademed Motmot *Momotus momota*, may begin to dig its burrow nearly half a year before the eggs are laid, although it has not been found sleeping in a tunnel before the breeding season. Apparently it was from a family propensity to begin the preparation of the nest burrow long before the advent of the nesting season that the Blue-throated Green Motmot's peculiar sleeping arrangements have evolved, as an adaptation to the cool highlands. No lowland motmot is known to use its burrow as a dormitory.

On a mountain in New Guinea, Ripley (1942 : 265) found a rail *Rallicula leucospila* sleeping in pairs in piles of dead leaves. On the same island, Gilliard (1958 : 150) discovered three individuals of *R. forbesi* sleeping in a nest of leaves and bark 11 feet up in a pandanus tree at 9,500 feet above sea level. In another small rail *Laterallus leucopyrrhus* in captivity, both parents were on the nest at night in the incubation period, but after the young hatched the female brooded them by day and the male by night (Kendeigh 1952 : 199). I know too little about rails to classify their sleeping habits, but some may belong under the present heading. One would like to know, too, more about the sleeping arrangements of the kiwis of New Zealand, which use an elaborate system of underground tunnels for lodging (Cottrell 1955).

2*C*. *The young lodge with one or both parents until they become self-supporting*. A number of neotropical wrens exemplify this stage in the evolution of the dormitory habit. In the Southern House Wren *Troglodytes musculus*, adults sleep singly in a wide variety of situations, including holes in trees, buildings and banks, the centre of a bunch of growing green bananas, and other unexpected sheltered spots. Their nest sites exhibit the same wide diversity as their lodges, and I have several times found them feeding young in one of a pair of saddle bags. Toward the end of the fledglings' first day in the open, the parents lead them to a shelter, which may be the nest they have just left, but is frequently a nook more accessible to young birds unskilled in flight. The parents direct the young wrens to their sleeping place by flying repeatedly from them to it and going in and out in their presence. After the youngsters are safely ensconced, they may receive a few more meals, and their mother may join them for the night, although sometimes they sleep without a parent. The mother is especially likely to lodge with them if they return to the nest. In this case, they may continue to sleep in the nest space until about the time the next brood hatches, when they are evicted by their parents. But some young House Wrens, stubbornly resisting the adults' efforts to drive them away, sleep beside their mother while she broods the nestlings of the following set. In these circumstances, I have known young of the first brood to help feed those of the second

brood, while a member of the second brood gave the same attention to the third brood, The last brood of the year may remain with the parents somewhat longer than earlier broods; but long before the following breeding season they disperse, and the territory is occupied only by the parents, who sleep in separate nooks (Skutch 1953).

As far as known, the sleeping arrangements of the Rufous-browed Wren *Troglodytes rufociliatus* and the Ochraceous Wren *T. ochraceus* of the Central American highlands follow the pattern of their more familiar and widespread congener (Skutch 1960). The Northern House Wren *T. aëdon* and the European or Winter Wren *T. troglodytes* also lead their fledglings to a shelter, at least on occasion (Bent 1948 : 126; Sherman 1952 : 113; Armstrong 1955 : 228–232); but in these northern representatives of a tropical genus sleeping arrangements are complicated by migration or winter's stress, and they do not properly belong with the year-round users of dormitories. We shall return to the European Wren in another chapter.

The Lowland Wood Wren *Henicorhina leucosticta* of the tropical American forests builds nests of two kinds, both of which are covered, with an opening in the side. The deep, substantial breeding nests are so well concealed in the lowest vegetation that they are rarely found. The thin-walled, pocket-like dormitories, which often have so little sill that an egg would roll out of them, are built a yard or two up in fairly exposed situations and frequently attract attention. Sometimes these dormitories are occupied by an adult with one or two fledglings, but through most of the year they shelter only a single sleeper, whence I infer that families disperse after the young can take care of themselves (Skutch 1940, 1960).

In the Riverside Wren *Thryothorus semibadius*, globular nests with an antechamber that is entered through a downward-facing doorway, usually placed in the vegetation overhanging a stream, are used for both breeding and sleeping. As a rule, adults sleep singly, but once I found a dormitory with three occupants, evidently a parent with two young who seemed old enough to feed themselves. The Highland Wood Wren *Henicorhina leucophrys* builds a somewhat similar nest, in which both parents sometimes lodge with one or two fledglings. In this species, however, the parents continue to sleep together after the young birds separate from them. One who has experienced the penetrating dampness of the forests of the Subtropical and Temperate altitudinal zones where Highland Wood Wrens dwell can appreciate the benefit they derive from sleeping with their mates rather than singly like their lowland relatives (Skutch 1940, 1960).

The Blue-and-white Swallow *Pygochelidon cyanoleuca* breeds from Patagonia to Costa Rica in such diverse sites as burrows in banks, cavities in trees, crevices in masonry, and beneath the roofs of houses. In the non-migratory tropical forms of this species, the nest space also serves the constantly mated pair as a dormitory throughout the year, and they may also enter it by day to escape hard rain. After they build their shallow, cup-like nest of straws and weed stems and line it with feathers, one member of the pair sleeps in the bowl while its mate rests on the rim; and this arrangement is usually followed until the nestlings fly. The young swallows return to sleep in the nest space with their parents, and they may continue to do so for some weeks after they become self-supporting. Soon, however, they go elsewhere, leaving the parents to sleep in the cranny where they bred (Skutch 1952).

In the Red-winged Starling *Onychognathus morio* of South Africa, the breeding pair often roost throughout the year on their nest site, which may be a hole in a tree, a niche in a cliff, or a shelf or cranny in a building. Here they sleep close together but apparently not in contact. The fledglings of the first brood lodge with their parents until five to seven days before laying is resumed, when they are driven off at roosting time. The young of the second brood are permitted to remain longer with their parents, on the average for five or six weeks, before they are similarly driven away (Rowan 1955).

Possibly the Verdin *Auriparus flaviceps*, an aberrant member of the Paridae that inhabits arid regions in southwestern United States and northern Mexico, should be included here. At all seasons, apparently, the adults sleep singly in closed structures of interlaced twigs with a doorway in the side. The winter lodges of the males are smaller than the breeding nests, with a less ample lining of feathers. The young return to sleep in their nursery long after they are fledged, but I can find no information as to whether a parent lodges with them (Bent 1946 : 432–434).

Rails, coots, and gallinules sleep on platforms which raise them above the damp or water-covered ground where they forage, and to such structures they lead their downy chicks to be brooded. The American Coot *Fulica americana*, whose zeal for building seems to equal that of certain wrens, constructs display platforms, nests for eggs, and nests for brooding. Often more than one egg-nest is built before laying begins, and those which do not receive eggs may be used for sleeping. The non-incubating parent may also roost on a display platform until it disintegrates; but unlike most birds that sleep in dormitories, the roosting coot soils its nest with its droppings. When the eggs begin to hatch, the parents construct a brood nest, and here the female covers the older, more active chicks while the male warms the remaining eggs and the newly hatched young on the egg-nest. Broods of chicks from 6 to 15 days of age may be divided at night, each parent covering some of them on a separate brood-nest. One mother slept with her offspring on a brood-nest 46 days after the last of them hatched, but apparently she roosted beside rather than brooded them. Thereafter, the young occupied the platform by themselves, while their parents slept on floating debris near by (Gullion 1954).

Like the coot, the Sora Rail *Porzana carolina*, the Virginia Rail *Rallus limicola*, and the Moorhen *Gallinula chloropus* brood their young on " dummy nests " or platforms of vegetation which raise them above the water or wet ground (Terrill 1943 : 177; Grey 1927 : 184). I once found a full-grown Grey-necked Wood Rail *Aramides cajanea* sleeping on a very substantial platform, too flat to hold eggs, situated as high as my head in a bush beside a small swampy opening (Skutch 1959 : 77). Although, since special structures are involved, we include the sleeping arrangements of these members of the Rallidae under the heading of " dormitories ", actually their downy young are protected in much the same way as the chicks which a quail or pheasant broods on dry ground; in both cases, the roof above them is the parent itself.

2*D*. *The young lodge with both parents long after they are self-supporting*. As an example of a wren that has attained a higher degree of social integration than the species we have already considered, we take the Banded-backed Wren *Campylorhynchus zonatus*. This starling-sized member of the cactus wren group is irregularly distributed from southern Mexico to northwestern Ecuador, and from sea level up to about 10,000 feet. At all altitudes it builds bulky globular nests, at times almost a foot in diameter, with a round doorway in the side, and it uses these structures for both sleeping and breeding. A single parent, doubtless the female, normally spends the night with the eggs and nestlings. One or two, and apparently at times as many as five, additional birds help the parents to feed the nestlings, and these attendants lodge together in a neighbouring nest. After the fledglings emerge, they are led in the evening to sleep in the nest that they have left, or in a similar structure in the vicinity, and here the parents and their helpers may lodge with them. The dormitory may then contain up to 11 birds. This group moves from time to time to a new nest, apparently to avoid the vermin that have infested the old one, or because the wrens have been disturbed. It holds together until the approach of the following breeding season, and even then its youngest members may remain with the breeding birds and help them to rear their nestlings (Skutch 1935, 1960).

In the Rufous-naped Wren *Campylorhynchus rufinucha*, a cactus wren that inhabits more or less arid country from southern Mexico to northern Costa Rica, up to four birds, all able to take care of themselves, were found lodging in bulky nests in November,

when there was no evidence of breeding. In the forests of Panama, parties of four or five Song Wrens *Leucolepis phaeocephala* slept in elbow-shaped nests hung over the vertical fork of a sapling in the undergrowth, and these also were evidently families whose youngest members had become fully self-supporting (Skutch 1940, 1960).

The sleeping habits of the Black-headed Mannikin *Spermestes nigriceps* of East Africa seem to resemble those of the Banded-backed Wren. They roost in old brood nests, and when these disintegrate, several birds unite to construct a dormitory nest, in which as many as 11 individuals may pass the night (Van Someren 1956 : 477).

Although some of the woodpeckers never tolerate another fledged one in the hole with them, there is a group of more sociable species in which family bonds are more enduring. An example is the Golden-naped Woodpecker *Tripsurus chrysauchen*, which inhabits the rain-forests and clearings on the Pacific side of southern Costa Rica and adjacent parts of Panama. The nest hole is carved by both sexes in a dead tree or limb with fairly sound wood, usually high above the ground. Male and female sleep together in the nest throughout the periods of laying, incubation, and rearing the nestlings. Although they may lay four eggs, I have never known them to rear more than three young, which leave the hole when about five weeks old. In the afternoon of their first day in the open, their parents lead them back to the nest cavity. Thereafter the hole, which is kept scrupulously clean, serves the family for sleeping and also on occasions as shelter from rain; some parents call their fledglings to the hole when a hard shower begins, whereas other parents go in leaving their offspring out in the rain, where they come to no harm; or one parent may stay dry in the hole while the other clings to the lower side of an inclined trunk.

I have only once known Golden-napes to attempt a second brood; and on this occasion the single young woodpecker of the first brood, a female, slept with her parents and the eggs or nestlings, although she was not seen to bring food to the latter. Rarely a Golden-nape reveals traces of the unsocial behaviour of other woodpeckers and tries to keep members of the family out of the hole in the evening. I have noticed this only in an occasional male, who opposed the entry of birds of both sexes; but often they forced their way in despite his pecks, and after that I could detect no further signs of discord. If all goes well, the family continues to lodge in the old nest hole until the following breeding season. A new hole seems invariably to be carved for the eggs; and about the time these are laid, the last of the previous year's brood depart, leaving the parents alone. Thus in the Golden-naped Woodpecker the nest hole has become the family home, in which the parents and their grown children lodge in comfort and security throughout the year. The Crimson-bellied Black Woodpecker *Tripsurus cruentatus* of eastern Ecuador and Peru, of which I have found five grown birds lodging together, appears to have similar sleeping habits (Skutch 1948 a).[1]

The sleeping arrangements of the piculets of the genus *Picumnus* closely resemble those of the Golden-naped Woodpecker. These diminutive woodpeckers are among the smallest of all birds. Unlike the larger members of the family, they do not support themselves with the tail as they climb over trees. Despite their short bills, both sexes carve a tiny, neatly finished cavity in very soft, decaying wood, and both sleep in it till the young fly. Then the parents lead the fledglings back to sleep in the nest; and I have known a young Olivaceous Piculet *P. olivaceus* to continue to lodge there while the parents hatched out the second brood. The piculets change their lodging more often than

* Since this was written, a pair of Gold-napes reared an exceptionally early brood of three, followed by a second brood of two. The three young woodpeckers fledged in May slept with their parents throughout their second nesting, and they sometimes brought a little food to the nest. After the second brood took wing at the end of July, the family of seven remained together, sometimes dividing up between two or three cavities in the same branch. Now in early November of 1960 the family remains intact. Seven is the largest number of woodpeckers of any species that I have found, or read of, occupying the same dormitory.

Golden-naped Woodpeckers, because the very soft stubs in which they are obliged to carve it do not last long. Hence I have not succeeded in following the vicissitudes of a single family from one breeding season to the next (Skutch 1948 b; Haverschmidt 1951).

Other woodpeckers in which a number of grown birds lodge together are the Blood-coloured Woodpecker *Veniliornis sanguineus* of the Guianas, in which Haverschmidt (1953) found one male and two females sleeping in the same hole, and the Acorn Woodpecker *Melanerpes formicivorus*, in which five grown birds may share a dormitory. In this woodpecker of western United States and Middle America, up to five birds attend a single nest with eggs or young, but their relationship has not been worked out (Skutch 1943).

The slender, middle-sized toucans called araçaris probably belong in this class. They differ from Golden-naped Woodpeckers and piculets in that, in both the Collared Araçari *Pteroglossus torquatus* and the Fiery-billed Araçari *P. frantzii*, only one parent sleeps with the eggs, although both pass the night with the nestlings. In one nest of the former species, five adults slept with the nestlings and all helped to feed them. In both of these araçaris, fledglings are led back to roost in the nest cavity along with their parents and the other attendants when these are present; but because of various mishaps, I have not succeeded in following the subsequent history of a family. I have repeatedly found five grown Fiery-billed Araçaris lodging in an old hole of one of the larger woodpeckers, while three or four other members of the same flock, who even by folding their tails over their backs to save space, could not squeeze into the crowded dormitory, took shelter in some neighbouring cavity. Although it is often assumed that other kinds of toucans, especially the large members of the genus *Ramphastos*, sleep in holes in trees, satisfactory evidence of this has not come to my attention (Skutch 1944 b, 1958).

2*E*. *Several families occupy a dormitory*. With its curious bill, the Prong-billed Barbet *Semnornis frantzii* of the highlands of Costa Rica and western Panama carves a cavity deep in fairly sound dead wood. Male and female share in this task, carrying the chips away instead of dropping them through the doorway to the ground, and when the cavity is large enough both sleep in it. They continue to pass the nights in the nest while they hatch their four or five eggs and rear their young; and after the latter emerge, they are carefully led back to sleep in the nest with their parents. In all this, the barbets closely resemble the Golden-naped Woodpeckers and the piculets. But, after some months have passed, one begins to find Prong-billed Barbets lodging in groups too large to be single families. I once discovered 16 of them sleeping in a hole that differed in shape from their nest cavities. These birds seem not to excavate new holes between breeding seasons; and if they lose their dormitories, several families may club together in any suitable cavity. In this they differ from woodpeckers, most of which preserve their territories and keep their families separate throughout the year. As the breeding season approaches, the barbets again become strongly territorial, the communal dormitories are abandoned, and each pair proceeds to carve a new hole (Skutch 1944 a).

In the Pied Barbet *Lybius albicauda* of East Africa, two adults slept in the hole with the eggs, but later four brought food to the nestlings. In the non-breeding season, up to six of these barbets may sleep together in a hole in a tree (Van Someren 1956 : 210–212). In the White-eared Barbet *Buccanodon leucotis* of the same region, four individuals brought food to a hole in a tree that contained four nestlings, and at least five have been seen entering a cavity to roost (Moreau & Moreau 1937 : 171–173). The sleeping arrangements of these African barbets appear to resemble those of the American Prong-billed Barbet, with the complication that helpers may join the parents of nestlings, or else two pairs breed together.

In the Pygmy Nuthatch *Sitta pygmaea* of the western United States and the highlands of Mexico, both sexes carve a cavity in decaying wood, and some pairs are assisted in this work by one to four additional birds. Unlike woodpeckers and barbets, the nuthatches

line their nest hole, and in this they may also be aided by one of their offspring of the preceding year. Male and female sleep in the nest cavity at all stages of the nesting, and when there is a yearling helper he does likewise. After the fledglings emerge, they are led to sleep in the nest or in some nearby cavity, where the parents lodge with them, as does the young bird who often helps to feed them. The parents and their offspring often continue to sleep together until the following spring, and even after breeding begins a young male of last year's brood may stay with the parents and share their labours. Sometimes, however, two neighbouring families with fledglings join together and sleep in the same hole (Norris 1958). This tendency of Pygmy Nuthatches to lodge with members of other families increases during the winter, especially at high altitudes where the weather is severe; and as many as 150 have been found roosting in an old pine trunk that contained several holes. At least 100 of these nuthatches occupied the same cavity. In some hollow trees where nuthatches slept there were numerous corpses of birds that may have died of suffocation, although other causes cannot be ruled out (Knorr 1957).

Of the White-breasted Nuthatch *Sitta carolinensis*, 29 have been found in winter sleeping in a hollow in an old dead Yellow Pine, and another lodged beneath the tiles of a roof (Bent 1948 : 18–19). We have already noticed that at times up to four Brown-headed Nuthatches may sleep together in a bird box in cold weather.

We have considered the barbets and the nuthatches after the Banded-backed Wrens, the Golden-naped Woodpeckers, and the piculets because their larger aggregations of roosting birds develop from a situation similar to that which we examined in the preceding section. It would be wrong, however, to suppose that the present class represents a higher development of the dormitory habit than the preceding class (2D). On the contrary, in birds like the Banded-backed Wren and the Golden-naped Woodpecker, the use of dormitories is more highly developed, because they build or excavate a new lodging whenever necessary. The larger aggregations of the barbets and nuthatches appear to result from their failure to prepare dormitories except in the breeding season, although in the nuthatches the desire to huddle together in freezing weather is a contributing factor.

INFLUENCE OF THE ENVIRONMENT

In the highlands of Central America, from 5,000 to 10,000 feet above sea level, the cold mountain nights seem as a rule to exert little influence on the sleeping arrangements of birds. Even at 8,000 and 9,000 feet, where for about half the year frost forms on open fields in clear and windless nights, most of the birds, including tiny humming-birds, appear to need no special protection. Wrens, swallows, woodcreepers and woodpeckers take shelter in dormitories, but so do members of these families in the lowlands. Probably the Banded-backed Wren's custom of sleeping in groups in thick-walled nests, which it follows at whatever altitude it resides, enables this member of a heat-loving genus to extend its range upward to nearly 10,000 feet. The same applies to the Southern House Wren's habit of taking shelter in crannies, where I have found it up to 9,000 feet. But the sleeping together of the male and female of the Highland Wood Wren appears to be a response to a cooler climate, since adult Lowland Wood Wrens sleep alone. A still more striking example of the modification of sleeping habits by climate is provided by the Blue-throated Green Motmot, of which the male and female sleep together in their burrow at all seasons, although such use of a dormitory is otherwise unknown in this generally thermophilous family.

On the high plateau of Peru, at about 13,000 feet (4,000 metres) or more, the climate is far more severe than anywhere in Central America, save possibly on the highest summits. Here, according to Dorst (1957 a : 25–26), 20 or more birds of diverse species may huddle

together for warmth beneath protecting blocks of stone. These sleeping groups contain the finches *Phrygilus gayi*, *P. plebejus*, *P. unicolor*, *Zonotrichia capensis*, and *Sicalis uropygialis*, and the ovenbird *Cinclodes fuscus*. The same author quotes an observation of Niethammer that in Bolivia, at 17,400 feet (5,300 metres), more than 200 individuals of the starling-sized fringillid *Diuca speculifera* massed together at night in a crevice in a glacier to keep each other warm. The stiff, close-set, sword-like leaves of the peculiar terrestrial bromeliad *Puya raimondii* also provide protected sleeping places and daytime refuge for the hardy birds of the high, bleak Peruvian Andes. Great numbers of Black-winged Doves *Metriopelia melanoptera* frequent these dormitories, roosting with their heads outward on the leaves, as close as possible to the centre of the plant. The Bare-faced Doves *Gymnopelia ceciliae* of the same region sleep in holes in walls (Dorst 1957 b : 595). These roosting doves and finches soil their sleeping places, whereas birds which make dormitories keep them clean.

Oreotrochilus estella, a common humming-bird of the high Peruvian plateau, frequently builds its nests within caves and mine shafts, and when not breeding it roosts in similar situations, its body temperature falling almost to that of the air. Such nocturnal torpidity, a sort of short-term hibernation, seems to be general in humming-birds when nights are cool. In the caves and tunnels where the humming-birds slept, several other kinds of birds sought refuge from the frigid Andean night, among them Sparrow Hawks *Falco sparverius*, Horned Owls *Bubo virginianus*, Streaked Spinetails *Leptastenura andicola*, and two kinds of terrestrial American flycatchers, *Agriornis montana* and *Muscisaxicola rufivertex*. In other caves a Bolivian Goose *Chloephaga melanoptera*, a Cinerous Ground Tyrant *Muscisaxicola cinerea*, a Black-fronted Ground Tyrant *M. frontalis*, and a Grey-headed Finch *Phrygilus gayi* were roosting or nesting. In these high mountains, flickers *Colaptes*, miners *Geositta*, creepers *Upucerthia*, shake-tails *Cinclodes*, cliff-swallows *Petrochelidon*, and ground finches *Sicalis* make use of holes and crevices. Altogether, a substantial proportion of the scanty avifauna of these bleak heights roosts in covered places (Pearson 1953, cf. Dorst 1956). In a cave at 13,500 feet in the Ecuadorian Andes, a number of humming-birds *Oreotrochilus chimborazo* and shake-tails *Cinclodes excelsior* were found sleeping (French & Hodges 1959).

High on Mt. Kenya in tropical Africa, the sunbird *Nectarinia johnstoni* seeks protection from bitterly cold nights by entering deep holes which the Mountain Chat *Pinarochroa sordida* excavates in the matted dead-leaf clusters of the Tree Groundsel *Senecio keniodendron*. One evening two females and a male entered such a cavity, suggesting that these sunbirds rest communally. Immature birds entered disused covered nests for resting and warmth, even by day (Williams 1951 : 586–587). In the limited literature available to me, I find no mention of similar sleeping habits of sunbirds at lower altitudes.

At high latitudes, as at high altitudes in the tropics, cold induces birds to sleep in closed spaces. In warm climates, finches seem rarely to roost elsewhere than amid vegetation; I am familiar with no Central American representative of the family that uses a dormitory. But I have already given examples of finches that sleep beneath rocks and in glacial crevices in the high Andes, and to this may be added two examples from northern regions. Near the Arctic Circle in East Greenland, in May and June, the Snow Bunting *Plectrophenax nivalis* sleeps about two or three hours each night in a crevice in rocks; his mate also builds her nest in a rock crevice (Tinbergen 1939 : 11). In more than usually severe sub-zero weather in New England, wintering Snow Buntings dug themselves into soft snow under the steep leeward edges of shallow drifts in an open field, until the face of the snow bank was pitted with oval depressions. Here the buntings huddled not only through the long winter night but during much of the day, leaving their shelter only long enough to seek food at nearby chaff piles (Bagg 1943). In their winter habitat, these niches in snowdrifts probably resembled their summer dormitories and nest sites more closely than anything else available to them.

The Rosy Finches *Leucosticte tephrocotis* nest and apparently also roost in crannies among rocks in the high mountains of western North America, where even in the breeding season the climate is almost Arctic. In winter, when they descend to lower altitudes, they roost gregariously in old nests of the Cliff Swallow, in caves and mine shafts, and in sheltered places on buildings (Shaw 1936; French 1959). Here, again, there is resemblance between the winter and summer sleeping places and the nest sites of a finch that inhabits a severe environment.

Swallows of many kinds seek protection in closed spaces. We have seen that Blue-and-white Swallows sleep in pairs, which for a while are accompanied by their young. In the high mountains of Guatemala, Black-capped Swallows *Notiochelidon pileata* spend the night in burrows, seven or eight sometimes roosting together. On chilly mornings, they may linger in their dormitory until the sun has risen high above the flowery mountainside (Skutch 1960). Although migratory swallows cannot, like these tropical species, lodge in a cranny throughout the year, their ability to find a sheltered retreat is at times of critical importance to them. The protection afforded by their closed, mud-walled nests of the preceding year may preserve the lives of Cliff Swallows if the temperature suddenly drops after their return from the south (Buss 1942 : 154–155). In abnormally cold weather in Florida, wintering Tree Swallows sought warmth by crowding together in holes in trees, but many succumbed from the combined effect, of cold and shortage of food (Christy 1940). Violet-green Swallows, arriving in the state of Washington in early spring, were caught at the end of March by snowy gales and freezing temperatures, from which some took shelter beneath the eaves of buildings and in similar protected places; yet many died from cold and starvation (Edson 1943 : 403). Likewise in Great Britain, in the fatally late spring of 1886, large numbers of Sand Martins took refuge from a severe May snow-storm in their burrows, where many perished (Coward 1928 : 256).

The effect of the environment is also evident in the sleeping arrangements of the Great Tit *Parus major*, which in the Netherlands roosts in a sheltered place against a tree trunk or amid foliage in summer, whereas in the winter months from November to March it sleeps in a natural cavity or in a bird box, always alone (Kluijver 1950 : 101). Blue Tits *Parus caeruleus*, which usually roost in ivy or other evergreens, seek protection in bitter weather in a hole or any closed space they can find. Likewise Long-tailed Tits, which ordinarily roost in a cluster in trees or bushes, cuddle together in holes in the coldest weather (Coward 1928 : 143, 147). Since titmice of numerous kinds do not use dormitories throughout the year, but only when cold makes such protection welcome, they do not as a rule lead their newly emerged fledglings back to the nest or to some other cranny, but install them amid foliage (Kluijver 1960 : 101; Howard 1952 : 66). The only exception to this rule that has come to my attention is a tropical African species, the Highland White-bellied Pied Tit *Parus albiventris*, in which the parents put their fledglings to bed in a crevice in a tree (Van Someren 1956 : 411).

Although adults of the European or Winter Wren *Troglodytes troglodytes* most of the time sleep singly, in old nests of their own or of some other bird or even, in mild weather, amid sheltering foliage, in midwinter they may huddle together for warmth. Armstrong (1955 : 275–282) believes that the combination of cold and damp is most effective in causing these wrens to roost in groups, where if sufficiently numerous they arrange themselves in layers or tiers, with their heads toward the centre. In the British Isles, 46 of these diminutive wrens have been found sleeping together in a bird box; while in northern United States, 31 individuals of another race crowded into a box that measured only six inches each way (Bent 1948 : 175–176). No comparable aggregation of sleeping wrens is known for any tropical species, although in the tropics wrens more consistently use dormitories.

Eastern Bluebirds *Sialia sialis* nest in boxes and other cavities, yet even in winter they seem usually to roost in trees, three or four together in a terminal cluster of dead

leaves. But at about 0°F two pairs forgot their usual enmity and took refuge in the same box (Thomas 1946 : 173–174). Although most members of the thrush family appear to roost in trees and bushes, Uganda Black Chats *Myrmecocichla nigra* sleep in pairs in tunnels in the earth, when they are not breeding (Van Someren 1956 : 295).

Even in families which ordinarily roost amid vegetation, cold weather may drive individuals to seek whatever closed space they can find. Thus, during a spell of freezing weather in Florida, 15 Myrtle Warblers *Dendroica coronata*, perhaps the hardiest of the wood warblers, were found dead in an out-building in the heart of the scrub (Ruff 1940). We need not repeat here more of the many recorded instances of birds, even of kinds that usually roost in the open, entering closed spaces in severe weather.

In view of the value of an enclosed place in preserving the warmth of sleeping birds, and of how frequently they seek makeshift lodgings when the temperature falls low, we are led to ask why the dormitory habit is so poorly developed where winter is severe. Why should nearly all our examples of the construction of special dormitories, and their use throughout the year, come from tropical and subtropical regions where they appear to be less necessary than in more rigorous climates? In the first place, birds rarely build special dormitory nests unless they have already adopted closed nests for breeding; and the evolution of these more elaborate structures seems to be correlated with the length of the interval between the start of building and the deposition of the eggs. Many permanently resident birds of the tropics devote weeks or months to the construction of their nests. Migratory birds of high latitudes, where the breeding season is short, cannot afford so much time for building; hence they have more rarely evolved the covered structures which can also be used for sleeping. It is significant that woodpeckers, which carve chambers for themselves in northern no less than in tropical lands, are among the northern birds which most consistently sleep in dormitories; yet no extra-tropical woodpecker is known to use its hole as a family lodging in the manner of *Tripsurus*, *Picumnus*, and the Acorn Woodpecker, which last is an essentially tropical species that reaches California and southern Oregon.

In the second place, the quest of food in cold and snowy weather obliges many birds to wander widely, and there is little advantage in having a permanent dwelling unless one is permanently resident. It is significant that Starlings *Sturnus vulgaris* resident in England sleep in winter in the holes in which they nest, whereas starlings that come from the Continent to winter in England take no interest in holes (Bullough 1942). The Red-headed Woodpecker *Melanerpes erythrocephalus* is exceptional among migratory birds in preparing a dormitory on its wintering ground. Sealed-in stores of acorns permit these woodpeckers to remain stationary on defended winter territories, each with its individual sleeping hole, which may be the bird's lodging for as long as six months (Kilham 1958). The tropical birds in which the dormitory habit is best developed remain on their territories throughout the year, and they rarely unite in large flocks in which family bonds are not evident, as do so many extra-tropical birds.

A third reason why so few birds of the temperate zones maintain dormitories may be that they would be dangerously conspicuous in leafless trees and bushes in the winter months.

One may also ask why even in tropical regions where most birds are permanently resident the dormitory-users are a small minority. Even if dormitories are not needed for warmth, to have a dry lodging during the torrential rains of the wet season would seem to be advantageous. Doubtless natural selection would have caused the more widespread use of dormitories if their advantages greatly outweighed their disadvantages. What, then, are the latter? In the first place, a dormitory nest is nearly always more conspicuous than a small bird roosting amid foliage; and since the structure remains in one spot, predators may remember its position. Some birds reduce this danger by having

several lodgings scattered over their territory; if an intruder is in sight of one when they are ready to retire, they slip into another. Since even in tropical regions dormitory nests of all kinds are usually widely scattered, predators are not likely to specialize on them; but if many kinds of birds built dormitories, their abundance might cause nocturnal predators to concentrate on them. Another disadvantage of dormitories is that lice and other vermin may infest them; the periodic changes of domicile of certain birds may be related to such infestation. Birds which employ their nests for sleeping as well as breeding nearly always refrain from defaecation while inside and so keep them clean. I have noticed that hole-nesting birds which do not lead their fledglings back to the nest often become careless of sanitation after the nestlings can climb up and take their meals through the doorway and the parents need no longer enter in order to feed them. But parents whose family will continue to lodge in the hole go in especially to remove waste matter.

After one has weighed all the advantages and disadvantages of dormitories, and taken account of some of the means of overcoming the latter, one may conclude that the chief reason why so few birds use them is that in mild climates, where conditions are most favourable for their development, they are rather redundant. Birds, like turtles, carry their houses with them, the chief difference being that the bird's feathery covering is far more flexible and convenient that the tortoise's carapace. When the bird's plumage is well oiled with the secretion of the preen gland, drops of water that fall on it roll off, as from any unwettable surface. Although I have given instances of woodpeckers, swallows, swifts, and other birds taking shelter from rain, frequently the possessors of dormitories fail to enter them even in hard downpours. By raising or depressing its feathers, a bird can adjust for changes in temperature. Constantly clothed in a garment that has many of the advantages of a house with a roof and ventilators that can be opened and shut, most birds seem to find a second covering of vegetable or mineral materials superfluous. Yet sometimes long-continued rain may penetrate a bird's plumage and render it flightless, as I have seen happen to a Prong-billed Barbet in a cold rainstorm that lasted for days. Probably this is the reason why this dweller in excessively wet mountain forests provides a dormitory for itself.

THE EVOLUTION OF SLEEPING ARRANGEMENTS

I have endeavoured to trace the evolution of the ways of sleeping of birds, from that primitive condition in which they pass the night on the surface of the land or sea or amid foliage to a more advanced stage in which they take advantage of natural shelters and finally of dormitories constructed by themselves. We have seen how these dormitories, at first occupied by single birds, have become the dwelling of the mated pair and finally of a family consisting of two or more generations. This story may be compared to the history of man's efforts to provide shelter for himself.

The first step toward the acquisition by birds of a sleeping place that shields them seems to have been the adoption of natural cavities as nest sites, or the making of burrows, holes in trees, or roofed nests to contain their eggs and young. Since nearly all birds construct nests of some sort, yet relatively few provide themselves with dormitories, it is logical to suppose that the use of a closed receptacle for the eggs preceded the employment of such a shelter for sleeping. I am not aware that any kind of bird habitually sleeps in a place more sheltered than that in which it rears its young; yet many species whose nests or nest-cavities would make dormitories fail to use them as such. The chief reasons for this neglect appear to be the lack of sufficient cavities for the whole population; the unsuitability of the nest for climatic conditions that prevail after the breeding season, as when warm downy nests become sodden after the rains begin (e.g. those of the Black-eared Bushtit), or nest burrows in river banks become subject to inundation in the rainy

season; the infestation of nests by vermin; the too great conspicuousness of such nests; and the adequacy of the bird's feathers as a sole protection against the elements.

Once the bird has learned to find or make a sheltered receptacle for its eggs, the next step is to sleep in the same or a similar receptacle at times when it neither incubates nor broods its nestlings. At first, each individual occupies its shelter alone, resenting the intrusion of its mate, and failing to provide for its newly fledged young the same protection that it enjoys. If the mate desires an equally comfortable sleeping chamber, it must build or find one for itself. Such a situation prevails in the woodcreepers, at least two kinds of American flycatchers, the Bananaquit, a number of woodpeckers, wrens, and other species.

The next advance is the admission of the mate to sleep in the nest where the eggs are being incubated and the nestlings brooded. We find this situation in a motmot, a starling, a number of swifts, barbets, woodpeckers, swallows, titmice, nuthatches, weaver birds, and others. From the point of view of the preservation of the species, perhaps this is an undesirable habit, for it subjects the whole breeding population to certain of the numerous hazards that render the existence of eggs and nestlings precarious. In general, only birds whose nests are more than ordinarily inaccessible to predators, as those in burrows in high banks, in deep holes in trees, on cliffs or the vertical walls of buildings, can afford to adopt this custom. In some species which have advanced to the next or final step in the evolution of the dormitory habit, the parents rarely sleep together while they have eggs or nestlings; several kinds of wrens lead their nestlings back to sleep in the nest, yet the male does not ordinarily pass the night with his incubating or brooding partner. But he may do so if he loses his own dormitory, or in certain other circumstances—which suggests the possibility that these wrens have passed through the phase in which both parents sleep in the breeding nest and found it an unprofitable arrangement.

The final stage in the perfection of the birds' sleeping arrangements is attained when they provide shelter for their fledglings newly emerged from the nest. The dormitory to which the parents lead their young may be the nest in which they were reared, or some similar retreat which has the advantage of freedom from parasites, of being more accessible to unpracticed wings, or of affording a readier escape from nocturnal attack even if less cunningly concealed—as is true of the dormitory nest of the Lowland Wood Wren compared with its breeding nest. These careful parents are physically incapable of carrying their babies, although in rare instances they push them, but they do the next best thing: they show them over and over how to reach the chosen roost. A number of woodpeckers, toucans, barbets, swallows, nuthatches, wrens, etc. have reached this stage.

The time that the young remain beneath the parental roof is variable. It may be merely until they can shift for themselves, as in the Southern House Wren and the Red-winged Starling. It may be until the following breeding season, as in Golden-naped Woodpeckers and Prong-billed Barbets; or some of the young birds may remain with their parents even through the next breeding season, now helping to attend their younger brothers and sisters, as in the Banded-backed Wren and the Pygmy Nuthatch. Occasionally Barn Swallows, House Martins, and Southern House Wrens continue to live with their parents long enough to help them attend a later brood of the same season.

Cold, such as occurs in winter at high latitudes and at night on tropical mountains, leads birds to seek whatever protection they can find, as by roosting in crannies in rocks or buildings, in the densest foliage, or even beneath snow and in clefts in glaciers, sometimes in compact clusters of numerous individuals of the same or even of diverse species. Often the bird's life depends on the availability of such protection. But rigorous conditions have not favoured the development of the dormitory habit; these birds of harsh environments seem rarely to prepare lodgings for themselves, nor to preserve the family

structure that is often associated with the possession of special dormitories. These refinements are found, not where life is most difficult, but where it is easiest for the birds, in the mild climates of tropical and subtropical regions where they reside throughout the year.

SUMMARY

As a rule, only birds which breed in roofed nests or those built in enclosed spaces sleep in their nests when not incubating or brooding young. The chief exceptions are rails, coots, and gallinulse, which build platforms to raise them above the water or wet ground while they sleep, and Curved-billed Thrashers, which roost on open nests in thorny cacti.

The first step in the evolution of the dormitory habit appears to be sleeping in the covered breeding nest itself before the eggs are laid or after the fledglings depart. In the simplest case, only one parent occupies the breeding nest. But in a number of species, the second parent uses the nest as a dormitory even while it contains eggs and nestlings, and sometimes unmated helpers roost with the parents. A further advance is made when the fledglings are led to sleep in the nest they have just left.

The next advance is the construction of special dormitories, not intended for eggs. These usually resemble the breeding nest, but differences in form or site are sometimes found, especially in tropical wrens. Only birds which make or acquire dormitories, in addition to their breeding nests, are likely to enjoy such lodges through the year. In them, self-supporting individuals may sleep singly, or in pairs, or with their dependent offspring. In the final stage of the evolution of the dormitory habit, the young lodge with their parents long after they are self-supporting. Often each family remains separate throughout the year; but sometimes, probably in consequence of the loss of dormitories, several families club together in the non-breeding season. Numerous examples of each of the foregoing arrangements are given.

In a harsh environment, as at high latitudes and above timberline on tropical mountains, many birds seek closed spaces for sleeping, and their lives may depend on the availability of such protection. Nevertheless, the dormitory habit is best developed in mild climates where the birds are permanently resident.

APPENDIX

SLEEPING WITH EGGS OR NESTLINGS BY BOTH PARENTS

We rarely find both parents sleeping in a nest in which breeding is in progress, yet in the text a number of instances of this were mentioned. Other cases that have come to my attention could not be classified because fuller information on the sleeping habits of the species is not available. The present list includes all the cases known to me of both parents sleeping with eggs and/or nestlings. References are given only when the authority has not already been cited.

Rallidae. *Laterallus leucopyrrhus*, during incubation.

Psittacidae. Yellow-headed Pygmy Parrot *Micropsitta keiensis*, in which six adults were found with two " babies " in a termitarium (Hindwood 1959 : 13).

Apodidae. Common Swift *Apus apus*, White-rumped Swift *Micropus caffer*, Palm Swift *Cypselus parvus*, *Colletoptera affinis*, Chimney Swift *Chaetura pelagica*, Grey-rumped Swift *C. cinereiventris* (Sick 1959 : 475), Lesser Swallow-tailed Swift *Panyptila cayennensis* (Haverschmidt 1958). In swifts the second parent sleeps on or close beside the nest at all stages of the nesting

Momotidae. Blue-throated Green Motmot *Aspatha gularis*, throughout the nesting.

Capitonidae. Prong-billed Barbet *Semnornis frantzii*, Pied Barbet *Lybius albicauda*.

Ramphastidae. Collared Araçari *Pteroglossus torquatus*, in which a single parent sleeps with the eggs, but up to five adults with the nestlings; Fiery-billed Araçari *P. frantzii*, in which both parents sleep with nestlings but only one with the eggs.

Picidae. Golden-naped Woodpecker *Tripsurus chrysauchen*, Olivaceous Piculet *Picumnus olivaceus*, Lafresnaye's Piculet *P. lafresnayei*, in all three of which a young bird of the first brood may sleep with the parents while they incubate the next set of eggs; Sundevall's Piculet *P. minutissimus* (Haverschmidt 1951).

Hirundinidae. Barn or European Swallow *Hirundo rustica*, Wire-tailed Swallow *H. smithii*, Cliff Swallow *Petrochelidon pyrrhonota*, Blue-and-white Swallow *Pygochelidon cyanoleuca*, Dusky Sand Martin *Riparia paludicola*, Purple Martin *Progne subis*; House Martin *Delichon urbica*, in which young of two earlier broods may continue to sleep in the nest; Black-capped Swallow *Notiochelidon pileata*, in which both parents sleep at least with nestlings.

Paridae. Long-tailed Tit *Aegithalos caudatus*, Common Bushtit *Psaltriparus minimus;* Black-eared Bushtit *P. melanotis*, in which one or two male helpers may sleep with the parents and nestlings.

Sittidae. Pygmy Nuthatch *Sitta pygmaea*, in which a helper may sleep with the parents; Brown-headed Nuthatch *S. pusilla*.

Troglodytidae. Banded-backed Wren *Campylorhynchus zonatus*, Highland Wood Wren *Henicorhina leucophrys*, Southern House Wren *Troglodytes musculus*, in all of which the male only exceptionally sleeps in the breeding nest.

Motacillidae. African Mountain Wagtail *Motacilla clara* (Moreau 1949 : 184).

Sturnidae. Red-winged Starling *Onychognathus morio*.

Ploceidae. Bronze-headed Mannikin *Spermestes cucullatus*, Black-headed Mannikin *S. nigriceps*, Barred Waxbill *Estrilda astrild*, Crimson-cheeked Blue Waxbill *Uraeginthus bengalus* (all from Van Someren 1956); Zebra Finch *Poephila guttata*, with nestlings (Morris 1954 : 292).

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