WEAVERBIRD NEST AGGREGATION AND EVOLUTION OF THE COMPOUND NEST[1]

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ABSTRACT.—Possible steps in the evolution of the compound nest are considered by comparing three different species of weaverbirds (Ploceidae) of the subfamily Plocepasserinae, the Sociable Weaver (*Philetairus socius*) of southern Africa, the Grey-capped Social Weaver (*Pseudonigrita arnaudi*) of East Africa, and the White-browed Sparrow Weaver (*Plocepasser mahali*) of East Africa. We develop a multiple factor theory of the origin of the compound nest recognizing that the relative importance of the different factors will vary with circumstances and in different places. Gregarious breeding is typical of many weaverbirds, and is favored by security from predation and by social stimulation of nest building and breeding. Security and gregariousness are enhanced by the roofed nests characteristic of all Ploceidae, often by nesting in thorny trees, and sometimes by nesting close to colonies of aggressive insects. Feeding in large flocks often well away from the colony tree is characteristic of *socius* and *arnaudi*, both of which often nest in large colonies, whereas *mahali*, which lives in small colonies, generally keeps close to its colony tree. Year-round residence in one tree is characteristic of the Plocepasserinae, in contrast to the Ploceinae, or true weavers. The former subfamily also more characteristically lives in arid climates, uses dry grasses for nest materials, and builds nests during both breeding and nonbreeding seasons. In the dry climate old nests may persist for many months. Aggregation of nests into masses with two or more nests in physical contact is common in the Plocepasserinae and is favored by the persistence of old nests through the dry season, by building of thick nests at any time of year, and sometimes by nesting in association with aggressive social insects. Some massing of nests in *mahali* and *arnaudi* is likely to occur by mere chance, especially in larger trees and colonies. Temperature regulation is related to size of nest mass and to body size in a reciprocal fashion. The Plocepasserinae sleep in their nests the year round; the larger *mahali* sleeps one bird to a nest while the two smaller species, *arnaudi* and *socius*, often sleep in groups of two to five birds to a nest. Group sleeping and consolidation of nests into large masses have been shown to have thermal advantages during the cool nights of the arid tropical and subtropical habitat. Consolidation of nests also helps solve the problem of any shortage of nest sites. A common roof, built on by all, is seen over nest masses of *socius*. This thick communal roof gives added thermal advantages, and we believe also enhances protection from some predators. The tendency of *arnaudi* to build new nests directly under and fused to old nests, suggests that such old nests may have been precursors of a communal roof in evolution. —*Department of Biology, University of California at Los Angeles, Los Angeles, California 90024, and Los Angeles County Museum of Natural History, Exposition Park, Los Angeles, California 90024.* Accepted 3 June 1975.

IN contrast to the case in the social insects, the compound nest is a rarity among birds, and the best example is the nest of the Sociable Weaver (*Philetairus socius*) of the Kalahari Desert and other parts of southern Africa. In many ways the nest of this species is the most spectacular structure built by any bird.

More detailed and comparative study of nests, nest sites, and behavior of the sparrow weaverbirds (Plocepasserinae), the subfamily to which the Social Weaver belongs, has long been needed. The object of this report is (1) by surveying representative genera of sparrow weaverbirds to attempt to establish a gradation in pattern from colonies containing nests well separated from one another to the huge nest masses of *Philetairus* that may contain up to 60 or more individual nest chambers in a sort of gigantic apartment house arrangement, and (2) to attempt to delineate the ecological and social conditions under which nest massing takes place to varying

[1] This paper is dedicated to the memory of Professor Alfred E. Emerson.

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degrees and levels of specialization. We are not in this study particularly interested in trying to contribute evidence to the establishment of specific geneologies, nor do we think our general objective of seeking ecological and social correlations with variations in nest structure and massing is greatly dependent on knowledge of precise taxonomies. Still, a brief discussion of the phylogeny of the Plocepasserinae is useful for perspective.

In 1927, after a study of skeletal material, particularly of skulls, Sushkin concluded that *Plocepasser, Pseudonigrita,* and *Philetairus* form a small group of closely related genera and united them into one subfamily, the Plocepasserinae. Chapin (1954) adopted this subfamily, and we followed his 1954 taxonomy in our monograph on weaverbird nests (Collias and Collias 1964). This arrangement of genera but not this subfamily was adopted in the "Check-list of birds of the world" (Peters 1962). Chapin helped arrange the phylogenetic sequence of genera in the Ploceidae for the check-list.

In 1970 Sibley reviewed the literature on classification of the Ploceidae, and he added some evidence based on a study of egg-white proteins. He pointed out a similarity in mobility of the ovalbumin fraction between *Philetairus* and *Passer*, which he tentatively grouped together with the the Plocepasserinae into a family, Passeridae. He also pointed out that as the egg-white similarity was based on protein mobility rather than on presence or absence of a distinctive protein, the taxonomic significance of this similarity might be small. Recently Walter Bock (pers. comm.) discovered a unique skeletal element, the preglossale, present in the tip of the tongue of *Passer*, but absent, together with its associated muscle, from *Sporopipes*, *Plocepasser*, *Pseudonigrita*, and *Philetairus*. This finding tends to strengthen Suskin's original grouping of the latter three genera into one subfamily, the Plocepasserinae, and it would seem that *Philetairus* is about as closely related to *Pseudonigrita* as to any other genus. The taxonomic relations of *Sporopipes* are uncertain and require further study. In this report "Plocepasserinae" is used as a convenient term for the genera *Plocepasser, Pseudonigrita,* and *Philetairus*.

The nest of *Philetairus* is distinctively different from that of other weavers, but on the whole is closest in its structure to that of *Pseudonigrita* of East Africa (Collias and Collias 1964). The main differences are in the extent of compounding of individual nests, the presence of a communal roof, and in the presence of only one entrance to each nest chamber in *Philetairus*. *Plocepasser* and *Pseudonigrita* have two entrances to each nest, except when the birds are breeding, when they plug up one entrance. This report focuses on a comparison of the degree of nest aggregation in these two genera and in *Philetairus*. In East Africa we particularly studied *Pseudonigrita arnaudi*, the Grey-capped Social Weaver, and *Plocepasser mahali*, the White-browed Sparrow-Weaver.

Study Areas and Methods

Prior to the field studies on East African Plocepasserinae that we are reporting here, we made two brief visits to South Africa where we had watched nests of *Philetairus* under nonbreeding and breeding conditions. In July 1957, the middle of the southern winter, we visited colonies of this bird in the Western Transvaal, and in October 1969 we studied colonies, many of which contained nestlings, along the Kuruman River and in the Kalahari Gemsbok National Park. Our visits each lasted about 12 days.

In the spring of 1957 in Kenya we studied breeding colonies of *Pseudonigrita arnaudi* and *Plocepasser mahali* (Collias and Collias 1964). We wished to observe these species outside their breeding season, which normally coincides with the rains. During the summer of 1973, a season of exceptional drought, we

TABLE 1

OCCURRENCE OF COLONIES OF *Pseudonigrita arnaudi* IN RELATION TO PLANT COVER

Plant-cover index[1]		Number km	Percent km	
Grass	Bush-tree	surveyed	with colonies	Remarks
0	0, 1	32	0	No grass or trees
1	1	13	54	Good habitat
1	2	25	72	Good habitat
1	3	6	33	Rather dense
2	0	5	0	No trees
2	1	23	57	Good habitat
2	2	23	74	Good habitat
2	3	8	0	Dense cover
3	1	12	0	Dense cover

[1] 1 = trace to 1/3, 2 = 1/3 to 2/3, 3 = 2/3 to complete cover.

traveled some 2,500 km while surveying colonies of *Pseudonigrita arnaudi* in parts of East Africa from 30 June to 14 September. We also saw many colonies of *Plocepasser mahali*. With the exception of one nest of *mahali* that still contained nestlings on 4 July following the breeding season, none of the many nests of either species we saw contained eggs or young, so we can take this season as a good example of the nonbreeding season. We were able to confirm the fact that the birds remain permanently at the colony trees the year round. A few individuals of each species were captured with mist nets and color-banded, and we were able to follow certain individuals of *mahali* for a time, but the several *arnaudi* we caught and banded proved very shy at this time of year, and most were not seen again.

These two species nest in conspicuous colonies in open country. As we drove along the roads we counted all colonies within clear view, about 100 m on each side of the road, and in many places estimated the height of colony trees, made sample counts of the number of nests in each colony, and their degree of massing, i.e. the number of nests in physical contact with another nest. We collected nests for later analysis, as well as specimens from the colony trees and of the grasses in the nests for later identification. We also made notes on the general nature of openness of the surrounding vegetation and documented the various types of colony, of nests, and of habitats with photographs.

The Ploceidae generally nest in colonies. For consistency we shall use the term "colony" to mean all the nests in one tree. If two or more nests are in physical contact we call this aggregate of nests a "nest mass." If the nest mass has some communal feature, such as a common roof, which may be built on by all birds, we call the nest mass a "compound" nest.

RESULTS

Figs. 1 and 2 when compared with 3 and 4 illustrate some degree of gradation between the compound nest mass of *Philetairus socius* and the variously grouped nests of *Pseudonigrita arnaudi*.

Relation to habitat.—Fig. 5 shows that in general colonies of *arnaudi* in East Africa occur below 5000 feet elevation (1524 m), and coincide with the semiarid acacia savanna, i.e. areas of mixed grass, thorn bush, and thorn-trees. Colonies were most common in fairly open country having intermediate degrees of grass, bush, and tree densities (Table 1). *Plocepasser mahali* is also characteristically found in arid savanna and often nests in the same sort of trees as does *Pseudonigrita arnaudi*, but its nesting colonies are much more likely to be found near human habitations.

Relation of massing of nests to size of tree and colony.—*P. arnaudi* nests in a variety of trees and, in general, the larger the species of tree, the more nests it contains, e.g. *Acacia tortilis* and *A. xanthophloea,* in contrast to the small *A. drepanolobium* and *A. thomasi* (Table 2). Even for the same species of tree the number of nests is 3 to 4 times greater in trees more than 20 feet high than it was in smaller trees, when the species of trees for which we have most data are considered. More interesting was the fact that the average number of nest masses per tree was

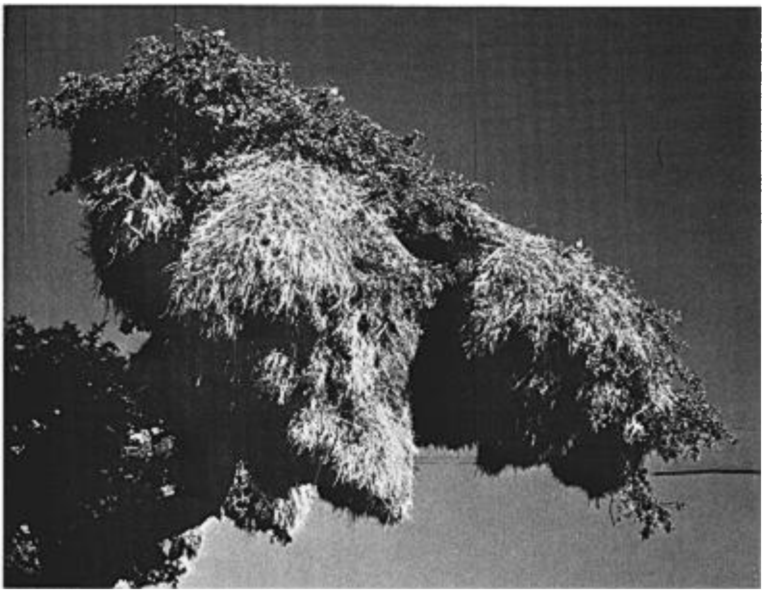

Fig. 1. Side view of the roof and nest mass of a *Philetairus socius* colony in a Camelthorn tree (*Acacia giraffae*), near Barberspan, Western Transvaal, South Africa, 1957.

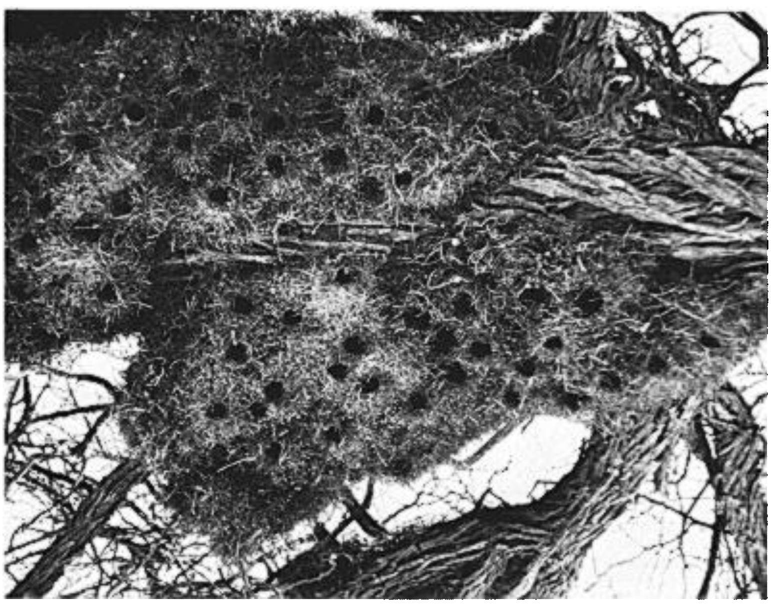

Fig. 2. Underside of a nest mass of *Philetairus socius* showing the many individual nest chambers, Kuruman River, Cape Province, South Africa, 1969.

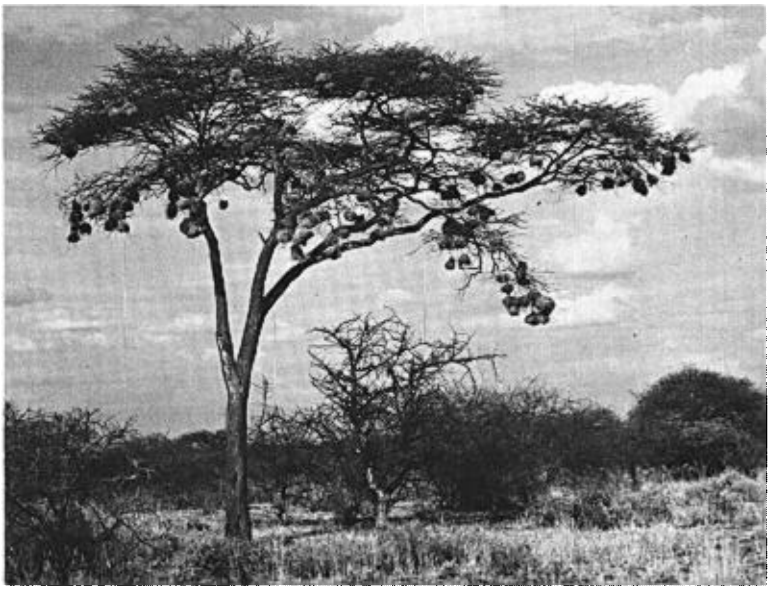

Fig. 3. A large colony of *Pseudonigrita arnaudi* in an *Acacia tortilis*, Amboseli Game Reserve, Kenya, 1973.

Fig. 4. Nest of *Pseudonigrita arnaudi* with ten nests in physical contact, near Hunters Lodge, Kenya, 1973.

TABLE 2

PRINCIPAL SPECIES OF TREES USED BY NESTING COLONIES OF *Pseudonigrita arnaudi* IN KENYA

Species of tree	Number of trees	Height (feet)		Number of nests in tree	
		Average	Range	Average	Range
Acacia thomasi	44	17	8–30	4	1–24
A. senegal	31	16	10–23	13	1–87
A. drepanolobium	12	9	6–10	9	1–20
A. xanthophloea	13	27	12–45	21	2–41
A. tortilis	73	24	9–13	30	1–158
Balanites aegyptica	19	22	15–28	14	2–62

significantly greater in the larger trees than in the smaller ones (Table 3). The percent of nests in masses was also much greated in the larger trees, this difference being particularly well-marked in *Acacia tortilis* (the umbrella thorn), which has a large, spreading, flat-topped crown, compared with *Acacia thomasi*, which has a small narrow crown with whiplike branches.

There was little or no difference in the average number of *arnaudi* nests per nest mass in small and large trees, for either species of tree (Table 3). The situation is different when we look at variability in number of nests per nest mass, this being much greater in the large colonies (Fig. 6). Of special interest are the rare cases of large nest masses each composed of 6 to 12 nests more or less fused together (Fig. 4) because such masses come closest to the number of nest chambers in the compound nest of *Philetairus*. During one breeding period of *Philetairus* in the Kalahari, Maclean (1973: 223) noted that the number of chambers in 22 nest masses in 14 trees ranged from 4 to 50 (average 16); in the next breeding period 19 nest masses contained from 6 to 50 (average 13).

Under what conditions do the rare instances of large masses arise in *arnaudi*? As all of them are to be found in large colonies, it would seem to some degree a matter of chance—the more nests in a tree the more nests will be in physical contact. If it were a purely random matter, one might expect the rare instances to fit into a Poisson distribution. One of the properties of this statistical distribution is that it is determined entirely by the mean (Dixon and Massey 1969) which in this case ranged from 2.3 to 2.6 (Table 3). But even assuming a Poisson distribution here, there would still be extremely little chance of obtaining nest masses as large as six or greater (Dixon and Massey 1969: 533). Some more systematic factor must be responsible for the more extreme massing. The birds show some tendency to defend their nests from

TABLE 3

NUMBER AND MASSING OF NESTS OF *Pseudonigrita arnaudi* INCREASES WITH SIZE OF TREE[1]

	Acacia thomasi		*Acacia tortilis*	
	Small	Large	Small	Large
Range in height (feet)	8–20	21–30	9–20	21–40
Average height (feet)	16	26	18	28
Number of trees	32	12	19	27
Nests per tree (average)	3	10	11	48
Nest masses per tree (average)	1	2	1	8
Percent of nests in masses	36	46	22	44
Nests per mass (average)	2.4	2.3	2.4	2.6

[1] Comparing small and large trees for *A. thomasi*, $z = 3.27$, $P = 0.001$; for *A. tortilis*, $z = 2.39$, $P = 0.008$ (Dixon and Massey 1969: 116).

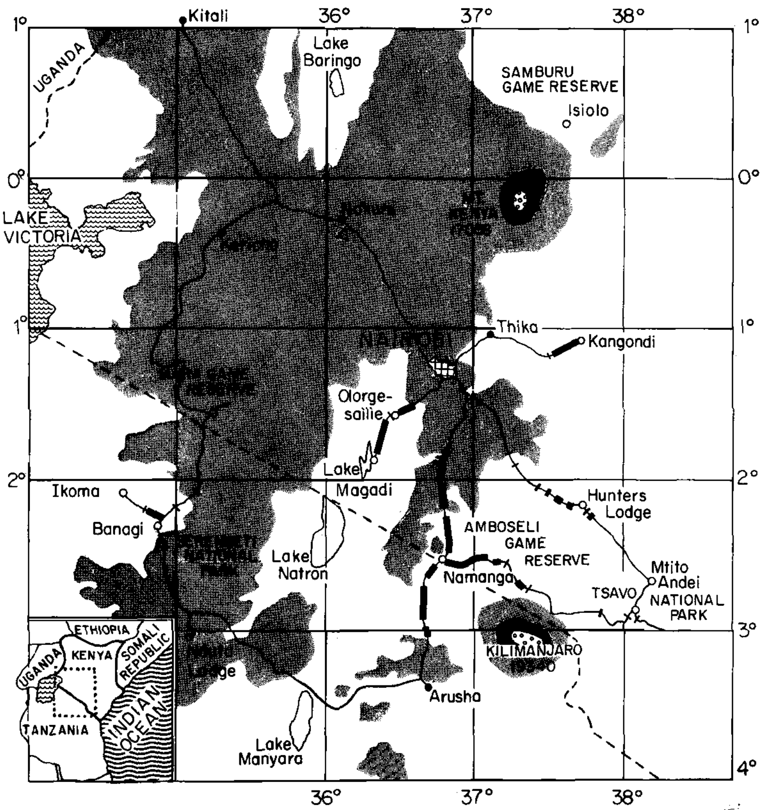

Fig. 5. The roads surveyed for colonies of *Pseudonigrita arnaudi*, July–August 1973. Inset to lower left shows its general location in East Africa by dotted lines. The location of colonies visible from the road is shown by black bars across road; colonies closer together than 3 km road distance are shown as continuous black bars. Highlands above 5000 feet (1524 m) are shaded. (Map based on Atlas of Kenya, 1962 ed.)

other birds, and possibly nest massing is increased by a tendency of individual pairs to build new nests near their old nests, combined with the fact that many old nests last from one year to the next in the dry climate the birds inhabit.

If we compare the percentage of all nests in physical contact for *arnaudi* and *mahali*, we find a very similar distribution of different sizes of nest masses for both species (Fig. 7). We saw no *mahali* colonies with more than 5 nests in a mass, but we found some *arnaudi* colonies with 6, 8, 10, and 12 nests massed together. In part this difference is associated with the much greater size of some of the *arnaudi* colonies compared with *mahali* colonies. Colonies of *arnaudi* contained from 1 to 157 nests in a tree (196 colonies, average 18.6), of *mahali* only 3 to 32 nests (34 colonies, average 13.9).

Factors that help determine size of colony—*P. arnaudi* colonies are often larger than *mahali* colonies for at least three reasons. These are differences in (1) feeding habits, (2) body size, and (3) sleeping habits. In all three respects *arnaudi* resembles *Philetairus socius*, as well as differing from *mahali*. Size of colony tree does not seem to be an important difference between *arnaudi* and *mahali*, and even when *mahali* colonies occur in large trees there are generally many fewer nests than is true of *arnaudi* colonies. Colonies of *socius* are usually in large trees.

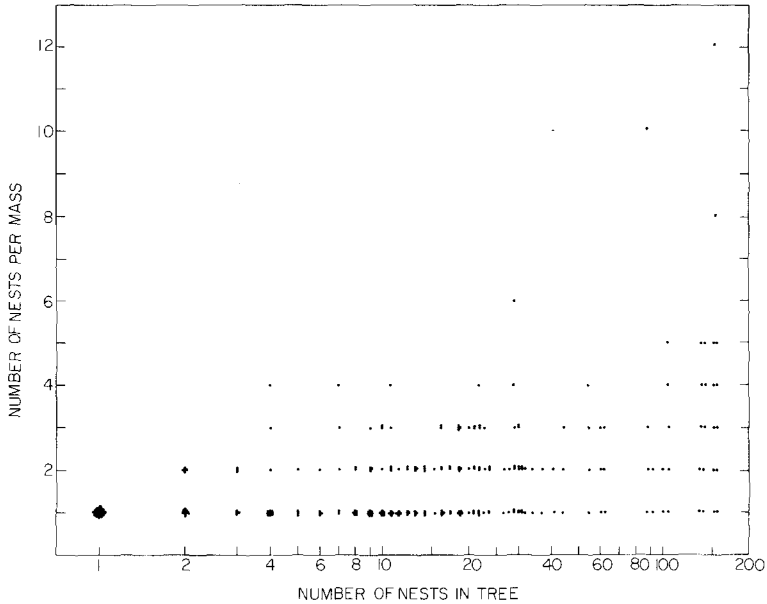

Fig. 6. In colonies of *Pseudonigrita arnaudi* the variability in size of nest masses is greatest in the larger trees. A semilogarithmic scale is used for size of colony (abscissa).

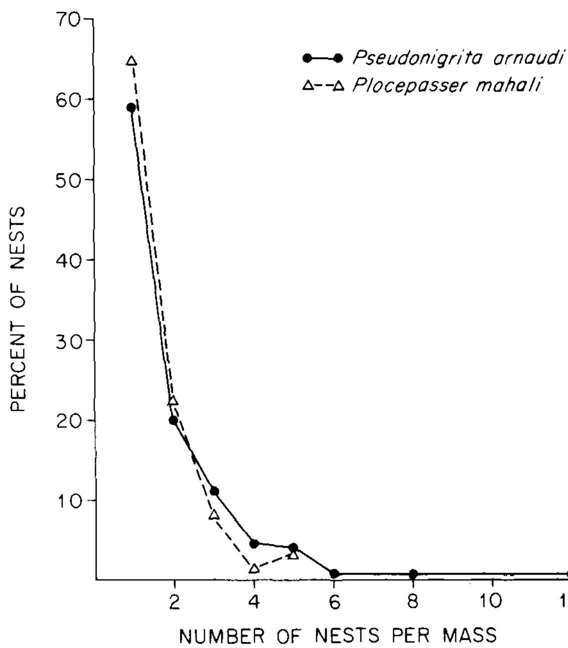

Fig. 7. Percentage of nests in different sized contact groups is very similar in the two species indicated, but the size of nest mass reached is greater for *Pseudonigrita arnaudi* than for *Plocepasser mahali* colonies.

TABLE 4

Plocepasser mahali SLEEPS ONE BIRD TO A NEST; THE SMALLER *Pseudonigrita arnaudi* USUALLY SLEEPS IN GROUPS

Species	Number of birds	Percent of nests occupied	Number of birds per nest			
			1	2	3	4 to 7
Plocepasser	35	30	35	0	0	0
Pseudonigrita	161	72	15	42	51	53

Many years ago, Friedmann (1935) in a review of bird societies of the world noted that birds whose reproductive area is the same as their feeding area are generally solitary nesters, whereas those with spatially distinct nesting and feeding grounds are often colonial breeders, provided nesting places safe from predators are available. During the nonbreeding and dry season, *arnaudi* is often absent from the colony trees during a good part of the day, and may be found in feeding flocks of 10 to 300 birds in the adjoining country or in more distant places in the morning and afternoon. In contrast, the *mahali* we watched during the nonbreeding season often fed in small flocks or as scattered pairs or individuals close to the colony tree, usually within 50 m. Like *arnaudi* the *mahali* feed generally on the ground. As Maclean (1973) showed, *socius* often feeds in flocks well away from the colony tree throughout the year, although generally within 1.5 km. Both *arnaudi* and *socius* also feed beneath or near the colony tree at times.

The smaller body size of *arnaudi* means that a given area or amount of food can support more individuals than of the much larger *mahali*. The average body weight of 13 *arnaudi* we captured in Kenya was 18.3 g, of 2 *mahali* 45.5 g. This difference in body size has important implications for the temperature regulation and therefore for the sleeping habits of the birds. In three different places where we studied *arnaudi* and *mahali* the ambient nighttime minimum temperatures ranged from 17.2°C to 22.2°C at the time of our study. During the cool tropical night the small *arnaudi* often conserve body heat by sleeping in groups of up to five or even more birds in a nest, whereas the larger *mahali* sleep singly (Table 4). In *mahali* colonies most of the nests remain unoccupied at night whereas in *arnaudi* colonies most of the nests in the tree are occupied. *Philetairus socius* often sleeps in groups of 2 to 5 birds to a nest chamber (White et al. 1975). Group sleeping in *arnaudi* and *socius* means that more birds can be accommodated in one tree and by a given number of nests, and is one factor helping to account for the greater number of individuals in their colonies than with *mahali*.

Massing of nests and security from predators.—Other factors than size of colony may facilitate the massing of nests together. In northwestern Tanzania where we found the small southern race *dorsalis* of *Pseudonigrita arnaudi*, many of the birds were nesting in the small whistling thorn (*Acacia drepanolobium*), which is an ant gall acacia (Dale and Greenway 1961). The galls on these little trees were inhabited by colonies of aggressive ants that instantly swarmed out and attacked us whenever we touched the tree in an attempt to collect a nest. These ants must furnish an effective defense for the birds against a number of predators. The added security to the birds would be expected to enhance the attractiveness of ant gall acacias as nesting sites. As shown by Table 5, in 57 colonies of *arnaudi* in ant gall acacias 19% of the nests were in physical contact, whereas none of the nests were massed together in 81 colonies of *arnaudi* nesting in the same general area in small specimens of

TABLE 5

MASSING OF NESTS OF *Pseudonigrita arnaudi dorsalis* IN THE SERENGETI NATIONAL PARK, TANZANIA, IN SMALL ACACIA TREES

Acacia species	Ant-galls present?	Number of trees	Height of trees	Percent trees with massed nests
A. drepanolobium	Yes	57	6–14	19[1]
A. senegal	No	81	15–25	0

[1] Ten trees with nests in pairs, one tree with three nests in mass.

Acacia senegal comparable in size to the other species of acacia but not having ant galls. On a previous trip to East Africa we had found an acacia crowded with ant galls and nests of the northern race of this bird (*P. a. arnaudi*) in which nine nests were in physical contact (Plate 8 in Collias and Collias 1964).

We never found *mahali* nesting in association with ants, but these birds are much larger than *arnaudi* and their small colonies may engage in cooperative group defense. Thus we watched one colony cooperate in driving away a flock of wood hoopoes that happened to pass through their colony tree. We also saw this colony drive off two strange *mahali* that invaded the colony. We saw no such cooperative attacks in the many colonies of *arnaudi* we observed.

Consolidation of nests of a colony into a few large masses in Philetairus.—The Sociable Weaver generally nests in large acacia trees, such as *Acacia giraffae*, with strong, heavy boughs capable of supporting the large nest masses characteristic of this bird. This species of acacia does not occur in East Africa where *Pseudonigrita arnaudi* is found. For a comparable situation we took only 62 colonies of *arnaudi* that were in large acacia trees of three other species (*tortilis, senegal,* and *xanthophloea*), and we found an average of 5.7 nest masses per tree, with 77% of the nests in contact with other nests. We then compared these figures with corresponding ones for 150 colonies of *Philetairus* from a roadside survey we took alongside the Kuruman River southeast of the Kalahari National Park in 1969. Nest masses, besides being larger, were fewer in number in a colony tree in *Philetairus* than in *Pseudonigrita*. In *Philetairus* as the separate masses grow they often fuse together. All of the nest chambers of *Philetairus* are consolidated into communal nest masses, unlike the case in *Pseudonigrita*, and there were on the average only one or two nest masses per tree in *Philetairus* colonies.

Possible origin of the compound roof to the nest of Philetairus.—Having the nest entrance opening directly downward and below the nest probably arose in evolution before the communal roof, as this entrance orientation is present today in *Pseudonigrita* as well as in *Philetairus*. Quite often *arnaudi* builds a new nest directly beneath and broadly fused to an older nest, which could then be the precursor of a much thickened roof in evolution.

We sampled at random 52 contact pairs of nests of *arnaudi*, each consisting of an old and a new nest, and in 48 of these the new nest was built on the same drooping branch or twigs immediately below or distal to the old nest. It is easy to distinguish the pale brownish-yellow fresh nests with their many projecting grass stems from the dark gray old and weathered nests with the grass ends broken or flattened down on the nest's outer surface.

Use of many twigs as well as of long dry grass stems reinforces and strengthens the roof of *Philetairus* nests as Maclean (1973) described in the Kalahari Desert. In this use of twigs in the roof *Philetairus* is convergent with the buffalo weavers (Bubalornithinae), but *Philetairus* does not always use many twigs in the nest roof. We encountered some *Philetairus* colonies in cultivated country in the Western Transvaal near the eastern border of the range of the species (Collias and Collias 1964). In this region where suitable twigs were apparently scarce, though the birds used some twigs, both thorny and nonthorny in the nest roofs, they supplemented them with many more dry stems of an herbaceous composite that grew abundantly near the nest trees and which we were told was an introduced weed. The roof of these nest masses consisted largely of dry stems or straws of various grasses (Fig. 1). Some of the twigs on the roof were obviously too large for the birds to carry up (a conclusion later confirmed by repeated observation of aviary housed *Philetairus*) and probably just fell on the roof from overhanging branchlets.

DISCUSSION

This discussion elaborates a multiple factor theory of the origin of nest aggregation and of the compound nest in the evolution of the Ploceidae with special reference to *Philetairus* and its more immediate relatives in the Plocepasserinae. We will discuss each factor as it relates to other factors in an attempt to delineate the role of each factor of evolution in an interacting system. Also by studying cases of convergent evolution, as between the sparrow weavers (Plocepasserinae) and the true weavers (Ploceinae) or other birds, we should gain some idea of the most favorable conditions for the origin of nest aggregation and of the compound nest.

Maclean (1973) suggested for *Philetairus socius* that "a paucity of trees such as occurs over most of its range today would have favored the evolution of a communal nest so as to fit as many pairs as possible into the limited number of available nest sites." He noted in the Kalahari that where there was only one tree per mile that he judged to be suitable for nesting by *Philetairus*, it was almost sure to be occupied. But as the number of trees increased up to 49 trees per mile the percentage occupation by the birds fell to less than 3%.

Generally *Philetairus* colonies are to be found in large trees, but *Pseudonigrita arnaudi* nests in a wide range of tree sizes. In other words the range of choices of suitable nest sites available to this species is so wide that it seems much less likely to suffer from a shortage of nest sites than is *Philetairus*. Places that might conceivably have a shortage of potential nest sites would be expected to favor crowding of the birds into the few sites available.

As shown by the results of this report, large size of a colony in *arnaudi* increases the probability of physical contact between nests. In turn, increase in colony size is favored by nesting in large trees, by sleeping more than one bird to a nest, and by otherwise favorable conditions of food supply and nesting materials.

Social stimulation may help stimulate more nest building and breeding than takes place in very small colonies of the same species, especially by extending the breeding season as has been shown experimentally for the Village Weaver, *Ploceus cucullatus* (Collias et al. 1971). Deserted colonies of *Pseudonigrita arnaudi* are likely to be very small, and may have lacked sufficient social stimulus to keep growing, although other unknown causes may terminate a colony. In the Amboseli Game Reserve we saw 26 such colonies, mostly in *Acacia tortilis*, in which all the nests were dark gray, old, and faded, with an average of only 4 to 5 nests per tree. Although the Plocepasserinae may build nests the year round at their colony sites, the relationship of social stimulation to gregarious breeding and to rate of nest building in this subfamily has not been investigated.

A general and important difference between the Plocepasserinae and the Ploceinae is the permanent residence of the former in the colony trees. Year-round occupancy of the nesting tree by the sparrow weavers at least for sleeping in the nests is favored by the arid climate they inhabit and the use of dry grasses for nest materials. Old nests have thick walls and sturdy construction and in a dry climate may last for months and from one breeding period to the next. *Plocepasser*, *Pseudonigrita*, and *Philetairus* may build new nests onto old nests in the same tree from year to year.

In the true weavers or Ploceinae, parallel evolution with the Plocepasserinae has resulted in the considerable massing of nests seen, for example, in the large colonies of the Chestnut Weaver (*Ploceus rubiginosus*) (Collias and Collias 1964). Physical contact of nests is also very common in the crowded colonies of Speke's Weaver (*Ploceus spekei*). In an active colony of this species some 14 km north of Nakuru, Kenya, 24 nests were in physical contact with at least one other nest and 24 were not. Both species, like the Plocepasserinae, often inhabit semiarid or arid savanna. In general, the Ploceinae, unlike the Plocepasserinae, desert their nesting trees in the dry season, so one can conclude that permanent residence is not a requirement for nest massing, although it enhances the tendency to massing.

The advantage of nest massing to thermal regulation confers a benefit and a positive selection pressure that may have led to increasing consolidation of nests in evolution. White et al. (1975) found in *Philetairus socius* in the Kalahari that a large nest mass heats up from the sun more slowly during the day than a small mass and loses heat more slowly at night. Group sleeping in the nest chambers helps add heat to the nest mass during the cold winter nights of the Kalahari when the temperature may fall to freezing or even lower. Any thermal advantages of consolidation of nests in the Plocepasserinae is reinforced by other positive selection pressures, as consolidation also helps relieve the problem of shortage of nest sites in suitable trees.

Increased security from predators may permit colonial breeding and nest massing irrespective of the nature of the agency enhancing security, whether it be thorns, ants, bees, wasps, or hawks, eagles, or vultures nesting in the same tree with the weaverbirds (Collias and Collias 1964). In a review of bird-insect nesting associations Moreau (1936) showed that a number of species of weavers and other birds build alongside nests of aculeate Hymenoptera in Africa and Asia, as do some icterids in America. In Nigeria, McLaren (1950) noted that nests of the Bronze Mannikin (*Lonchura cucullata*) when built near the nests of red weaver ants (*Oecophylla smaragdina*) were concentrated closer together, in contrast to the solitary nests found in trees not having the protection of the ants. Similarly in Ghana, Grimes (1973) recently found a significant association between the occurrence of nests of Heuglin's Weaver (*Ploceus atrogularis*) and of nests of red weaver ants in the same tree.

We have shown in the present report that *Pseudonigrita arnaudi* in ant gall acacias have a greater tendency to place their nests in physical contact than when nesting in acacias of comparable size but lacking the protection of the ants. We also saw ant colonies in the characteristically inflated base of the thorns of *Acacia giraffae* trees containing *Philetairus* colonies near Barberspan in the Western Transvaal in 1957 (Collias and Collias 1964), but Maclean (1973) found no ant colonies associated with *Philetairus* in acacias in the Kalahari. Trees of different species may have only an occasional or a more or less regular association with ants (Wilson 1971). The theory we wish to advance is that a protective association with ants or other dangerous animals may allow or increase the tendency for birds to aggregate their nests whenever and wherever this favorable circumstance occurs. Possibly in *Philetairus* the large, communal roof has replaced or reduced the need for other security measures, such as nesting in close association with aggressive and dangerous insects.

Security from predators enhances nest aggregation and massing, but there may also be a feedback relationship, in that crowding of many individual nests together in turn may enhance the security of the more central nests, either by more effective warning of the presence of a predator, or simply by satiation of predators when breeding is highly synchronized (Elgood and Ward 1963). Maclean (1973) found that most of the successful clutches in his study of *Philetairus* were in the two largest colonies, which also had the largest nest masses, and he suggested (p. 238) that "the very size of the nest masses might mean that a cobra eats its fill from the more peripheral chambers before it reaches the others, so that at least some young will survive." Furthermore the ability of *Philetairus* to utilize its nest for breeding at any time of the year when other conditions are favorable makes it possible for this bird even to breed in winter when its chief enemy, the cape cobra, is hibernating (Maclean 1973, Bartholomew et al. 1976).

Small birds such as most passerines have many enemies and only exceptionally breed in colonies (Friedmann 1935). Very small birds, such as *Sporopipes* (Collias and Collias 1964), and the Estrildidae (Immelmann 1965), generally are much less likely to breed in close colonies than are most weaverbirds, and pairs usually nest in separate trees or bushes or in only small colonies. *Sporopipes squamifrons*, the Scaly-feathered Finch, often occurs in the same habitat and geographic range with *Philetairus*, and can frequently be seen under the same tree. Whereas the Sociable Weaver weighs on the average about 27 g, the Scaly-feathered Finch weighs only about 11 g (66 birds in Rhodesia, average weight 10.9 g) (Ginn 1973).

We may now speculate on the origin and evolution of the communal roof. Having a roof over each individual nest is the most general characteristic of the weaverbirds as a family and helps predispose them to close nest aggregation by screening birds in the nests to some extent from each others' territorial defense reactions, as Emlen (1952) has shown for Cliff Swallows (*Petrochelidon pyrrhonota*), a species renowned for its large breeding aggregations in which the individual mud nests are often in physical contact.

As we have seen, *Pseudonigrita arnaudi* often build a new nest directly beneath and fused to an older nest. The latter might perhaps then be the precursor of the communal roof in evolution. Having the nest entrances open directly downward as in *Pseudonigrita* we think was a preadaptation favoring the origin of a communal roof. The nest entrance is the center of the territorial defense reactions of the birds and one would expect more tolerance of neighbors on or near the roof than near the entrance. Building on a common roof might be permitted where no trespassing near the entrances would be tolerated, as is now seen in *Philetairus*.

Once a roof appeared its further elaboration in evolution would be favored by its thermal advantages and whatever added security it might afford from predators. In fact the enhancement of security from many predators by the presence of a communal roof could well be a key feature in the evolutionary development of the compound nest of birds, a viewpoint already elaborated to some degree elsewhere

(Collias and Collias 1964). Such protection might be especially effective against many bird and mammal predators, rather than against snakes. The compound nests of the Sociable Weaver, of the Black Buffalo Weaver (*Bubalornis albirostris*) of Africa, and of the Monk Parakeet (*Myiopsitta monachus*) of Argentina all resemble each other in containing a great many twigs, which are often thorny. Hudson (1920) suggested that the roof of the Monk Parakeet nest protected the birds against the depredations of opossums. The Palm Chat (*Dulus dominicus*) of Haiti builds a compound nest which also is a mass of twigs, and Wetmore and Swales (1931) were of the opinion that "the stick nest is without question a safeguard against owls and other similar predators."

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