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BEHAVIOR OF THE GREY-CAPPED SOCIAL WEAVER (*PSEUDONIGRITA ARNAUDI*) IN KENYA

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ABSTRACT.—We observed color-banded individuals of the Grey-capped Social Weaver (*Pseudonigrita arnaudi,* Ploceidae) in Kenya during breeding and nonbreeding periods. In each colony, one to several groups centered about different families slept in their nests the year round in the same acacia tree (considered a colony). Nest territories were generally not defended against members of other groups in the same tree. Birds from other colonies, however, were usually attacked whenever they landed in the colony tree. The birds foraged on the ground in communal feeding areas and were organized into dominance hierarchies but did not defend feeding territories. Members of different groups from the same colony tolerated each other when feeding on the ground more than they did birds from other colonies. Aggression was rare or absent between members of the same group. The roofed nests had two entrance or exit holes opening below, one of which was closed in a brood nest before eggs were laid and opened again just before or after the young left the nest. Both members of a pair incubated. Other birds in adult plumage and immature birds from previous broods often helped the pair build nests and feed nestlings. The behavior of *P. arnaudi* is compared with that of the related *Plocepasser mahali* and *Philetairus socius* and resembles the latter most closely. *Received 2 April 1979, accepted 10 December 1979.*

THE weaverbirds (Ploceidae) are excellent subjects for investigating the evolution of avian sociality, particularly in relation to nest-building behavior. The object of this report is to describe the social behavior of the Grey-capped Social Weaver[1] (*Pseudonigrita arnaudi*) and to compare its nest and behavior with that of related species. Aside from a brief, preliminary report (Collias and Collias 1978a), there has been no previous general study of the social and breeding behavior of this species. We have described its nest-building behavior (Collias and Collias 1964). It and two species that we previously studied, *Plocepasser mahali,* the White-browed Sparrow Weaver of East Africa (Collias and Collias 1978b, 1978d), and *Philetairus socius,* the Sociable Weaver of southwestern Africa (E. Collias and N. Collias 1978, 1980), have often been united together into one subfamily, the Plocepasserinae, in the Ploceidae. Their taxonomic relations have recently been discussed by Bock and Morony (1978) and by Bentz (1979), who support the idea of a close relationship between them on morphological grounds. Bentz has grouped them with *Sporopipes* and *Passer* into one subfamily, the Passerinae.

[1] We prefer the name Grey-capped Social Weaver to Grey-headed Social Weaver (Mackworth-Praed and Grant 1960, Williams 1963) for the English name, because the former is much more accurate (Fig. 1a).

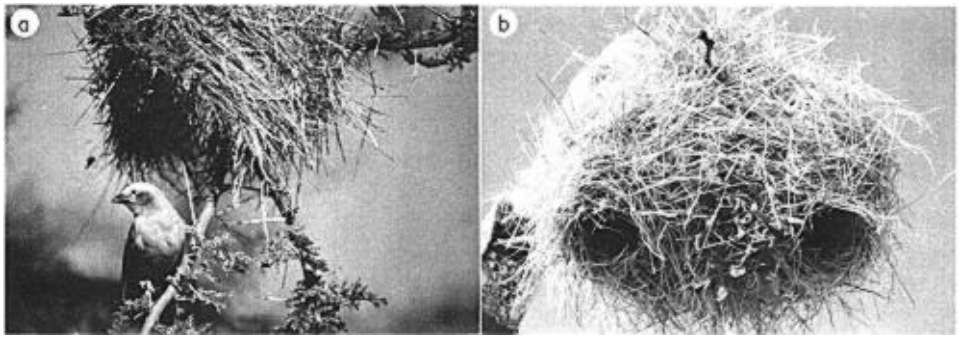

Fig. 1. (a) Grey-capped Social Weaver beneath its nest; (b) nest viewed from below showing two entrance or exit holes.

STUDY AREA AND METHODS

We observed *Pseudonigrita arnaudi* during April–July 1978 in the Rift Valley of Kenya at the Olorgesailie National Prehistoric Site (1°35′S, 36°27′E; elevation 980 m), 70 km southwest of Nairobi. We made additional observations and took a census of nests at the Amboseli National Park (2°40′S, 37°10′E; elevation 1,100 m) in southeast Kenya. The study areas consisted largely of semiarid acacia savanna, most of which was grazing country used by various game animals and by the pastoral Masai for their cattle. In general, there seems to be a close correlation between the distribution of *P. arnaudi* and Masai country. At Olorgesailie, the three colonies (by a colony we mean all the resident birds and nests in one tree) we observed most closely were within 50 m of our doorstep. Colonies of this species are not usually found near human habitation, however.

Using mist nets and a drop trap, we captured 50 adult and immature birds. These birds plus another 13 nestlings were each banded with two individually distinctive color bands, the same on each leg. The sexes are identical in appearance, and we usually inferred sex from behavioral criteria; near the end of the study one male bird was sexed by laparotomy as a check on these criteria. Immature *P. arnaudi* are readily distinguished by their dull brownish-gray crowns in contrast to the gray-white crowns of the adults. The birds were very tame and easily observed from a few meters at Olorgesailie.

Two entrance or exit holes are present in the bottom of every nest (Fig. 1b), except that one is plugged up in brood nests. We periodically checked the contents of plugged nests. Over a wide area we counted the number of nests present in different colonies and the proportion of brood nests.

Rainfall and some temperature records were kindly furnished to us by various officials or research workers. We also measured temperature changes with a maximum-minimum mercury thermometer in our open hut. Map data were taken from the Survey of Kenya maps. We measured distances between colonies with the mileage recorder in our vehicle and an optical tape measure.

BREEDING SEASON

Breeding of *P. arnaudi* is generally associated with rainfall. At both study areas there is a long dry season from June to September and two main periods of rainfall from March to May and November to December. Total rainfall for the first half of 1978 was 470 mm at Olorgesailie (measured by the resident manager). During our study period in May–July, the average maximum temperature was 28.8°C (24.4–30.6°C) and the average minimum temperature was 18.5°C (16.1–20°C).

In the Nest Record Scheme of the Ornithological Sub-Committee of the East African Natural History Society, most breeding records of *P. arnaudi* in Kenya are for April, May, and June (Hazel Britton pers. comm.). During the dry season (June–Sept) of 1973, an exceptionally dry year, we found no breeding at all by this species in several parts of Kenya (Collias and Collias 1977). In 1978, an exceptionally wet year, Grey-capped Social Weavers had already been breeding for some time when we arrived in Kenya at the end of March. At Olorgesailie, breeding ended about a

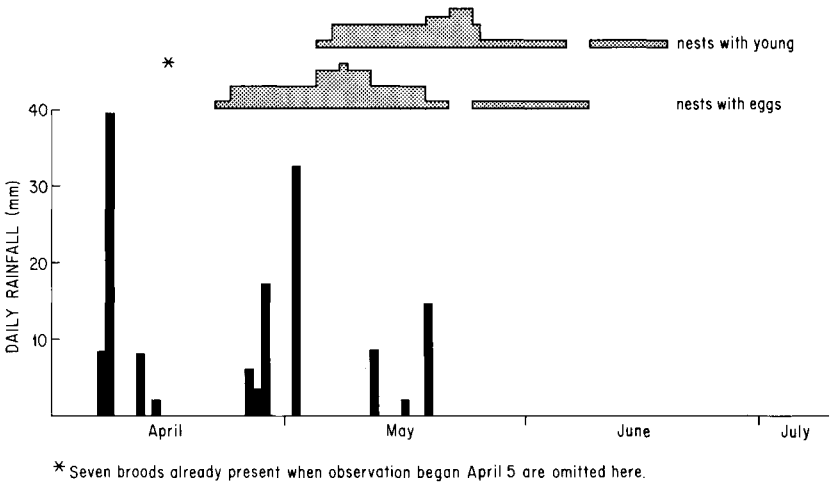

Fig. 2. Daily rainfall at Olorgesailie during the period of our study in 1978, as related to breeding activity of *Pseudonigrita arnaudi*. The smallest step in shaded graph represents one nest with eggs or young.

month after the rains ceased (Fig. 2). The rains in the dry savanna country of Kenya are erratic and breeding may occur at any time of year if there is sufficient rain. According to the Nest Record Scheme (see above), G. R. Cunningham-van Someren has found *P. arnaudi* nests with eggs during every month of the year along the Magadi road that leads to Olorgesailie (except December, when he did not visit the area).

At Amboseli on 28–29 April 1978, during active breeding of the birds, we counted 260 nests of *P. arnaudi* in 21 colonies along a 5.3-km stretch of the road leading east from the new National Park Headquarters. Of these nests, 34% had only one hole and thus, apparently, were or had been brood nests. We often heard nestlings and saw adults carrying food. We repeated the census of these same colonies on 28–29 May, after the rains had stopped and breeding had largely ended, and found 312 nests, of which only 10% possessed one hole. Very little breeding activity was apparent, and it is likely some of these one-hole nests were not active but had been preyed upon and abandoned.

We considered the possibility that, when compared with very small colonies, social stimulation in larger colonies might help to prolong breeding (Collias et al. 1971). Assuming that one-hole nests were or had been brood nests, we counted the frequency of different nests in 32 colonies at the Olorgesailie study area and at Amboseli during late April. In 12 small colonies, each with 2–10 nests (average 4.5), 26% were brood (one-hole) nests, compared with 32% in 20 larger colonies, each with 11–60 nests (average 28.6). There was no significant difference in the relative frequency of brood nests between small and large colonies, although there seemed to be a tendency toward a smaller proportion of brood nests in very small colonies (Chi-square 2.8, $P = 0.1$).

Population Density

The three colonies we studied most, Banda 1, Central, and Picnic colonies, occurred in a 0.4-ha portion of the Olorgesailie study area (Fig. 3). The colony trees

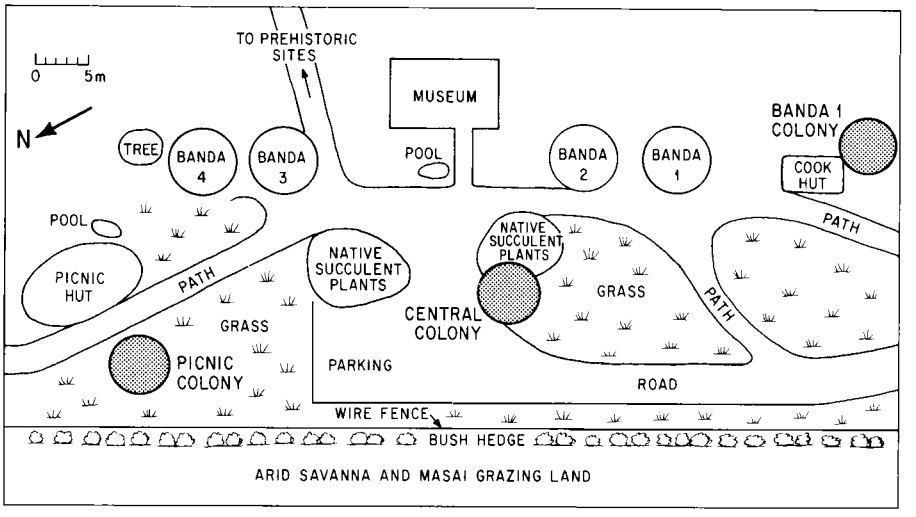

Fig. 3. Map of study area at the National Prehistoric Site, Olorgesailie, Kenya, showing location of the three principal colonies (shaded) observed.

were 38 and 35 m apart. Banda 1 Colony was in an *Acacia mellifera* 5.2 m high; Central and Picnic colonies were in *Acacia tortilis* trees 7.0 and 5.5 m high, respectively. At the close of the breeding season, 40 birds resided in these 3 colonies, equivalent to about 100 birds/ha in the immediate vicinity of the colony trees. The birds ranged out to an unknown distance but spent most of their time within about 100 m of the colony tree during the breeding season. There were no definite or defended boundaries between colonies.

In the 3 main study colonies during April–June, 7 of the 15 clutches that were laid failed during the egg or nestling stage. In Banda 1 and Central colonies, we banded almost all the birds in April, enabling some estimate of changes in population size during the long rains. Mortality of adult and immature but independent birds in this period was slight, and population size increased by 15%, from 26 birds present in April to 30 in July at the close of breeding. More nests were built after the onset of the dry season, when freshly dried and strong grass stems became more available. During the same period of time the average number of nests per bird in these two colonies increased from 0.6 to 1.0.

Colony Structure

The nests in a colony tree and the birds owning them were organized about family groups. We judged group membership based on sleeping, resting, building, breeding, and territorial behavior. Three of the eight families had adult helpers as well as immature birds, but we had no information on the genetic relatedness of these adult helpers. The distribution in the tree of groups in the Central Colony is shown in Fig. 4. The distance separating nests belonging to the same group or family varied from physical contact to 2–3 m. Each group had only one brood nest at a time.

Banda 1, Central, and Picnic colonies consisted of 1, 5, and 2 groups, respectively. Only two birds incubated each brood nest. One of these birds, presumably the male, was much more aggressive than the other, presumed to be the female. The Southwest

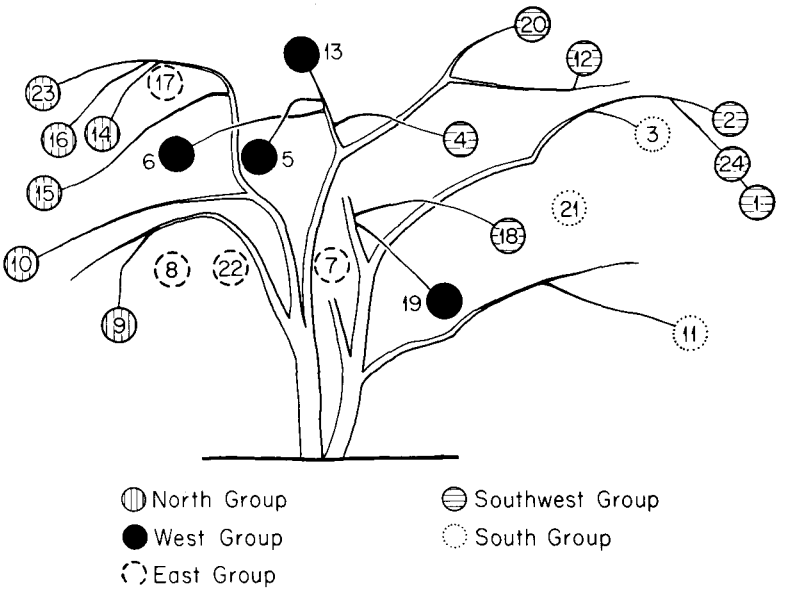

Fig. 4. View of Central Colony from west side showing location of nests belonging to the different groups in the acacia tree. Those nests numbered 3, 4, 5, 7, 10, and 13 were brood nests.

Group of the Central Colony contained a second pair of adults in addition to the dominant breeding pair. The number of independent young birds in immature plumage varied from zero to five per family. In Picnic Colony, the Northeast Group, situated near the entrance of a nearby picnic hut, began building a nest near the Southwest Group in the opposite side of the tree after losing their brood from an unknown cause.

The different families or groups in the same tree did not normally seem to defend territories against each other. They did not often trespass other than to join in mobbing some predator in the tree. Conspecifics from another colony that landed in the tree near a nest were customarily driven out by the owners of the nest or, in their absence, sometimes by a neighbor. In six groups tested, a mounted specimen of *P. arnaudi* fastened to a twig near a brood nest elicited vigorous attacks, particularly by the adult breeding pair. In the territorial display, which is often given to intruders, the wings are drooped and vibrated while the short tail is cocked upward but held still, and the bird utters a fairly loud and somewhat plaintive *chee-chee-chee*. This display was also given to the mounted specimen.

We have occasionally seen groups of unbanded *P. arnaudi* battling persistently for the same nests. In one case in the Amboseli area, 10 fights for 2 neighboring 2-hole nests, involving 6 birds, were seen in 1 h.

Each group roosted in its own nests. One to five (average, 2.4) birds slept in a single nest. At dusk the birds often went in and out of different nests for a time before settling down for the night. If, after entering a nest alone for the night, a bird was not joined by another, it often left that nest to enter one in which there was another bird. Only about two-thirds of the nests were occupied at night. Both parents might sleep in the brood nest with small nestlings in their first week, but only the female roosted there after the nestlings grew large and were in their third

TABLE 1. Domination:subordination (D:S) ratios (number of birds dominated:number of birds to which subordinate) in a local population of *Pseudonigrita arnaudi* in Kenya, 1978.

	Number of birds	D:S totals	D:S average/bird
Sex differences			
Adult males	7	107:17	15:2
Adult females	7	21:28	3:4
Age differences			
Adults	27	157:81	6:3
Immatures	21	32:86	2:4
Residency			
Local birds	36	186:138	5:4
Strangers	11	3:34	1:10
Different colonies			
Central	22	144:75	7:3
Picnic	8	33:37	4:5
Banda 1	6	9:26	2:4

week. During the height of the dry season, when the birds were away from the colony tree much of the day, they invariably showed up again in the evening, often shortly before time to roost (Collias and Collias 1977).

DOMINANCE RELATIONS

There was a consistent dominance hierarchy involving all the individuals of the three study colonies. This hierarchy was determined by noting pecks or threats and avoidance interactions between banded individuals at millet or bread crumbs placed on the ground at varying distances from the colonies. Dominance relations were consistent between any two individuals among the three colonies, regardless of the location of their interactions. Thus, out of 65 paired encounters between different birds in which 2 or more pecks were observed, there were only 4 exceptions to consistency with the first peck. This relationship was highly significant by a binomial test ($z = 6$, $P < 0.00003$, Siegel 1956: 41). It follows that even one paired encounter is almost invariably sufficient to indicate which of two birds is dominant and which is subordinate. We observed 298 (43%) of the 703 possible paired relations between 38 color-banded individuals of the 3 colonies, as calculated by the formula $n(n - 1)/2$. Of 276 possible paired relations in Central Colony, 74% were seen.

Tolerance within family groups was much greater than between family groups occupying the same tree. Within the five groups of Central Colony and within the two groups of Picnic Colony, a total of only 36 pecks or threats was observed. In contrast, 169 pecks or threats were seen between birds belonging to these two colonies but from different family groups in the same tree. The dominance of a family depended largely on its adult breeding male. Twelve of the 15 possible paired encounters between the 6 adult males of Central Colony were observed, and there was no exception indicated by these data to a linear order of dominance. Most dominant were BO, AO, and RR. However, BO was never seen to interact aggressively with AO or RR.

The number of different birds aggressively dominated by a given individual in relation to the number of birds to which it was subordinate is the domination:subordination ratio. Table 1 shows such ratios for the banded birds we

studied as they relate to sex, age, and residence. Adult males were far more aggressive and dominant than were adult females. Within a mated pair there was complete tolerance in that no male was ever seen to peck or threaten his mate. Adults dominated immature birds. There was no difference between the average body weight of adult males (19.9 g, $n = 7$) and adult females (19.9 g, $n = 7$), but adult birds (19.8 ± 0.27 g, $n = 25$) were a gram heavier than independent immature birds (18.8 ± 0.20 g, $n = 17$) ($t = 2.54$, $P < 0.01$).

Local birds from the three colonies dominated strangers from other colonies at grain or bread stations near their home colony. Some of the strangers must have been birds high in dominance, and fights with strangers were not uncommon. The largest colony, Central, had a greater proportion of dominant birds than did Picnic Colony, whose birds in turn were generally more dominant than birds from the small Banda 1 colony. Dominance relations on the ground among these three neighboring colonies, however, depended upon the individual birds involved rather than their home colony.

Foraging Behavior

Grey-capped Social Weavers feed on grass seeds and insects, but we made no attempt to analyze crop contents systematically. Insects especially are fed to nestlings, and we could see the birds bringing caterpillars, grasshoppers, and various other insects to their nests. Generally, the insects were captured within about 50 m of the colony tree. Birds from different colonies might form foraging flocks at any time of year but particularly during the dry season, when they spent much of their time in the fields. As a feeding flock drifted along, individuals left behind would fly up to rejoin the main body. The species also has a flight call, a loud *sreep!*. The birds feed on bare ground between tall stalks of bunch-grasses, such as the common needle grass *Aristida adscensionis*. The pale grey cap is conspicuous, made more so by pecking movements, and may serve as a visual cue indicating good food concentrations to other birds. Occasionally at a concentration of grain we heard clicking notes. At all times of year the birds seem to spend most of their time foraging. During the dry season (August) of the very dry year of 1973, when food was presumably scarce, 10 adult-plumaged *P. arnaudi* had an average weight of only 18.3 ± 0.32 g, significantly ($t = 3.25$, $P < 0.005$) lighter (7.6%) than the average of 25 adults (19.8 ± 0.27 g) in the long rains of April and May of the very wet year of 1978, in the same general region of Olorgesailie.

We used artificial feeding with millet to keep the birds near their own colony tree or to concentrate them near other colonies or in intervening ground. Whenever we placed a pile of grain on the ground near Central or Picnic colonies, it was usually not very long before local birds were joined by birds from 1 or more of 8 colonies located 100–150 m away and near the entrance gate to the prehistoric site. At first, one or two of the more dominant resident males would repeatedly and vigorously chase away the newcomers, but as more strangers arrived the aggression of the local males was simply swamped by the sheer numbers of the other birds. Eventually, the local males seemed to tire, would give up trying to drive off the strangers, and would join the flock in busily eating the grain.

Of perhaps 80–90 birds from entrance colonies, we color-banded 12 individually. Some visited the vicinity of Central and Picnic colonies much more frequently than did others, and these birds may have served as scouts or leaders to the grain that

we scattered near the other colonies. Of 53 visits recorded after these 12 birds were banded, more than half (28) were by only 3 birds.

There were two small pools of water at the station, and the *P. arnaudi* could be seen singly or in small groups visiting these pools to drink at almost any time from dawn to dusk.

Between about 1630 and 1730 the birds from the 3 study colonies and the entrance colonies often formed into a large, loose flock that foraged over the countryside to a distance of at least 150 m from their colonies, in the direction of a river about 2 km away. Before the pools were built at the prehistoric site, we had seen *P. arnaudi* drinking at this river at that time of day in the dry season of 1973.

BREEDING BEHAVIOR

We have previously described the nest-building behavior of *P. arnaudi* in some detail (Collias and Collias 1964). A nest freshly built in July 1978 and essentially complete measured 18 cm long, 16 cm high, and 16 cm wide, with 2 entrances, each 1.5 cm in diameter. The inside of the roof was lined with feathery grass tops. This nest consisted of 1,600 straws or grassheads and 161 rootlets. Nest building is generally a communal affair. Recently fledged young and older young of previous broods often help the parent to build, and three to six birds could be seen building a nest. Young birds often merely picked up grass heads from the ground and dropped them, and generally did less building than adults. Of 8 nests we watched being built, an adult male built the most on 6 nests, an adult female on 1, and an immature bird on 1.

Pair formation, which is an inconspicuous affair, may involve the building of a nest by the male to attract a female. Male LW (Central Colony) built most of two nests by himself and was then joined by another adult bird (OY, presumably a female), and then only this pair worked on the two nests. All birds in Central Colony were banded at this time, and OY was a new bird, coming from some other colony.

During the pre-egg stage, members of a pair begin spending much time close together. For example, in the case of RR and AB, the male persistently followed his mate about, and the pair often went off to the adjoining field where they may have copulated, as we never saw them copulate when they were at or near the colony tree. At times the male repeatedly engaged in what seemed to be a precopulatory courtship display. He would hop toward his mate, turn his back to her, and, while holding his head and body upright and tail usually down, drop his wings and vibrate them vigorously. Rarely, the male uttered a series of faint, light *chip* notes, but usually he remained silent.

We observed only two copulations, both apparently homosexual copulations between adult males and presumably merely expressions of dominance. The bottom bird in each case held the body horizontal, with its head raised a bit and tail cocked upward, and drooped and vibrated its wings. This is the same sort of posture adopted by many female passerine birds soliciting copulation and is practically identical with the territorial display of *P. arnaudi*. In one instance, male AO, which normally resided on the east side of the tree, came and perched next to a nest of male RR on the west side of the tree, assumed the horizontal display posture just described, and was mounted by RR in a complete copulation. The sex of the two birds was judged from the fact that they were far more aggressive and dominant than were their respective mates.

TABLE 2. Feeding of nestlings by *Pseudonigrita arnaudi* based on 637 feedings at nine nests.

Groups	Hours observed	Number of birds[a]	Birds feeding	Number of nestlings	Feedings·nestling^{-1}·h^{-1}
Banda 1	4.5	6 (5 ad, im)[b]	6	2	8.4
Picnic					
Southwest	1.0	3 (♂, ♀, im)	3	1	27.0
Southwest[c]	2.0	3 (♂, ♀, im)	3	1	25.5
Northeast	2.5	6 (4 ad, 2 im)	5	2	17.0
Central					
East	4.0	2 (♂, ♀)	2	1	13.8
South	4.5	2 (♂, ♀)	2	1	9.6
Southwest	7.8	7 (2♂, 2♀, 3 im)	3	3	8.7
West	4.5	6 (♂, ♀, 4 im)	2	2	6.3
North	2.0	3 (♂, ♀, im)	3	3	6.1
Average	3.6	4.2	3.2	1.8	11.4

[a] Excluding nestlings.
[b] ad = adult plumage, im = immature.
[c] A second nesting by Southwest Group.

One of the two entrances to the nest is closed by the birds before the 2–3 eggs of the clutch are laid, and it is opened again just before or just after the young leave the nest. Male and female take turns incubating the eggs, which hatch in about 14 days. Six nests were observed for details of incubation. On the average, females sat on the eggs (19 sessions, average 8.5 min on) about three times as long as did the males (22 sessions, average 2.5 min) during incubation sessions. Females spent more of their time on the eggs than off (11 times off, average 4.2 min), while the reverse was true of the males (14 times off, average 6.8 min). Only one bird sat on the eggs at a time (87 sessions, average 6.3 min on, combining both sexes), and the eggs were left uncovered 23% of the daylight hours (83 times both birds off, average 1.9 min). Incubating birds were watched going to roost twice; on one occasion only one bird entered the nest for the night, on the other night both birds did. During periods of general alarm in the colony initiated by outbursts of many alarm cries, incubating birds usually slip out of their nests and fly off. On returning, if the period of absence had been prolonged, a bird might sit for a longer period than usual,

The nestlings spend about 20 days in the nest before leaving and are fed various kinds of insects and, late in the nestling period, grass seeds as well. Six of the 8 family groups we observed closely had helpers, and in half of these 6 groups all the birds fed the nestlings (Table 2). There were 1–3 nestlings per nest, and the rate of feeding per nestling per h varied greatly, from 6.2 to 27.0. The average feeding rate was 11.4 visits per nestling per h, which is rather high for passerine birds (cf. Skutch 1976). Of 195 feedings (24 h at 6 nests) in which the sex of the feeder was identified, 48% were by the adult males and 52% by the adult females of the 6 pairs. Of 266 feedings (20 h observation) at these nests, 74% were by the 12 adults of the pair of adults that had incubated, 18% by five helpers in adult plumage, and only 8% by four immature helpers. Six broods with helpers fed an average per nestling of 15 times/h, compared with 10/h for 3 unassisted broods.

Larger nestlings (in their third week) were fed at an average rate per nestling of 15.0/h (9 nestlings, 327 feedings at 5 nests over about 12 h), a higher rate than for small nestlings, which were fed at a rate of 9.8 (9 nestlings in their first week, 136

feedings observed at 4 nests over 8.5 h). After feeding a nestling, an adult at times was seen to leave with a dropping, which it let fall to the ground.

After leaving the nest, a fledged bird was fed insects and grain, often by only one of the presumed parents, which it persistently followed about from place to place. In one case we watched three fledged young of the same group on the day and the day after they left the nest. Three different adults fed them 177 times in 3 h, averaging 19.7 feedings per young per h, a very high rate. Fledged young were fed for 3–4 weeks. Many young birds did not disperse far, if at all, from the area in which they were raised. In January 1979, 9 of 18 *P. arnaudi* we had color-banded 8–9 months earlier as immature birds at the 3 study colonies were still in the same small area (G. R. Cunningham-van Someren pers. comm.).

RESPONSES TO ENEMIES

Being a small bird, the Grey-capped Social Weaver has a host of enemies. When alarmed, it may move into the dense upper canopy of the colony tree when the latter is an umbrella thorm (*Acacia tortilis*) or fly to nearby bushes or trees with dense foliage in which it can hide. It gives a loud, sharp, high-pitched alarm, *tseep!,* to all sorts of enemies, including snakes, hawks, owls, hornbills, didric cuckoos, mongoose, jackals, or dogs, or to any large bird or person that disturbs its nests. A bird often remains in the nest with the eggs or small nestlings until a finger is actually inserted into the entrance, whereupon the bird suddenly flies out. We saw a Harrier Hawk (*Polyboroides typus*) hang from a nest with its feet and capture a *P. arnaudi* in its beak just as the weaver left the exit hole of the nest. Sometimes eggs disappear from nests without a trace. In two nests from which nestlings disappeared, a hole was found torn in the roof. Such holes were not uncommon in our nest census in both one-hole and two-hole nests. Some may have been a result of predation by Gabar Goshawks (*Melierax gabar*), which we have seen extracting nestlings of Village Weavers (*Ploceus cucullatus*) after tearing a hole in the roof of the nest (Collias and Collias 1971, 1978b). We have also seen a Superb Starling (*Spreo superbus*) peck at and pull materials out of the roof of a *P. arnaudi* nest.

Any sudden movement alarms the social weavers, but movement is not necessary. A motionless stuffed specimen of a Spotted Eagle Owl (*Bubo africanus*), whether placed in the colony tree or in a bush or on a fence several meters from the colony tree, induced strong "mobbing," the social weavers crowding and fluttering about the owl giving their alarm cries. After about 15 min the birds generally ignored the mount. A rubber latex model of a 2.5-m mamba induced similar intense mobbing when placed in the tree near the nests, but, curiously enough, this same snake model was virtually ignored when placed on the ground near the tree. The social weavers fed on grain near the model, and some even perched on its coils.

Cut-throat Finches (*Amadina fasciata*) and Chestnut Sparrows (*Sorella eminibey*) may use nests of the Grey-capped Social Weaver for raising their own broods (Payne 1969, 1977). The former may use old nests, but the latter usurp new nests of the social weavers. In Picnic Colony, a pair of *A. fasciata* slept in an old weaver nest. When chased away from a nest by the social weavers, the finches and sparrows, which are small birds, persistently returned; Payne (1969) noted that the disturbed social weavers eventually deserted their nest to *Sorella*. Like Payne, we have seen *Sorella* copulating next to a *P. arnaudi* nest, while a few meters away the *P. arnaudi* fed their nestlings in other nests.

TABLE 3. Major differences in behavior between three species of Plocepasserinae (Ploceidae) belonging to different genera.

Trait	*Plocepasser mahali*	*Pseudonigrita arnaudi*	*Philetairus socius*
Average weight	42 g	20 g	27 g[a]
Colony size	Small	Small to large	Medium to large
Nests	Usually separate	Usually separate	Compound
Sleep in nests	Singly	1–5/nest	1–5/chamber[a,b]
Feeding territory	Yes	No	No
Modal clutch	2 eggs	3 eggs	4 eggs[a]
Incubation	By one female	By the pair	By the pair
Nestlings fed	Communally	Usually communally	Usually by pair only[a]

[a] Maclean (1973).
[b] White et al. (1975).

DISCUSSION

There are two species of social weavers of the genus *Pseudonigrita,* the Grey-capped Social Weaver and the Black-capped Social Weaver (*P. cabanisi*). Both are restricted to eastern Africa. Their ranges overlap to some degree, and birds of both species may nest in the same tree. The gray or gray-white crown and black bill of *P. arnaudi* are opposite in color to the black crown and white bill of *P. cabanisi.* The tendency toward opposite coloration in the two species may represent character divergence that aids in species recognition in zones of sympatry. We have not made a detailed study of the behavior of *P. cabanisi* but elsewhere describe its nest-building behavior, which is very similar to that of *P. arnaudi* (Collias and Collias 1964).

Plocepasser mahali, Pseudonigrita arnaudi, and *Philetairus socius,* which have often been considered members of the same subfamily (Plocepasserinae), share many similarities in behavior (Collias and Collias 1964, 1977, 1978b, 1978c; Maclean 1973). They inhabit dry African savanna, are gregarious breeders, and reside in their colonies the year round. Their roofed nests are thatched rather than woven and are constructed mainly of dry grass stems. The social organization of colonies is based on nesting and sleeping units that apparently are, to a large extent, based on extended family ties. Young birds tend to remain with their family for some time after they become able to feed themselves. Nests are often built communally, and other birds may help parents feed the young. All three species forage in flocks and are organized into peck orders, but with considerable tolerance within families. All feed on grass seeds and insects, but the young are given mainly insects. The sexes appear identical, and copulation is rarely observed. The incubation period is about 2 weeks long, and the nestling period is rather prolonged for passerine birds, lasting 3 weeks or even longer.

Some important differences in the behavior of these three species in different genera of the Plocepasserinae are summarized in Table 3. Small colonies, usually of only 4–6 birds, characterize *P. mahali,* while *P. arnaudi* has larger and more variable colonies of 2–60+ birds. Individuals of *P. mahali* sleep singly in different nests, while the much smaller *P. arnaudi* often sleeps with two or more birds in a nest, presumably as an aid to keeping warm during cool nights. Unlike *P. socius,* both of these species have two entrances in each nest, one of which is closed in nests used for breeding. All *P. mahali* colonies studied consisted of single breeding units. Pairs were not obvious, however. We found that, after 2 yr, half of the surviving birds had moved to a neighboring or other nearby colony (Collias and Collias 1978d).

The key to the behavior of this species, in the sense of determining other behavior patterns, seems to be its defense of a food territory within which the members of the colony do all their foraging. Incubation is by one female only, freeing the dominant male and the rest of the group for increased vigilance in territorial defense. All five *P. mahali* colonies in which we counted feeding rates had communal feeding of the young, whereas in *P. arnaudi* in 1 of the 8 breeding units only the 2 parents fed the nestlings, despite the presence of 4 immature but independent birds in the group. The fledged young of *P. mahali* were generally also fed communally, but only rarely those of *P. arnaudi.*

We have suggested that one function of communal feeding of nestlings or fledged young by birds in addition to parents is to help compensate for harassment by predators by maximizing available foraging time. Thus, out of 124 h observation of 4 colonies of *P. mahali,* about 18% of the time birds were prevented from foraging by the presence of a predator, particularly the Gabar Goshawk (Collias and Collias 1978b, 1978c). After the hawk flew away, the different sparrow weavers fed their young in rapid succession. Other theories of communal, cooperative, or group breeding in birds include more efficient detection and defense against predators or individual ("selfish") and kin selection. These theories have recently been reviewed by Fry (1977), Brown (1978), Emlen (1978), and Stallcup and Woolfenden (1978). There is no necessary antithesis between our suggestion (which may or may not involve kin selection) and these different ideas. The question is one of their relative importance as explanations in different situations.

In contrast to *P. mahali,* the greater gregariousness of *P. arnaudi* is associated with greater tolerance of neighboring families, permitting several family groups to nest in the same tree. The greater number of individuals in a colony of *P. arnaudi* and of *P. socius,* compared with the small groups of *P. mahali,* requires a larger feeding area, and different colonies share common feeding grounds. At the same time, the relatively large flock size both within and between colonies results in searching over a wider area of country. The difference in flock size is consistent with the theory of Ward and Zahavi (1973) that gregarious breeding and large roosting groups in birds serve as information centers for guidance to unpredictable food resources.

The individual nest chambers of *Philetairus socius,* unlike the nests of the other two species, never have more than one entrance at any time, and it seems the communal roof of the gigantic nest helps provide added security from predation, permitting the aggregation of nest chambers (Collias and Collias 1964, 1977; Collias 1980). The thick roof of the nest, we think, has helped reduce pressure from hawk predation on nestlings. Building of a compound nest with a communal roof is the main difference in behavior of *P. socius* from *P. arnaudi* (Table 3). The behavior of the two species is otherwise very similar. The communal nest-building habits of *P. arnaudi* seem preadapted to the evolution of a compound nest, as does the strong tolerance between different family groups in the same tree.

The question arises as to why the Grey-capped Social Weaver has not evolved a compound nest as the Sociable Weaver has done. One reason may be that its two-hole nest helps meet the enemy problem in a different way insofar as adults are concerned. White et al. (1975) furnish another clue with their finding of more stable temperature regulation in *P. socius* in larger nest masses. Such temperature regulation is especially important in the cold winter nights of the Kalahari Desert where the temperature may fall to −10°C. In contrast, *P. arnaudi* inhabits a much warmer

climate with minimum temperatures in different parts of its geographic range of only 10–22°C. In the Kalahari Desert, Maclean (1973: 225) found that the eggs of *P. socius* were "seldom left uncovered, at any time during incubation." We found the eggs of *P. arnaudi* in Kenya were left uncovered 23% of the day, while, in an aviary colony of *P. socius* at Los Angeles, the eggs were uncovered only 6% of the day. Whereas only one parent is in the nest with the eggs during the day in *P. arnaudi,* both parent *P. socius* were in the nest together with the eggs 29% of the day (observed 111 h).

It seems possible, as Bartholomew et al. (1976) have suggested, that the geographic range of the Sociable Weaver may be limited by rainfall, as a large water-soaked nest mass would be subject to decomposition and deterioration. The annual rainfall in its desert environment is only 8–600 mm in different places (Maclean 1973: 183). In contrast, the Grey-capped Social Weaver inhabits semiarid savanna where, for example, the annual rainfall in 1977 was measured at 640 mm (Magadi) to 1,011 mm (near Nairobi). The maximum number of *P. arnaudi* nests we observed in physical contact varied from 12 (1973) to 20 (1976) during very dry years to only 6 in a very wet year (1978) in the same general areas.

The sheer amount of nest material required to build the gigantic nest mass of *P. socius* must be a problem to the birds in terms of time and energy. They build on their nests the year round, as do other species of Plocepasserinae, but in addition *P. socius,* unlike *P. arnaudi* and *P. mahali,* often makes one grass stem do the work of two by clipping a straw or grass head into two pieces with its beak and inserting both parts into the nest (Collias and Collias 1978). This procedure not only saves in flying time and effort but also helps consolidate and strengthen the large nest, as does the use of twigs in the roof, a material not used by the other two species.

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