COOPERATIVE BREEDING BEHAVIOR IN THE WHITE-BROWED SPARROW WEAVER

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ABSTRACT.—We observed color-banded individuals of *Plocepasser mahali*, the White-browed Sparrow Weaver (Ploceidae), in Kenya during dry and rainy periods. Colonies usually consisted of five or six birds that slept singly in different nests in one tree and spent more than half of each day foraging in small group territories near the nest tree. The birds of a colony built nests the year round and all might join in building a new nest. Each colony was organized into a dominance hierarchy, but with strong intragroup tolerance. Each colony had only one breeding nest at a time, eggs were incubated intermittently by one female, and all or nearly all birds of a colony fed the one or two young. The most dominant bird took the lead in territorial defense, but did relatively little feeding of the young. Loss of the most dominant bird to a predator resulted in the invasion of a group's territory by a neighboring group. When a hawk or other predator was present all foraging and feeding stopped, and about 18% of foraging time was lost by such harassment. After the predator departed the adults fed the young in rapid succession, thus helping to compensate for the delay, a clear advantage of cooperative feeding. In its communal nest-building and cooperative feeding, this species resembles *Philetairus socius*, the Sociable Weaver of southwestern Africa. *Received 4 August 1977, accepted 1 January 1978.*

IN Kenya the White-browed Sparrow Weaver (*Plocepasser mahali*) of the family Ploceidae is common in acacia savanna where it nests in small colonies in trees. The object of this report is to describe the behavior of this species with special reference to communal nest building and cooperative breeding. Cooperative breeding, in which more than two birds care for the young, is widespread in tropical birds but only recently has its importance become widely recognized (*in* Frith and Calaby 1976, Skutch 1976). No species of *Plocepasser* seems to have had its breeding behavior described in any detail and, except for *Philetairus socius*, the Sociable Weaver of southwestern Africa, cooperative feeding of young has not been reported in African Ploceidae before (Grimes *in* Frith and Calaby 1976: 671–673).

We undertook the present study chiefly in the hope of shedding some light on the evolution of behavior in the Sociable Weaver, especially of its communal nest building and compound nest. We have described elsewhere the nest and nest building of *Philetairus socius* (Collias and Collias 1964, 1977, 1978). Maclean (1973) has given a comprehensive account of the general biology of this species, while White et al. (1975) and Bartholomew et al. (1976) have described the thermal significance of its large nest.

STUDY AREA AND METHODS

The study area was about 350 km north of Nairobi in the Samburu-Buffalo Springs Game Reserve, an area of dry bush and acacia savanna. The Samburu Reserve lies just north of the Ewaso Ngiro River; the contiguous Buffalo Springs (Isiolo) Reserve is just south of this river.

We stayed first at Buffalo Springs. The White-browed Sparrow Weavers nested in *Acacia tortilis* trees near the thatched huts for tourists. The ground was stony with a sparse growth of grasses and herbs, and a scattering of bushes and acacia trees. Nearby was a stream bed, partly dry, but with pools of water and a dense growth of trees and bushes. The nests of each colony of sparrow weavers were all or nearly all in a single tree. We used mist nets to capture the birds at four adjoining colonies, weighed them with a Pesola scale, and color-banded them with individual combinations. The dark tail feathers have pale

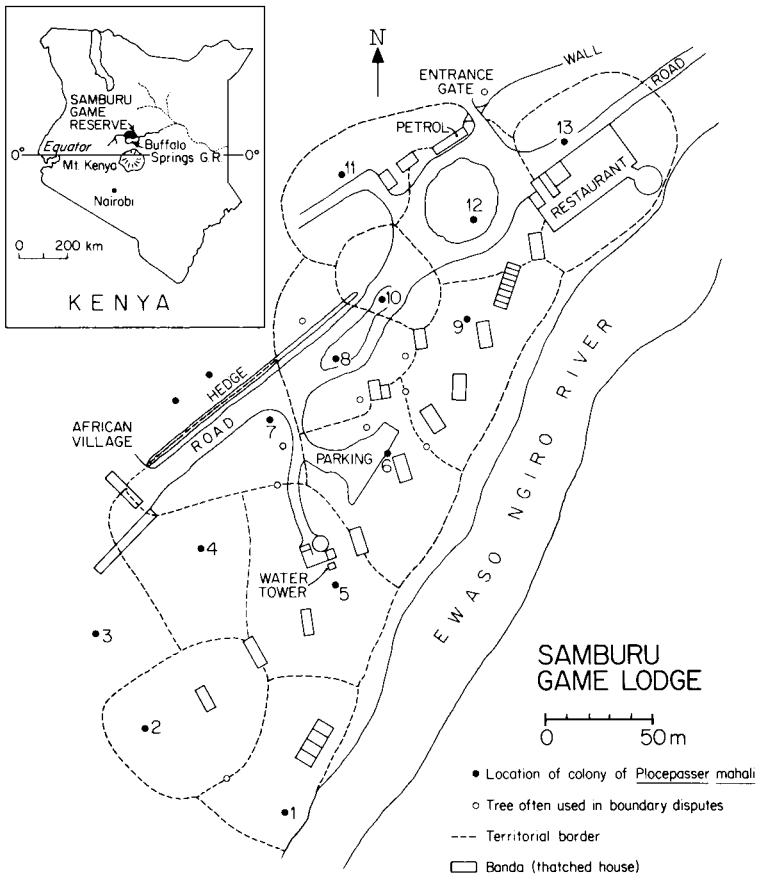

Fig. 1. *Plocepasser mahali* group territories at Samburu Game Lodge, Kenya, March–June 1976.

tips, and some individuals could be distinguished at close range by differences in tail moult pattern as well as in their white wing bars. The sexes appear identical in this species and we did not generally know the sexes of the birds.

We set up a parallel study at the Samburu Game Lodge area along the Ewaso Ngiro River about 20 km to the west (Fig. 1), where we also mist-netted and color-banded the birds in four adjoining colonies. Here also *Plocepasser* had their nests in isolated *Acacia tortilis* trees next to the thatched huts. The ground in many places was carpeted with grasses maintained by watering from garden hoses, and patches of bushes were interspersed with open ground. Along the river was a dense gallery forest where the Sparrow Weavers seldom ventured.

We observed the Sparrow Weavers for 1,210 h from 9 March to 21 June 1976. The birds were protected, accustomed to people, and easily observed. We repeatedly counted all birds and nests at each colony. Every nest in each colony was given a number. The two study areas were mapped with aid of a compass and by pacing distances.

After breeding began we checked contents of most nests from a ladder placed on the roof of a vehicle. A few nests beyond reach we judged to have eggs if a bird regularly entered the nest and remained for a time, or to have nestlings if adults brought food to the nest. Possible brood nests were initially identified because one of the two bottom entrances characterizing the nest of this species was plugged up, but presence of only one entrance was not positive evidence that eggs or nestlings were present since one hole is plugged up well before eggs are laid.

Rainfall records for the Samburu Lodge area were furnished by the manager and the East African Meteorological Department. No official records of rainfall were kept at the Buffalo Springs area, and we merely kept qualitative records, while the manager of the area recorded days of rain or no rain for us

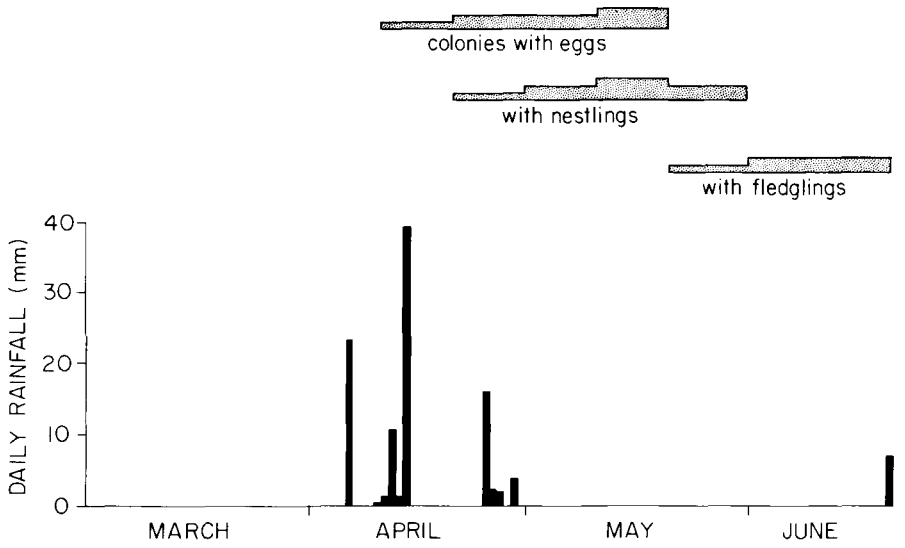

Fig. 2. Breeding of *Plocepasser mahali* in relation to rainfall at Samburu Game Lodge, Kenya, March–June 1976. Each step in bars for colonies with eggs, nestlings, or fledglings represents three colonies.

when we were away. We measured maximum and minimum air temperatures during the period of our study with a mercury thermometer in our open hut.

Breeding Season and Population Density

Temperature in the reserve is generally equable, averaging between 20°C and 30°C in different months. A dry season occurs from June to September. Rainfall peaks in April and November, but rainfall is not great and is erratic from year to year. In March–May 1976 the rains largely failed at Buffalo Springs and the sparrow weavers did not breed there. At Samburu Game Lodge good rains in April set off some breeding activity, but the rains failed in May, and except for one renesting no eggs were laid after 10 May (Fig. 2). Rainfall was abnormally low for March–May 1976, with only 97 mm of rain recorded, all of it in April, compared with 53, 124, and 49 mm for these same months in 1975, when 580 mm were recorded for the year.

No colony of sparrow weavers had more than one breeding nest at a time. In 17 colonies at the Samburu Game Lodge area, eggs were laid in 13, hatched in 8, and young fledged in only 5. Although the usual clutch is 2, rarely 3, eggs (Mackworth-Praed and Grant 1960: 863), only 1 of the 5 brood nests fledged more than 1 young, and 1 of these 2 fledglings was lost in its first month. Only one colony made more than one breeding attempt and this after losing its first brood. In the Nest Record Scheme of the East African Natural History Society, P. L. Britton records nestlings being fed by *Plocepasser mahali* at Buffalo Springs on 30 December 1974, so this species may also breed after rains late in the year.

Four colonies at Buffalo Springs occupied an area of 1.7 ha, or 0.43 ha per colony. At Samburu 13 colonies occupied 4.7 ha, an average of 0.36 ha per colony.

Population size changed little during the study. Of 83 adults present in the 17 Samburu colonies at the start of breeding, 74 were still present after breeding ended; adding 4 surviving fledglings gave 78 birds at the end of the study. Adults averaged

4.9 (3–7) per colony in the middle of April, and 4.4 (3–6) after the middle of June. These same adults had 200 nests (average 12/colony) near the start of breeding in April, reduced to 176 nests (average 10/colony) after breeding ended. At Buffalo Springs, 22 adults in the 4 study colonies (5–6 birds each in early April) were reduced to 20 by the latter part of June (4–6 birds per colony). Taking both areas together, 105 birds present before the beginning of the rainy season were reduced to 98 birds by the time the breeding season was near its close and the dry season well advanced.

Feeding Behavior and Daily Routine

The sparrow weavers foraged on the ground throughout the day in frequent brief periods, and in between would sit and rest or preen in a tree or bush, or work on a nest. While foraging they ate small seeds off the ground, or nibbled green or brown grass seeds off the heads of living, growing grasses, including *Digitaria velutina, Eragrostis papposa, Cenchrus ciliaris*, and *Dactyloctenium aegyptium*. We repeatedly saw the birds bite off a small green grass shoot, nibble at the succulent growing base, drop it, and take another. During the dry but not the wet season the sparrow weavers often dug in the bare soil with their beaks, but we did not know what type of food they were securing.

After insects became abundant following good rains in April, the sparrow weavers would make short runs after insects on or near the ground, or go 30–40 cm up into the air to capture flying insects. We often saw insects in their beaks, particularly small brown or green caterpillars and small moths. In searching for insects they inspected the underside of broad leaves on herbs, and with their beaks rolled over small stones, clods of earth, palm nuts, and pieces of elephant droppings. We never saw them foraging in trees, even during the rainy season, although they would rest in trees.

These birds averaged more than half of each day looking for food, irrespective of season or time of day. We followed one bird at a time for 1 h, timed important aspects of its behavior with a stopwatch, and also enumerated different behaviors. Sixteen birds in a 30-h time sample on a bird-hour basis averaged 33 min foraging, 31 territorial calls, one border dispute, and visited 1 or 2 nests for a total of 6 visits (in 5 of which they brought nest materials). Any general inhibition of behavior caused by presence of a predator is omitted from these data, which summarize observations made only when the birds were not threatened by a predator. The birds seldom spent more than 5–10 min of each hour resting and preening; we did not time rest periods but estimated rest time by subtracting time allotted to other activities.

Air temperature ranged from a daily minimum of 19–21°C to a daily maximum of 26–33°C during late March to early June at Samburu. There was little difference in foraging time between the relatively cooler and warmer hours of the day. Frequency of territorial vocalizations varied little during different times of day, although the birds averaged fewer border disputes during the cool hours of morning than they did later in the day. They also made more nest visits and did more nest building before 1100 than later in the day.

Dominance Hierarchies and Group Territories

The home range about the nesting tree was the same as the defended area or territory of each group (Fig. 1). The average distance between nesting trees of 6

different colonies at Buffalo Springs was 56 m (32–85 m); for 13 colonies at Samburu, 50 m (37–66 m).

Within each of five colonies in which dominance relations were determined the individuals were organized into a simple linear peck order. A dominant bird would approach with head and beak held high and plumage sleeked. The subordinate bird would then move away, sometimes drooping its wings and displaying its conspicuous white rump, or else it would freeze on the ground, crouch low with beak pointed down and, while facing away from the aggressor, often utter a low growl. The cause of aggression was sometimes food, but often was not evident. Dominance interactions were generally very rare between most individuals of a colony.

Colonies 6 and 7 rarely defended the territorial border between them, and most individuals of these groups frequently visited any part of the territory of the other group and were often tolerated. However, within these two colonies the rate of aggression was several times that observed within two other colonies that rigorously excluded all intruders from their territories (N. Collias and E. Collias 1978).

Dominance rank was closely correlated with body weight (35–49 g) in four of five colonies. The Spearman Rank Correlation Coefficients (Siegel 1956) between the two factors were 0.97, 0.97, 0.90, and 0.70, and were statistically significant in all but the last case. In each colony the most dominant bird was the heaviest, was most likely to sing, and go last to roost each evening, and to initiate defense of the group territory. Once the most dominant bird of a group was captured by a hawk, and within a few hours the nesting tree of its colony was invaded by the birds of a neighboring group. After a series of battles the intruders eventually returned to their own territory. In contrast, loss of a bird intermediate in the peck order of another group had no apparent effect on the group's relations with its neighbors.

Generally all birds of a colony participated in defense of the group territory about once an hour. The cause of boundary disputes was not usually evident. The birds uttered many loud territorial defense calls, flew to the boundary, clustered together and faced the opposing group on the other side of the border. Trees at or near the boundary were favorite defense sites, but sometimes the two groups faced each other on the ground forming two "battle lines."

Territorial displays resembled aggressive displays of individuals in that head and beak were raised and plumage sleeked, but differed in that loud territorial calls were given. Often the wings were drooped and the birds displayed their white rumps. Usually one or more birds would pick up a bit of grass or leaf and hold it aloft like a tiny flag while facing the other group. Fights were uncommon, but sometimes two individuals, usually the most dominant birds, would grapple with their feet and tumble about on the ground, pecking hard at each other. After much calling back and forth, border disputes ended by each group flying back toward the center of its territory.

NEST-BUILDING BEHAVIOR

White-browed Sparrow Weavers build in both dry and rainy seasons. Nest histories were followed in four colonies over a 14-week period covering the normal time of the long rains. Each colony had 5 or 6 birds and built an average of 3 or 4 new nests. During the same period the birds of each colony tore down an average of 6 nests, a net loss of 2 or 3 nests. Three of these colonies were at the Samburu study area. In one colony at Buffalo Springs only about 20% of nests present at the start of observations were torn down by the birds, compared with 40 to 70% torn

TABLE 1. Building on particular nests by different individuals[a]

Birds in order of dominance	Pieces of nest material added to			
	Sleeping nest	New nests	Other nests	Total pieces
Colony 8				
AY	27	54	2	83
U	16	23	2	41
OB	0	19	2	21
GB	20	43	8	71
GR	10	21	1	32
LL	27	19	2	48
Colony B-5				
RR	36	33	31	100
LL	23	108	17	148
AA	77	105	92	274
YY	67	71	4	142
BB	0	24	13	37
Total	303	520	174	997

[a] Colony 8 observed 9.5 h on 6 days, Colony B-5 for 16 h on 10 days

down in the Samburu colonies. Possibly the slower turnover rate of nests at Buffalo Springs was related to the fact that the rains largely failed there.

Nest building is stimulated by rainfall. Since the birds build with old dry grasses (rarely adding some dry stems of herbaceous dicots), they need not wait for new grasses to grow before building. On 12 April the first rain of the season fell at Buffalo Springs, a hard shower lasting from about 0900 to 1100. In the 3 h 15 min immediately after the rain, birds of Colony B-5 brought 140 straws to their nests, an average of 43 per hour. In contrast, in the preceding hot, dry days nest building was at a much lower rate, although it varied greatly from day to day. In the latter half of March and the first week of April, in 32 h we saw the birds of this colony enter their nests with a piece of nest material 688 times, an average of about 22 times an hour. On the day of the first rain the birds shifted their main building efforts away from their sleeping nests and worked especially on three nest starts, one of which was begun right after the rain. A new nest was also started in the adjoining colony the day of the first rain.

Old nests were often used by the birds for materials for other nests and so might gradually be destroyed. A bird builds a new sleeping nest and the old one deteriorates. Nests were deserted when their position on a twig shifted until the entrances had an abnormal orientation. Nests blown down by the wind were a favorite source of materials for other nests.

The length of time it took to build a nest varied greatly. Four nests were built from start to finish within 10–18 days. The shortest time for a nest to be built was 5 days, the longest 5–6 weeks. One nest in the B-5 colony went from start to near completion in about 5 weeks, and then with failure of the rains was reduced to a ring stage for the remainder of the 3-month observation period. We have described details of nest construction in *Plocepasser mahali* elsewhere (Collias and Collias 1964).

The birds gathered nest materials by picking up pieces of detached grasses, clipping off stems of still standing dry grasses, or pulling up grass runners from the ground as House Sparrows (*Passer domesticus*) do. They preferred dry, brown grasses, and selected these at Samburu among a plethora of green lawn grasses. Nest

TABLE 2. Communal feeding of young in different colonies

	No. adults in colony	No. adults fed young	Feedings per nestling		Feedings fledged young	
			H obs.	Fed per h	H obs.	Fed per h
Colony 2	5	4	6.5	10.9	—	—
Colony 6	6	7[a]	16.5	9.3	29.3	16.3
Colony 8	6	6	17.7	15.8	8.0	14.2
Colony 12	5	6[a]	4.7	13.6	10.5	12.0
Colony 13	5	5	25.2	7.0	—	—

[a] Rarely a bird from another colony fed young

materials were gathered from any spot in the group territory, and after foraging a bird generally returned to a nest with a grass in its beak.

We counted 983 pieces of nest material in a nest that had contained two freshly laid eggs. The outer shell consisted of 803 grass stems, grass heads, and grass runners. The inner lining was composed of 115 fine grass heads and 65 feathers, as well as one-half cup of plant down and soft bits of grass tops that were not counted. The nest proper measured 23 cm long, 18 high, and 15 wide, while the entrance tube was 11.5 cm long and 7 cm in diameter.

Some individuals worked at nests consistently more than others did (Table 1). Such differences were seen both in a colony that was breeding (Colony 8) and one that was not (Colony B-5). No very definite association of nest-building activity with dominance status existed, except that the most dominant bird (RR) in the B-5 colony frequently attacked and prevented another bird (BB) from building. The most important observation was that all birds cooperated to build a new nest. Nine of 11 individuals in 2 different colonies put most of their building effort into helping build new nests in their colony, and over half (52%) of the 997 pieces of nest materials carried by all birds in 25.5 h observation was to such nests. Next most work (30%) by each bird went to the maintenance of its own sleeping nest, while much less work (17%) was done on other old nests. The difference between work done on new and sleeping nests was statistically significant (Signed-rank test, $P = .005$, Dixon and Massey 1969: 341), as was the difference between work on sleeping nests and other old nests ($P = .019$). On the average each bird of these 2 colonies built on 7 different nests and did not build on 10 nests of the colony.

SEXUAL BEHAVIOR AND INCUBATION

Precopulatory courtship and copulation have not been described before for *P. mahali*. Despite many hours of observation only three copulations were seen. The first one occurred in a small tree at the Samburu study area at 1650 on 15 April, the day after the heaviest rainstorm in several years. No postural display by the male was noted, but he gave a musical trill just before he mounted the female. After he dismounted, both male and female flew off together. A second copulation occurred on 24 April on the ground under the nest tree of Colony 7 with the observer (N. C.) only 2 m from the birds. The female was the same bird that incubated in Colony 6, and often visited and was tolerated in the territory of Colony 7. It had rained the preceding night. A male had been following the female about on the ground for about 2 min when the female assumed a precopulatory stance without crouching, pointed her closed beak straight up, her tail held horizontal and vibrating, and uttered a faint, rather melodious but somewhat strained cry. At once the male gave

TABLE 3. Feeding of young by different adults in Colony 8

	Nestling		Fledged young		Total feedings	
Adult	Feedings	Percent	Feedings	Percent	Number	Percent
OB	100	37.7	47	41.2	147	38.9
GR	49	18.5	39	34.2	88	23.3
LL	50	18.9	13	11.4	63	16.7
GB	51	19.2	9	7.9	60	15.9
AY	14	5.3	6	5.3	20	5.3
U	1	0.4	(U disappeared after young fledged)			
Total	265 (16.2h)		114 (8 h)		379	

the precopulatory trill, mounted and brought his tail down beneath hers. Immediately after copulating the pair flew off together.

The incubation period of *Plocepasser mahali* was not precisely determined. By assuming that the first egg follows copulation by 1 day and subtracting the known nestling period from the date of this egg we estimated the incubation period in 1 nest at roughly 14 days.

In 7 colonies observed for 33 h over 18 days, incubation was intermittent. From 1 color-banded bird and by details of plumage of birds in 3 other colonies we found that only 1 individual was doing all the incubating. The incubating sex most probably was the female, identified as such during a copulation.

When the incubating bird was in her nest we assumed she was sitting on her eggs. With this assumption, the average time spent on the eggs was 10.6 min (67 times on), the same as the average time spent off (60 times) the eggs (i.e. away from the nest). The range of time spent away from the nest was 1–37 min, the same as for time spent inside the nest, with the exception of one long period of 65 min spent in the nest by one female during a light rain.

CARE OF THE YOUNG

In order to avoid undue disturbance of the birds we made only two checks of the interior of brood nests. Four nests fledged only one young each and in these nests only one nestling was heard during most of the nestling period. In Colony 12, which produced two young, the older fledgling attacked and pecked the younger fledgling on the day the latter left the nest and also on subsequent days when the younger bird was being fed. It is possible that such sibling rivalry exists in the nest during part of the nestling period, and may help to account for the death of the second nestling in some nests.

When the nestlings first hatched they were brooded by the same female that had incubated and in much of the same on-off pattern as for incubation. All or almost all the birds of the colony fed the young (Table 2). Six nestlings were each fed an average of 11.7 times per h. After leaving their nests 4 fledged young were each fed an average of 14 times per h, including the 2 young of Colony 12, which together received 24 feedings per h. After leaving the nest the young were fed for at least a month. The total amount of work done in raising a young one may be rather large in this species. According to Skutch (1976: 274), a wide variety of species of small birds are fed an average of 4–12 times per nestling per h. We observed feeding rates of 4 and 7/h/brood in two races of *Ploceus cucullatus* in which the usual clutch size is two (Collias and Collias 1971).

TABLE 4. Time lost for foraging and feeding young caused by the presence of a predator

	Nestlings		Fledged young	
	Hours observed	Percent of time lost	Hours observed	Percent of time lost
Colony 6	8.3	30.3	29.3	7.7
Colony 8	17.7	19.3	8.0	15.9
Colony 12	4.7	21.1	30.5	14.3
Colony 13	25.3	27.7	—	—
Total	56.0	24.7	67.8	11.7

The rate of feeding by different adults varied greatly (Table 3). Most of the feedings were by the brood female (39% in Colony 8, and in a 6-h sample 85% in Colony 6). The most dominant bird of the colony, presumed to be a male, did very little feeding (5% by AY in Colony 8 and only one feeding by BB of Colony 6). Very rarely a bird fed a young from another colony; thus BY and RW of Colony 7 each fed the fledgling of Colony 6, two and three times, respectively.

The young were mostly fed insects of various kinds and sizes. In Colony 6 the early nestling period coincided with a flush of small moths that the adults fed, wings and all; they also often fed small caterpillars. Toward the end of the nestling period they sometimes fed grass seeds.

When a predator was nearby the nestlings generally stopped their incessant calling, in part inhibited by the alarm chatter of the adults and in part we believe by the general and prolonged silence of the usually noisy adults after the initial alarm.

The departure of a fledgling from the nest was seen three times. The first one seen to leave the nest perched on the threshold ridge of the brood chamber, crawled down the entrance tube, started to fall, caught itself, and crawled back in again. A few minutes later at 0700, it again crawled partway down the entrance tube shortly after being fed, fell out, and fluttered over to an adjoining tree. A second bird left the same nest 2 days later at 0900 not long after being fed; it simply fluttered directly out of the nest to the neighboring tree, as did another young seen to fledge from a different nest.

We watched one fledgling all day after its initial departure from the nest. When fed and often between feedings it repeatedly uttered a thin, brief, very high-pitched begging note, but unlike young birds of many other species did not quiver its wings. It did not feed itself, but pecked lightly and ineffectively at acacia leaves and twigs, at other vegetation, and at the ground. Most of the adults fed it, especially the brood female, which uttered a series of soft low-pitched *wheep* notes when she went to it.

When the adults chattered as a Black Kite (*Milvus migrans*) flew close by, the fledged young froze and stopped calling. When the adults suddenly flew to the shelter of the trees at some alarm, it crouched immobile on the ground. Its brown and white pattern matched the appearance of the brown soil and small white stones and helped to conceal it. During another "hawk scare," E. C. watched this fledged young hiding in the leafy tree canopy absolutely immobile for 1 h 15 min until the danger was past and the adults resumed their normal territorial calling.

In the following days when the young one wandered onto the territory of neighboring groups of sparrow weavers, it was attacked by resident birds. It often froze in submissive posture, but this response did not stop the attack, and eventually it

would fly back to its home territory. Once when it was being pecked in another territory, some adults from its colony suddenly descended, landing near it, then flew off again, and their young one went with them. Learning territorial boundaries by the young one is facilitated as it frequently goes along with the adults whenever a border dispute erupts, especially after 2 or more weeks post-fledging. Even 4 weeks after fledging, young birds did not participate in border disputes but merely perched nearby.

During the week before the young fledged the adults all joined in building a new nest. This was seen in three colonies, and in each case the entrance of the new nest was left incomplete and opened conspicuously to one side instead of downwards as in most older nests. This conspicuous entrance was easier for a fledgling to locate and to enter, and attracted the fledgling in the evening. More often than not, a fledged young slept in the new nest apparently provided for its benefit, but sometimes it entered some other nest. If this other nest was the sleeping nest of an adult, the latter left it to the young one and entered another nest for the night.

Fledged young were fed throughout each day except during predator alarms. Mostly insects were given the first 2–3 weeks after fledging. Gradually the adults began feeding more seeds as well, but even during the fourth week insects were still being provided. The young began to feed themselves about the second week after leaving the nest. By the end of the fourth week they were still fed occasionally but usually foraged for themselves. At this time a young weighed the same as an adult and was virtually identical in appearance. One young bird was identified in the same small area where we had banded it as a fledgling by John T. Emlen (pers. comm.) 7 months later.

When some larger species such as a Lilac-breasted Roller (*Coracias caudata*) or Superb Starling (*Spreo superbus*) came very near to fledged young, the adult sparrow weavers would come together, chatter and dive at the other species, attempting to drive it away.

When a predator was present the adults stopped foraging and made no attempt to feed the young. This was particularly true in presence of a Gabar Goshawk (*Melierax gabar*), which, when young were present, attacked or threatened the colonies every day. The hawk attempted to hide in a tree in the territory, awaiting an opportunity to dash out and seize one of the birds. It might remain hidden for an hour or more, and such harassment often prevented the adults from feeding the young for prolonged periods. We measured the number and length of such delays during formal observation periods while counting feeding rates at a given nest or of a fledged young. Out of 124 h of observation of 4 colonies, in almost 22 h (17.6%) (Table 4), the birds were prevented from foraging by the presence of a predator, generally a Gabar Goshawk or an African Black Kite.

After the hawk or other predator departed, all the adult sparrow weavers fed the nestling or fledgling in rapid succession, and so compensated for the delay caused in feeding. The colonies lost about twice as much foraging time on the average when feeding nestlings as they did when feeding fledged young (Table 4). The Gabar Goshawk can probably tear open the roofs of nests of sparrow weavers to capture nestlings, just as we saw this hawk doing at nests in a colony of Village Weavers (*Ploceus cucullatus*) in the Samburu study area. In three nests of White-browed Sparrow Weavers from which a nestling disappeared, a large hole was torn in the roof.

ADULT RESPONSES TO ENEMIES

We observed a flock of various species of small birds scolding an Olive Grass Snake (*Psammophis sibilans*) about 1.2 m long. Besides *P. mahali*, the birds included White-headed Buffalo Weavers (*Dinamellia dinamelli*), a Slate-colored Boubou Shrike (*Laniaris funebris*), a Spotted Morning Warbler (*Cichladusa guttata*), and others. The snake was in dense brushy cover, two-thirds hidden in a rodent hole. The birds came within 30–60 cm of it, giving various scolding notes, but drifted off when the snake remained immobile.

The common alarm cry, a low hard chatter, was given to the overflight of a kite, to Pearl-spotted Owlets (*Glaucidium perlatum*), Fan-tailed Ravens (*Rhinocorax rhipidurus*), Vervet Monkeys (*Cercopithecus aethiops*), humans, and snakes, but the sparrow weavers did not usually hide then. The appearance of a Gabar Goshawk caused the sparrow weavers to fly instantly to hiding places in tree canopies without vocalizing. Sometimes the appearance of the Gabar Goshawk was signalled from a distance by the alarm screech of a Superb Starling, and invariably the sparrow weavers responded by taking instant cover.

On 15 June, an adult male Gabar Goshawk caught WW, the most dominant male of Colony 5. The instant of capture was not observed, but the hawk was seen to fly with its prey from a tree in Colony 6 territory into the nest tree of Colony 5. After a few minutes the hawk flew off with WW in its claws.

Another *P. mahali* was captured by an African Black Kite on or near the ground in the territory of Colony 8. The kite flew back up to a perch it had been occupying in the top of a dead tree, and at once began to pluck its still living and screaming prey. Very soon the sparrow weaver fell silent, while the hawk continued to pluck off its feathers for some 15 min and then flew off and delivered the carcass to its own fledgling, perched high in a tree in the gallery forest along the river about 70 m away. Almost immediately after the kite had captured the bird, the other sparrow weavers returned to their nest tree and began giving their customary territorial calls.

DISCUSSION

The breeding of the White-browed Sparrow Weaver apparently depends on the erratic rains of its arid habitat. Egg-laying is associated with a period of adequate rainfall, but should the rains subsequently fail the birds are probably subject to a period of increasing food shortage, and successful breeding may be reduced.

The fact that *P. mahali* spends over half its time foraging and defends its foraging grounds suggests the major importance of food supply. In contrast, nest building takes relatively little time and energy, compared, for example, with the Village Weaver in which nest building is the most demanding activity of the males, which defend individual territories (Collias and Collias 1967, 1971). White-browed Sparrow Weavers sleep singly and each individual tends to use one or two sleeping nests, which it maintains. All birds in the colony, however, combine to build new nests, and in this respect their behavior resembles that of *Philetairus socius*, in which several birds help build a new nest chamber although only one pair may occupy it when breeding (Maclean 1973, E. Collias and N. Collias 1978).

The nestling period of *P. mahali* is rather prolonged, lasting between 3 and 4 weeks, and after leaving the nest young are fed for over 4 weeks by the adults. In the presence of a hawk or other predators the sparrow weavers may lose much valuable time that could be spent foraging. Having more than two adults feed the

young in quick succession compensates for such delays once the predator has departed, and maximizes use of available foraging time. At Samburu the 5 colonies that fledged young each had 5 or 6 adults, whereas 5 of 8 colonies that failed had 4 or fewer adults.

Cooperative feeding of young in differing degrees has been described for three species of Ploceidae. Studies of northern populations of *Passer domesticus* have left a general impression that only the pair feeds in this species, but recently Sappington (1977) found multiple feeders at 63% of 254 nests in the southern United States. In *Philetairus socius*, Maclean (1973: 227) described the first case of cooperative feeding in the weaverbirds; he states, however, that usually only the pair of parents fed their young. We found cooperative feeding in all five colonies of *Plocepasser mahali* where we counted feeding rates, and generally all birds of a colony helped feed (Table 2). Just one brood nest per colony is characteristic of this species, as of most cooperative breeders (Frith and Calaby 1976, and cf. abstracts of I.O.C. papers on cooperative breeding in Emu, 1976).

Species in which more than two birds attend the nest and young are often extended families. The origin of cooperative feeding in evolution may trace to some predisposing condition such as persistence of family ties, favoring the initiation of feeding of siblings by older young (Skutch 1976: 375), combined with some selective advantage of such cooperative feeding. In some cooperatively breeding species there is evidence that the extra helpers may increase the number of young fledged (Frith and Calaby 1976). Such increased efficiency under environmental conditions where more young are needed would favor the maintenance and further evolution of cooperative breeding and group defense of a common foraging territory. The need to find food quickly and maximize use of available foraging time would increase the selective advantage of a group territory. This is not to deny, of course, that other selection pressures are also involved, or the need to investigate kinship relations to help us gain a more complete understanding of the evolution of cooperative breeding and group territory (Brown 1974, Ricklefs 1975, Frith and Calaby 1976: 655–693).

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