DISPERSAL IN A POPULATION OF WHITE-BROWED SPARROW WEAVERS

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ABSTRACT.—Dispersal behavior of a color-marked population of the communal White-browed Sparrow Weaver (*Plocepasser mahali*) was studied over a three-year period in Zambia, Africa. Birds invaded communal groups having a higher occurrence of preferred feeding cover more than groups with low occurrence. Successful invasions were negatively correlated with the size of the group, perhaps because of group territorial defense. Movements that resulted in a bird staying in a group for at least six months or that resulted in a breeding attempt during this period were more frequent in smaller groups than larger groups. These movements, combined with female helpers who became breeders at their natal site, were used to approximate birth-to-breeding distances. The mean distance of this sample was 205 m, with a skewed distribution toward short distances. Excluding cases in which birds bred in the natal group, there was not significant difference in distances traveled by males and females. Cohorts from a group periodically invaded a neighboring group, frequently resulting in the disappearance of the invaded group's breeding female. Her replacement was by a member of the invading cohort. Individuals who dispersed relatively far appeared unable to breed as quickly as birds dispersing a short distance. Monitoring resources within the neighborhood while remaining at the natal site may be an adaptive habit for making a sedentary life style compatible with a successful dispersal phase.

Studies of communal species suggest that one sex tends to breed in its parental area while the other disperses to neighboring areas (Woolfenden and Fitzpatrick 1978, Ligon and Ligon 1978). The adaptive significance of these traits is unclear, although the importance of territorial acquisition has been proposed (Woolfenden and Fitzpatrick 1978). While the fitness value of inheriting a profitable resource may favor residency at the natal site, it is also adaptive to seek new resources if breeding opportunities at that site are scarce. Acquiring such resources is the ultimate selective advantage of dispersal, and the mode of dispersal is likely to be affected by social behavior in communal species. Dispersal modified by the effects of kinship has been documented (Woolfenden and Fitzpatrick 1978, Ligon and Ligon 1978). How an individual disperses may therefore depend on the size of its communal unit, since social relations and opportunities for social behavior should increase with group size. Another determinant of dispersal may be the relative quality of resources among communal territories, because individuals should be more likely to disperse when their territories have poorer resources than elsewhere.

Here I examine how resource characteristics and social behavior influence patterns of dispersal in the communal White-browed Sparrow Weaver (*Plocepasser mahali*). In particular, I ask: 1) How does resource quality and communal unit size correlate with the frequency of movements among communal groups? 2) What factors influence the frequency distribution of dispersal distances for movements that result in breeding attempts? 3) In what way does social behavior influence an individual's chances of successfully invading and breeding in another group? I also consider the possible significance of these results to population structure in this species.

White-browed Sparrow Weavers are ploceid finches, locally resident and often common through East and Central Africa. They inhabit dry bush and acacia country, thorn scrub, and mopane woodland. Easy to watch, they live in groups of 2 to 12, although only one breeding pair occurs in a group. Other group members are typically family members and assist with rearing the young of the breeding pair. Birds forage entirely on the ground for seeds and insects; communal groups defend a territory with a permanent roosting/nesting site in the center. Nests are singly distributed in a tree or several closely spaced trees, with approximately two to three nests per breeding pair. Additional details on the natural history of this species are given by Collias and Collias (1978a, b) and Lewis (in press).

STUDY AREA AND METHODS

My study area was 1 km² of mopane woodland (named for its dominant tree, *Colophosper-*

mum mopane) on the east bank of the Luangwa River, directly across from the Luangwa Valley National Park in Zambia. For details of this area see Lewis (1981). The area contained 27 communal groups with a mean group size of 4.5. Ninety-five percent of the birds from all groups were color-marked with unique combinations of one metal and three plastic leg bands. Birds were captured from their roosting nests at night with a specially designed trap.

From August 1976 through August 1979, I censused and observed each group at least once every two weeks. Observation periods normally lasted two to four hours from 06:00 to 10:00. Behavior was monitored from concealed, elevated platforms overlooking each group's nesting sites. During the first two years there were three observers, but for the final year only one observer gathered data.

Local movements of birds within the study area were plotted on a marked quadrat grid, with each quadrat 61 × 61 m. My helpers and I monitored movements of banded birds to groups outside the study area by checking approximately 80 groups at least once each year within an arbitrarily chosen zone of 760 m surrounding the study area; we also checked approximately 600 birds beyond this zone in six plots up to 3.2 km from the study area in 1979.

I used four terms to refer to birds that moved from their current group to a new group: A "transient" was an individual who visited a neighboring group but was repulsed during the same observation period in which it visited. An "invader" visited and successfully remained in a group for two consecutive observation periods or more. If an invader persisted in its new group for as long as six months, I called it a "recruit." An invader could become a recruit sooner by attempting to breed in the group it invaded. Finally, a "founder" was a bird who helped to establish a new group away from its home site.

I assessed habitat quality for each of the 27 groups during the breeding season according to the relative occurrence within each group's feeding range of the preferred ground cover used for feeding. Preferred ground cover was a mixture of bare ground and sparse vegetation up to 0.5 m tall. Fifty m^2-plots were randomly located within a 60-m radius of each group's nesting tree (an area where approximately 75% of prey items for nestlings were taken) and ground cover was assessed for each plot. Relative occurrence of the preferred ground cover among the communal groups was then estimated. Details of this procedure are described in Lewis (1981).
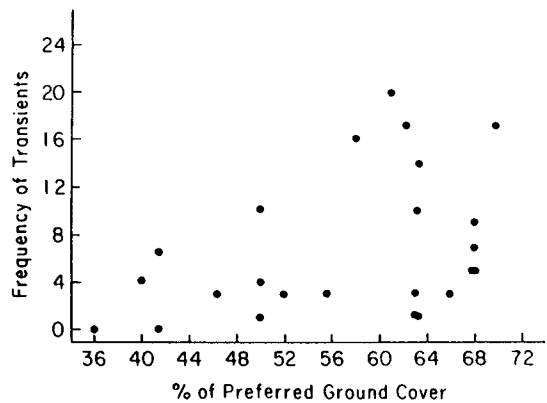

FIGURE 1.   Number of transients plotted against percent occurrence of preferred ground cover used for foraging at the group that transients invaded.

RESULTS

MOVEMENTS OF TRANSIENTS AND INVADERS

In this section I examine the factors possibly influencing the movement of transients and invaders among communal groups in this population. If birds shift their occupancy because of habitat quality, then groups occupying good habitat should have a greater frequency of transients than those with poor habitat. To test this prediction, I compared frequencies of transients per group (weighted by relative time of platform observations for a given group) with the group's habitat quality. Transient frequency ($n = 176$) was positively correlated with the relative amount of preferred ground cover at the invaded group (least-square linear correlation, $r = 0.37$, $P = 0.03$; Fig. 1).

Group members often defended their territory cooperatively by engaging in aerial fight and chasing invaders. Larger groups, therefore, should have been more successful in repulsing transients than smaller groups. This prediction was supported by a negative correlation between frequency of invaders per group and the size of the group (Kendall rank correlation, $r = -0.46$, $P < 0.001$). Furthermore, medium-sized groups had more members cooperating in chasing a transient than small groups (Mann-Whitney U-test, $Z = -2.29$, $P = 0.01$; Table 1). This trend was consistent between large and medium sized groups but was not statistically significant ($Z = -1.32$, ns).

Describing movements among groups also requires information on the source of dispersing birds in the population. For example, did each group contribute the same proportion of dispersing birds in the population? Because transients were often being chased, making their color-band combinations difficult to see,
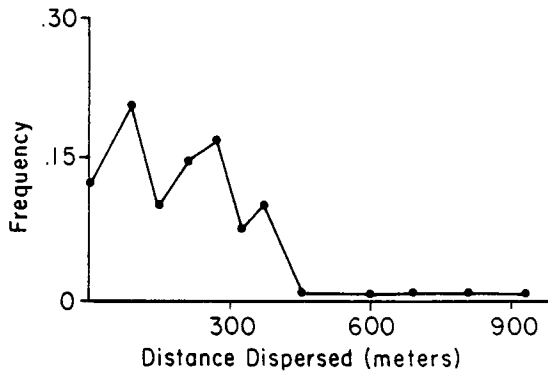
FIGURE 2. Distribution of dispersal distances approximating birth-to-breeding distances for the pooled sample of both sexes. Sex-specific dispersal given in text.

TABLE 1. Frequency distribution of number of individuals observed chasing an intruder out of small (2–3), medium (4–5), and large (6+) groups.

Small		Medium		Large	
No. of chasers	Freq.	No. of chasers	Freq.	No. of chasers	Freq.
1	14	1	17	1	16
2	8	2	16	2	20
3	1	3	8	3	10
		4	3	4	8
		5	2	5	3
				6	1

I answered this question from the invader data. The number of invaders originating from each group correlated positively with the size of their group (Kendall rank correlation, $r = 0.52$, $P < 0.001$). This result is not surprising since larger groups have more birds that can potentially disperse. I corrected this numerical effect of group size by determining the per capita rate of invaders leaving each group, and this value also correlated positively with group size (Kendall rank correlation, $r = 0.24$, $P < 0.05$).

RECRUITS AND GROUP FOUNDERS

In this section I examine three characteristics of dispersal: birth-to-breeding distances, randomness of these movements with respect to group size, and variation in reproductive success among dispersing individuals. Within the total sample of dispersing birds, recruits and founders were the most likely to breed and it was from these two classes that these characteristics were described.

My study had two obvious sources of error in estimating birth-to-breeding distances: 1) birds who became recruits or founders from outside the sampled population and whose origins were unknown, and 2) banded birds within the sampled area whose natal sites were also unknown. The first source of error was minimized by sampling only banded recruits. For the second, natal site was inferred for those birds observed as nest helpers; birds raised in a group almost always helped feed nestlings of that group, while unrelated recruits either did not feed nestlings or helped significantly less than a related helper (pers. observ.). A recruit that had previously contributed a major share of nestling feedings as a helper was therefore likely to be a natal member of that group.

DISPERSAL DISTANCES

Eleven of 42 banded recruits were in the peripheral groups surrounding the sampled, color-banded population. Additionally, five founders and seven other individuals did not disperse but bred at their natal group. Distances traveled by these 54 banded birds were used to approximate birth-to-breeding distances. Frequency distribution of these distances was strongly skewed toward short movements ($\bar{x} = 205$ m, SD = 172; Fig. 2). The sampling survey beyond the peripheral zone to 3.2 km from the study area failed to locate any banded birds, suggesting the absence of any longer distance mode of dispersal than described in Figure 2.

In this sample of 54 birds, sex was determined for only 26. Their respective dispersal distances indicated considerable overlap by sex, although males dispersed significantly farther than females ($\bar{x} = 245$ m, SD = 73, $n = 8$, males; $\bar{x} = 170$ m, SD = 135, $n = 18$, females); (Mann-Whitney U-test, $Z = 2.07$, $P = 0.02$). Excluding birds who bred at their natal site, dispersal distances were more similar ($\bar{x} = 245$ m, SD = 73, $n = 8$, males; $\bar{x} = 201$ m, SD = 116, $n = 11$, females); (Mann-Whitney U-test, $Z = 0.91$, ns).

During the three years, approximately 17 unbanded birds from outside the sampled area became either recruits or founders in the marked population. Assuming that the distribution of distances in Figure 2 was typical of these sparrow weavers for surrounding areas, peripheral groups were the likely sources of most, if not all, of the unbanded immigrants. For example, the study population had approximately 110 birds and the number of birds within the peripheral zone (760-m belt) surrounding the study area was about 290. During 1978–1979, 11 unbanded invaders entered the study population and at least four banded birds moved to the peripheral population during this same period. The 11 birds were a maximum count since they were censused continually. The four banded birds represented a minimum since they were censused only once and losses during the year could not be accounted for. If the per capita dispersal

rate was uniformly equivalent for both areas, the expected number of birds to move from the peripheral zone to the color-banded population was at least $290/110 \times 4 = 10$ to 11 birds, which was the number observed.

MOVEMENT PATTERN OF RECRUITS

I assumed that group size was likely to be important in the spatial distribution of recruits in this population. Since group size remained relatively constant among years (Lewis, in press), through bimonthly censuses groups were divided into three categories based on mean size over three years: small (2–3, $n = 8$), medium (4–5, $n = 8$), and large (6 or more, $n = 11$). The pattern of movements among these categories for recruits (Fig. 3) suggests that more recruits left than entered large groups, with a reversed trend for small and medium groups. The number of recruits entering a group was negatively correlated with the size of the group (least-square linear correlation; $r = -0.34$, $P < 0.01$).

In addition to the possible effects of improved territorial defense with a larger group, other explanations for this unequal flow of recruits are: 1) higher turnover of breeding birds in smaller groups, 2) replacement of breeding females in large groups by a female from the same group, 3) greater production of potential recruits in large groups, and 4) social facilitation of dispersal in large groups. The first three explanations are substantiated by the reproductive success and mortality patterns documented for this population (Lewis 1981). The fourth explanation may also be relevant since large groups periodically produced bands of group cohorts who invaded neighboring groups.

Six such cohort invasions were observed and all were from large groups. Four of these invasions preceded the disappearance of the current breeding female and were likely to have caused her removal. In one case, we were able to observe in detail the invasion of a group of three birds. On 15 January 1977, four birds from a neighboring group invaded the first and intense fighting between the groups ensued. The female of the first group, GG-BW, vigorously chased the invaders and fought with one of them. Intense chasing continued throughout the day. On the following day, GG-BW was not present and she never returned. Within less than a month, an invading female had mated with the resident male and had begun incubating her own eggs. Another cohort member remained and helped rear her young.

VARIATION IN REPRODUCTIVE SUCCESS

The reproductive history of recruits (Fig. 4) indicated a large variation in their breeding
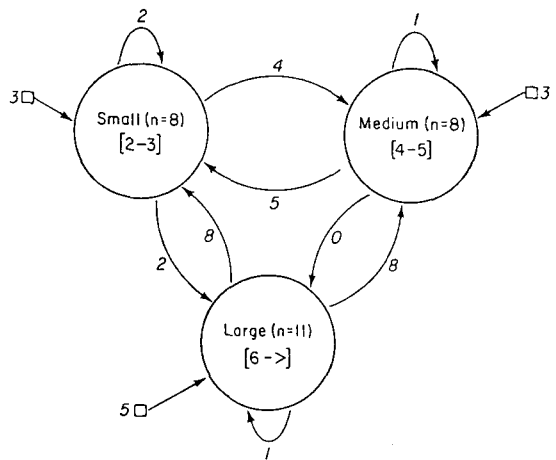

FIGURE 3. Pattern of movements for recruits among group size categories from September 1976 to August 1979. Movements from outside the sampled population are indicated by arrows with a square. Number of groups and the group size for each category are indicated inside the circle.

performance. Some recruits bred more successfully than others in their first year. Distance a recruit traveled may have been an important factor in this variation. For example, in each of the six cohort invasions, a member of the cohort group soon attempted breeding, and some or all of the accompanying birds remained as nest helpers. These invasions represented 24% of the breeding attempts by recruits; the mean distance for these six invasions was only 120 m (vs. 250 m mean distance for the sample of banded recruits).

In addition to cohort dispersal, other evidence supported the possible correlation of short distance dispersal with early reproductive success. The mean distance traveled by banded recruits within the color-marked population was 210 m ($n = 31$, SD = 131) and mean distance traveled by banded recruits to peripheral groups was 390 m ($n = 10$, SD = 320). This difference should also reflect the greater distance traveled by unbanded recruits from peripheral groups into the sampled population. Of the approximately 30 unbanded birds that invaded the sampled population, only 3 became breeding recruits and in each case there was a time lag of at least six months before the birds successfully mated. This delay may have been caused by waiting before shifting to a breeding opportunity at a nearby group. In contrast, of the 54 banded invaders within the population, 20 attempted breeding and only 2 delayed longer than six months before mating. These two birds also dispersed relatively long distances (440 m and 350 m).

FIGURE 4. Reproductive success from 1976–1979 for two classes of recruits: a) residency in the invaded group for less than one year, and b) residency in the invaded group for one to two years. Reproductive success categories: A = individuals not mated, B = mated but failed to fledge young, C = fledged one young, D = fledged two, and E = fledged three.

DISCUSSION

COMPARISON WITH OTHER SPECIES

An estimate of birth-to-breeding distances in this sparrow weaver indicated a skewed distribution toward short distances. In this, *P. mahali* resembles two other communal species for which comparative data on dispersal are available: the Florida Scrub Jay (*Aphelocoma c. coerulescens*; Woolfenden and Fitzpatrick 1978) and the Green Wood-Hoopoe (*Phoeniculus purpureus*; Ligon and Ligon 1978). In contrast, the weaver differs greatly from the dispersal range reported for three well studied non-communal species: the Great Tit (*Parus major*; Greenwood et al. 1978), the Red-billed Fire-Finch (*Lagonosticta senegala*; Payne 1980), and the Pied Flycatcher (*Ficedula hypoleuca*; Berndt and Sternberg 1969). These non-communal species each have a mean birth-to-breeding distance three to five times that of the weaver, and they contain more territories

within their birth-to-breeding distances than does the weaver.

These differences in dispersal between communal and non-communal species might be related to spatial and temporal availability of required resources (Lewontin 1965). For example, in the Acorn Woodpecker (*Melanerpes formicivorus*; Ritter 1938, MacRoberts and MacRoberts 1976, Stacey 1979), resource availability varies greatly in parts of the range (Roberts 1979). In one area, food supply was insufficient to maintain year-round territories and birds migrated during the winter (Stacey and Bock 1978). This population was atypical by lacking the communal social structure representative of the species as a whole. Stacey and Bock suggested that oscillating carrying capacity contributed to increased dispersal, which lowered the stability of social units. Such uncertainties of necessary resources are likely to impose limitations on the natural selection of communal social behavior (Brown 1978).

P. MAHALI DISPERSAL—AN ADAPTIVE PROCESS

By remaining in its natal territory and maintaining a watch over neighboring territories, an individual can quickly move to an available breeding site. Such behavior was hypothesized by Selander (1964) and Brown (1969) for territorial species with saturated population densities that provide irregular and infrequent opportunities for non-breeders to reproduce. Under this form of dispersal, benefits of increased inclusive fitness can be gained by helping a relative (Hamilton 1964) while waiting for a reproductive opportunity elsewhere.

Kiester and Slatkin (1974) proposed a dispersal model in which individuals enhance their chances of acquiring food or a nest site by monitoring the neighborhood environment for availability of such resources. This habit facilitates opportunistic movements toward irregularly occurring opportunities. Their model extended the behavioral complexity of that proposed by Selander (1964) and Brown (1969) and offered a mechanism for making a sedentary life style compatible with a successful dispersal phase.

Field data support this model of dispersal for the White-browed Sparrow Weaver. First, the species is sedentary (Collias and Collias 1978a, b; Lewis, in press). Second, because breeding individuals disappear irregularly and infrequently (Lewis, in press), dispersal to these sporadic openings appears to be consistent with the opportunism of the model. For example, of 15 breeding males who disappeared, 12 were each replaced by another male within a month and typically within a week. In contrast, of 45

non-breeding adults that disappeared, only six were replaced by another adult within a month. Kiester and Slatkin's (1974) neighbor-monitoring model predicts this response, since to move quickly into a reproductive opening would require an efficient means of recognizing when such an opening occurs. Furthermore, dispersal distances were relatively short, indicating that any searching would have been close to a bird's home group. I often saw various social interactions with immediate neighbors (Lewis 1981) and they could be important in monitoring opportunities for breeding. Neighboring groups frequently engaged in bouts of chorusing and it is possible that the presence of particular members could be monitored from such vocal displays.

BEHAVIORAL PLASTICITY AND POSSIBLE SIGNIFICANCE TO SOCIAL FACTORS

Dispersal in this sparrow weaver occurs by any of the following behaviors: 1) an individual moves to a neighboring group where it replaces a breeding bird who has disappeared, 2) an invader resides in a group as a non-breeder while waiting for a reproductive opportunity at its present group or at a neighboring group, 3) cohort dispersal to a nearby group, and 4) group founding to a site previously unoccupied. In the second case, dispersal may serve as a springboard to another group. I suggest that this mode is important for long distance dispersal. For example, birds from outside the study area typically invaded the study population by entering a relatively small group before dispersing again to a breeding opportunity at a neighboring group. These birds were likely to have originated from inside the peripheral zone and distances traveled to their breeding sites would be considerably greater than the mean distance traveled by the sample of color-marked recruits. Furthermore, the sample of color-banded recruits indicated that those dispersing the greatest distances adopted this springboarding behavior.

Group defense may have affected why such birds did not initially invade larger groups. This does not explain, however, why these birds tended to disperse farther than average. I propose that birds adopting this form of dispersal are socially subordinate and are escaping their status by shifting long distances to where their previous status would be unknown. By "social bluffing" in their new location, they might enhance their chances of eventually obtaining a breeding position. This hypothesis remains to be tested.

Cohort dispersal typically led to either the eviction or an early disappearance of a breeding female at a neighboring group. Her replacement was always one of the cohort members. Cohort dispersal was not limited to the sporadic occurrence of breeding opportunities and occurred only in large groups. Hence, by cohort dispersal larger groups could increase their rate of successful dispersal over smaller groups. Social cooperation in this mode of dispersal was suggested by the fact that cohort members appeared to share in the invading effort and often remained to help raise the young of the member who succeeded to the vacated breeding position.

GENETIC IMPLICATIONS OF P. MAHALI DISPERSAL

Cohort dispersal, more frequent breeding opportunities at smaller groups, higher emigration rate at larger groups, and increased territorial defense with group size are all possible factors helping to generate the dispersal pattern illustrated in Figure 3. Despite the greater number of recruits entering small groups, the potential gene flow due to these recruits is relatively small, since most of the successful reproduction in this population is limited to large groups (Lewis 1981). Because breeding females are replaced by close relatives in large groups (Lewis, in press), a key factor in measuring gene flow in this species is the source of male recruits who enter and breed in these groups. Too few male recruits were seen during this study to evaluate their impact on gene flow.

The relatively high degree of philopatry for both sexes as indicated by the potentially short birth-to-breeding distances suggests that neighborhood size (Wright 1943, 1951) may be small for the White-browed Sparrow Weaver. Furthermore, the high variation in reproductive success among the communal groups in this population (Lewis 1981) lowers its effective population size (Crow and Kimura 1970). Under these circumstances, the chance of a zygote forming from gametes with common ancestry is improved, and the impact of this dispersal pattern on the species' population structure will be to increase inbreeding relative to that of most non-communal species. Such mating, known as background inbreeding, can occur despite the absence of close-kin mating (Wright 1951).

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