

COOPERATIVE BREEDING IN *LANIUS* SHRIKES. I. HABITAT AND DEMOGRAPHY OF TWO SYMPATRIC SPECIES

STEVE ZACK¹ AND J. DAVID LIGON

Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA

ABSTRACT.—Two sympatric species of *Lanius* shrikes were studied near Lake Naivasha, Kenya, in an effort to understand the ecological factors favoring the evolution and maintenance of cooperative breeding in one of them. The Gray-backed Fiscal Shrike (*L. excubitorius*), a cooperative breeder, occupied territories of significantly higher tree and shrub cover than did the Common Fiscal Shrike (*L. collaris*), which is not a cooperative breeder. Areas with greater vegetational cover held significantly more insects in the dry months of the year than did relatively open sites. Possibly associated with the shrikes' differences in habitats and resources was their significant difference in disappearance rates during the study. Turnover of individuals among gray-backs was about half that of common fiscals. Similarly, territorial stability (as measured by the percent of territories continually occupied during the 18-month study) was nearly twice as high in the gray-backs. Within the restricted acacia woodland gray-backs were dominant to common fiscals, and in four instances we observed gray-backs expel common fiscals from the latter's territories. We suggest that cooperative breeding in gray-backs is related to occupancy of a temporally stable, but spatially restricted, habitat of high quality. This in turn may lead to relatively higher survivorship in gray-backs and, as a result, their habitat becomes relatively "saturated." In such an ecological and demographic setting, options for juvenile dispersal are restricted, and one evolutionary solution is group living. Received 5 October 1984, accepted 11 April 1985.

COOPERATIVELY breeding birds have received considerable attention in recent years (see reviews by Brown 1978; Emlen 1978, 1984). Selander (1964) first suggested habitat saturation as a critical factor favoring the evolution of such social systems. Habitat saturation occurs when all usable habitat in an area is filled with breeding pairs. An important consequence of habitat saturation is the inability of nonbreeding birds to establish a territory in the local habitat. Retention of young in the natal territory until a breeding vacancy occurs is one response to habitat saturation. Cooperative breeding often is thought to be a result of such habitat restrictions and retention of offspring in the natal territory. Only recently, however, has the influence of habitat on the development or maintenance of cooperative breeding systems been investigated in a quantitative manner (e.g. Brown and Balda 1977, Gaston 1978a, Craig 1979, Dow 1980a, Trail 1980, Koenig 1981a, Brown et al. 1983).

Stacey (1979) related differences in group size, site tenacity, and reproductive rates between New Mexico and California populations of the Acorn Woodpecker (*Melanerpes formicivorus*) to differences in the degree of habitat saturation and in demographic patterns in the two areas. Koenig and Pitelka (1981) refined the habitat saturation hypothesis (emphasizing "resource localization" and "habitat localization") and postulated that a relative scarcity of marginal habitat is instrumental in the evolution of cooperative breeding. Atwood (1980) used this line of reasoning to explain why Santa Cruz Island Scrub Jays (*Aphelocoma coerulescens insularis*), which occupy areas with extensive marginal habitat, are not group-breeders, whereas Florida Scrub Jays (*A. c. coerulescens*), which are more habitat-restricted, do exhibit cooperative breeding (Woolfenden 1975, Woolfenden and Fitzpatrick 1978).

In this paper we compare two sympatric congeneric shrikes, one species a cooperative breeder and the other a more typical (for the genus) noncooperative breeder. We then consider the possible roles of habitat and resources in the evolution and maintenance of these two

¹ Present address: Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907 USA.

social systems. The Gray-backed Fiscal Shrike (*Lanius excubitorius*) is a cooperatively breeding species, with social units ranging in size from 2 to 9 or more birds. Gray-backs appear to be monogamous, with only one breeding pair per group (Zach MS). The supernumerary birds in a flock act as "helpers." The breeding biology of gray-backs is very similar to that described for another cooperatively breeding laniid, the Yellow-billed Shrike (*Corvinella corvina*; Grimes 1980). In contrast, the sympatric Common Fiscal Shrike (*L. collaris*) occurs only as breeding pairs (Zack MS). First-year Common Fiscal Shrikes disperse upon maturity, usually coincident with molt into adultlike plumage. Gray-backs are restricted to *Acacia* woodlands in east and central Africa, whereas common fiscals occur throughout most of the Afrotropical region in a variety of habitats—most commonly in open and disturbed (especially cultivated) areas (Hall and Moreau 1970, Britton 1980, Mackworth-Praed and Grant 1960).

STUDY AREA AND METHODS

Study area.—The study site is located on Morendat Farm near Lake Naivasha, Kenya, in the Rift Valley of east Africa (0°40'S, 36°23'E). Ligon and Ligon (1978) have described this area. The vegetation is characterized by a virtually monotypic stand of the yellow-barked acacia (*Acacia xanthophloea*) with an understory of Naivasha star grass (*Cynodon plectostachyus*) and a few species of perennial shrubs (most commonly *Achyranthes aspera*, *Hypoestes verticillaris*, and *Solanum incanum*). Thickets of *Euphorbia*, *Aloe*, or *Opuntia* occur uncommonly in woodland openings. To the east and south of the study site are more open areas with only scattered acacias. To the west toward Lake Naivasha is a denser woodland composed of several tree species. To the north is a large plowed field under constant cultivation (see Fig. 1). The farm is grazed by domestic cattle, domestic sheep, six species of native bovinds, and hippopotamus (*Hippopotamus amphibius*).

Rainfall measurements were taken from records kept by the farm managers of Morendat and adjacent Marula farms. Rainfall sometimes occurs in a bimodal pattern but is highly unpredictable in both timing and quantity. The general pattern is that of substantial rains in April–May with lighter rains during other months.

Shrikes were studied from June 1979 to December 1980 and from August 1981 to early January 1982. Birds were trapped in mist nets or caught in spring-loaded traps baited with large insects or small frogs, and then banded with a uniquely numbered alumi-

num band on one leg and a unique color combination of two color bands on the other. Nestlings of both species were similarly banded at 10 days of age. Groups (gray-backs) and pairs (common fiscals) were censused at irregular intervals, but generally at least once a month. Both species are sexually dimorphic in plumage, as females have auburn flanks (Grimes 1979) that, although difficult to observe in the field, are readily observed in the hand.

Both shrike species nested with the onset of the major rains. Most nests were inaccessible due to their height and frailty of the supporting limb. The number of fledged young was recorded from all successful nests for both species.

Habitat sampling.—Twelve gray-back and 6 common fiscal territories were measured using a modified point-quarter method (Cottam and Curtis 1956) as follows: Beginning 50 m east of the southwest corner of a given territory, a north-south transect was established. Each transect consisted of five 40-m intervals, with each interval having one randomly determined point. From each point, the distance (in cm) to the nearest tree (≥ 1.5 m in height) to the west, and then again from the random point to the nearest individual tree to the east, was measured. Occasionally, this led to repeated sampling of the same tree in relatively open areas. These measures formed the basis of the point-tree data. From each of these trees, the distance to its nearest neighboring tree was measured for use in dispersion estimates. Dispersion estimates are from the equation $\Sigma p^2 / (\Sigma p^2 + \Sigma n^2)$, where p is the point-to-plant distance and n is the plant-to-nearest-neighbor distance (Hopkins and Skellam 1954, Batcheller and Bell 1971). The diameter at breast height (DBH) was measured for each tree encountered. DBH measures were taken only once and were not used again if the tree was encountered more than one time. A 1-m² grid also was established at the original random point, and the percent coverage of perennial shrub cover was determined visually. This shrub measurement was repeated in 1-m² quadrats 5 and 10 m west of the point and 5 and 10 m east of the point, making five such measurements per random point. At each quadrat, tree cover was recorded (present or absent), permitting a relative measure of percent shade cover. This process was repeated 15 times per territory (3 parallel transects containing 5 random point lines spaced 75 m apart), giving 30 point-to-tree measures, 30 tree-to-tree measures, and 75 perennial shrub cover and tree cover measures. Five territories (2 gray-back and 3 common fiscal) were too small to accommodate three transect lines, and for these only two transects (for a total of 20 random point measurements) were sampled. All measurements were made in the woodland; no measures were taken in the plowed field. Three common fiscal territories (osf, gpf, and tf in Fig. 1) contained no acacias and were not measured. The plowed field

TABLE 1. Results of the vegetational sampling per territory for each species on Morendat Farm, Naivasha, Kenya. Territory names are the same as in Fig. 1. *n* refers to the number of random points sampled per territory from which two point-to-tree measures were made. Tree diameter at breast height (DBH) measures (sample sizes in parentheses) do not include repeat samplings.

Territory	<i>n</i>	Random point to tree (cm)		Shrub cover (%)		Tree cover (%) \bar{x}	DBH (cm)			Disper- sion
		\bar{x}	SD	\bar{x}	SD		(<i>n</i>)	\bar{x}	SD	
Gray-backed Fiscal Shrikes										
RM	30	1,451.5	739.9	9.24	16.34	34.7	(49)	34.4	42.7	0.524
NWW	30	1,450.4	889.9	10.52	19.88	49.3	(56)	42.8	42.8	0.480
RYU	30	1,864.1	1,007.1	10.40	17.36	28.0	(47)	39.6	15.9	0.624
BM	30	1,259.5	615.4	8.71	24.01	28.0	(42)	31.8	23.8	0.500
CW	30	949.2	582.9	3.88	9.78	45.3	(49)	24.1	26.1	0.550
KM	30	901.0	421.4	10.67	14.76	52.0	(57)	23.6	14.3	0.622
MN	30	1,346.6	653.2	4.27	13.87	50.7	(58)	35.0	17.7	0.552
NYM	30	1,348.9	793.8	9.76	19.71	41.3	(46)	35.3	28.4	0.529
PYM/NS	20	988.1	593.5	6.30	14.81	46.0	(33)	29.9	23.4	0.476
SK	30	836.7	444.5	16.00	27.44	56.0	(51)	25.6	23.5	0.608
MYN	30	641.1	420.6	22.67	28.36	64.0	(52)	16.0	16.9	0.508
HKK	20	1,919.9	850.6	3.30	8.84	10.0	(29)	17.3	17.9	0.586
Total	340	1,234.2	779.1	9.93	19.81	42.9	(569)	30.0	27.4	0.546
Common Fiscal Shrikes										
hf	30	1,987.8	1,253.3	5.40	17.80	29.3	(48)	49.0	50.3	0.656
vpf	30	1,419.4	817.7	5.96	12.20	45.3	(55)	33.2	38.5	0.560
cpsf	20	1,946.8	1,083.5	0.60	2.60	16.0	(31)	34.8	41.4	0.647
cpnf	20	1,482.9	725.0	12.70	21.50	50.0	(28)	34.5	24.4	0.575
whhf	30	1,634.7	1,255.0	1.67	8.32	25.3	(50)	16.0	17.5	0.613
wgf	20	1,790.1	854.4	5.70	18.46	20.0	(34)	37.4	20.7	0.545
Total	150	1,704.4	1,049.4	5.14	15.00	31.4	(246)	33.7	36.3	0.599

was used extensively by the common fiscals and to a lesser extent by the gray-backs for feeding. However, no measurements could be made of insect abundance there.

To assess prey availability, three pitfall trap grids (traps 10 m apart in a 5 × 5 configuration) were set up in areas of different vegetational structure (low tree density/low shrub cover, high tree density/high shrub cover, and an area of intermediate value for these measures; see Table 2 for values) to assess possible differences in the prey base of the insectivorous shrikes in different microhabitats. Pitfall traps were opened for 8-h daytime periods during alternate weeks throughout 1980. Cattle dip (a locally used insecticide sprayed on cattle) was put in each of the traps to retain captured insects. The insects were then stored in methanol and water until all "edible" insects equal to or greater than 1 cm in length could be measured to the nearest mm. The number of edible insects collected in pitfalls less than 1 cm was negligible. Edibility was assessed by direct observations of foraging and feeding shrikes throughout the study. Both shrike species appeared to have great overlap in the kinds and sizes of prey captured (Zack in prep.). Coleopterans, "naked" lepidopteran larvae (without urticating hairs), some hemipterans, and all

orthopterans were eaten by the shrikes, whereas no shrike was observed to eat hymenopterans or lepidopteran larvae with urticating hairs.

Vegetational characteristics of the grid sites were measured in the following way: Perennial shrub cover was estimated using the 1-m² grid described above, except that measurements were made 5 m west of each pitfall trap and shrub cover was recorded as either present or absent. Tree shade cover was recorded at these same points. Trees were mapped relative to the position of the pitfall traps, and DBH was measured for each tree.

Data were analyzed using SAS programs (SAS Institutes Inc., SAS Circle, P.O. Box 8000, Cary, North Carolina 27511).

RESULTS

Habitat and shrike distribution.—Significant differences existed between the territories of the two shrike species with regard to tree density (expressed in terms of random point-tree measures, one-way ANOVA, *df* = 1 and 489, *F* = 350.14, *P* < 0.0001) and percent perennial shrub cover (Kruskal-Wallis test, *df* = 1 and 1,222, *F* =

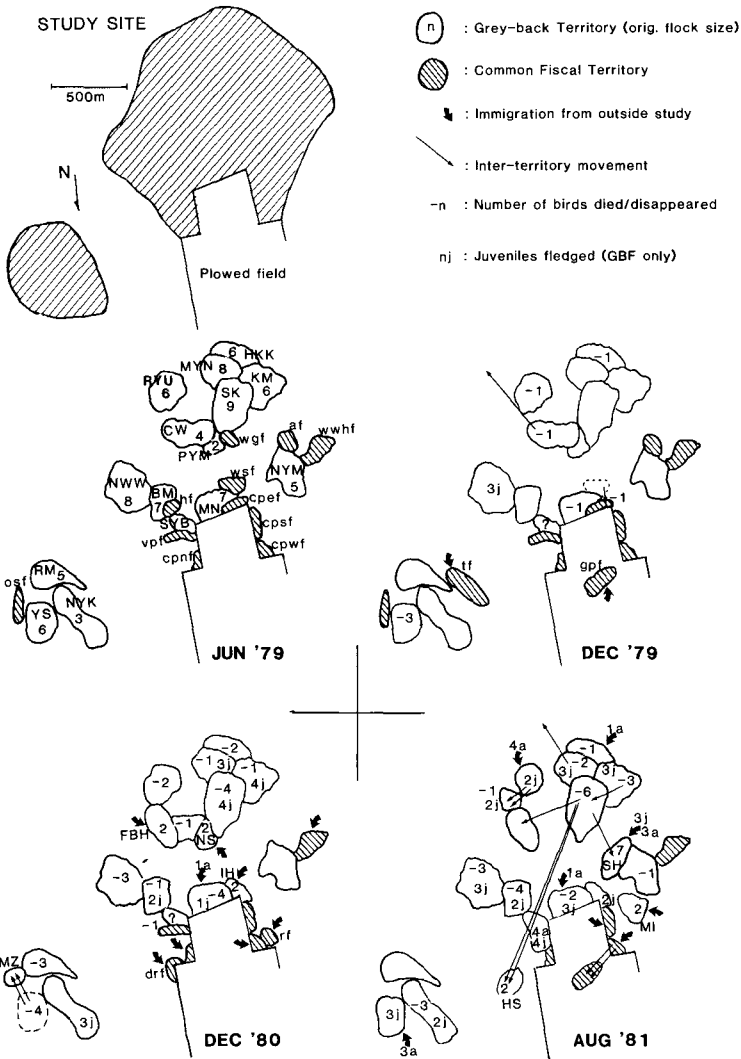


Fig. 1. The spatial and temporal pattern of Gray-backed Fiscal (open areas) and Common Fiscal (hatched areas) shrike territories during the study. The hatched regions in the upper left represent the area studied (birds of both species did occur on the eastern edge of these areas). Original flock sizes for gray-backs in June 1979 are indicated; for subsequent months, only changes are noted. Immigrations from outside the study area are noted by short, bold arrows and designate single individuals unless otherwise noted. Interterritory movements (birds of known origin) are indicated by long, thin arrows. The flock or pair letter designations correspond to those given in Table 1.

44.58, $P < 0.0001$). Gray-backed Fiscal Shrikes occupied territories of significantly higher tree density (lower point-to-plant distances) and higher perennial shrub cover than did common fiscals (Table 1). Gray-backs also occurred in habitat of higher tree cover than did the common fiscals (Table 1, G -test with William's correction, $G = 14.57$, $df = 1$, $P < 0.001$). Neither the pattern of tree dispersion (Kruskal-

Wallis test, $df = 1$, $0.05 < P < 0.10$) nor the DBH of acacias (one-way ANOVA, $df = 1$ and 814, $0.05 < P < 0.10$) differed significantly between territories of the two species.

Gray-backed Fiscal Shrikes were strongly associated with yellow-barked acacia woodlands throughout their range, contrasting sharply with the broad distributional pattern of the Common Fiscal Shrike. The data presented here

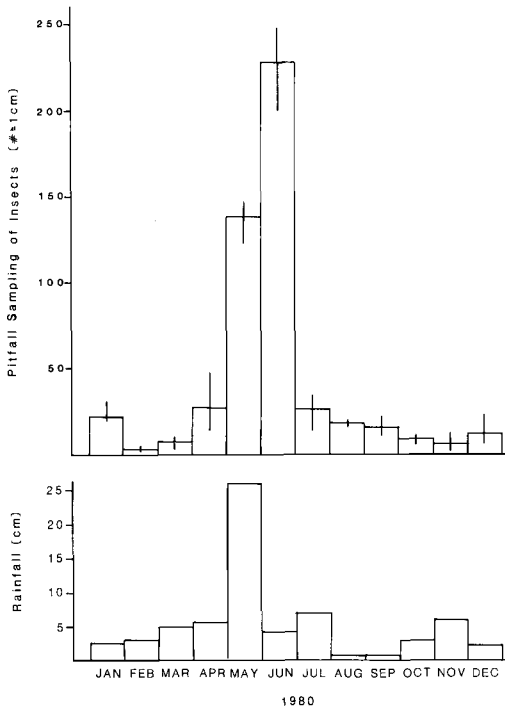


Fig. 2. Pattern of rainfall and "edible" insect (see text) abundance during 1980 on Morendat Farm. For each month, the mean value of insects sampled (two sampling periods, three grids) and the range of the grids are shown.

consider only common fiscal territories occurring in or at the edge of acacia woodland, and thus are a very conservative contrast of the differences in the habitat occupied by the two species. Common fiscals commonly were observed throughout the Rift Valley along roadsides and in many kinds of open country.

Behavioral interactions of Gray-backed and Common Fiscal shrikes.—Although the data showed a significant difference in habitat characteristics of territories of the two shrikes, the two shrikes can be highly syntopic on the study site. This was seen most clearly in June 1979 at the beginning of the study. Five pairs of Common Fiscal Shrikes held territories within the acacia woodland away from the plowed field (Fig. 1). This degree of overlap with the larger Gray-backed Fiscal Shrikes had not been observed during less systematic observations in the previous 4 yr. Both shrike species held exclusive territories against both conspecifics and each other. As the study area became increasingly drier during the months of August–Oc-

TABLE 2. Results of insect sampling during 1980 for the three grids of different vegetation cover.

Date	High cover (shrub = 52%, tree = 60%)	Inter- mediate (shrub = 28%, tree = 48%)	Low cover (shrub = 0%, tree = 12%)
2 Jan	4	2	1
15 Jan	1	0	1
2 Feb	5	7	2
22 Feb	4	3	1
13 Mar	17	34	10
26 Mar	5	13	4
11 Apr	99	92	100
24 Apr	137	156	100
8 May	112	128	110
23 May	11	17	37
6 June	5	11	21
20 June	9	23	7
4 July	15	11	10
18 July	5	5	8
29 July	6	7	13
18 Aug	6	8	8
31 Aug	6	8	2
13 Sept	5	2	4
29 Sept	7	2	3
15 Oct	5	0	2
31 Oct	15	2	3
14 Nov	8	5	3

tober 1979, aggression between the two shrike species became conspicuous. Such aggression was directly observed in 4 of the 5 woodland territories of the common fiscals. The gray-backs always won such encounters, apparently due to their larger size and numerical advantage. We noted persistent aggression by the gray-back flock BM (7 members) toward the common fiscal pair hf on 5 September (Fig. 1), in the form of displacement from perch sites and active chases. Final expulsion of the common fiscals took place on 5 October, when we observed several long chases that culminated in a single gray-back chasing the male Common Fiscal Shrike up and over the tall canopy and out of sight. This pair of common fiscals was not seen again, and from that time on members of the gray-back BM flock foraged regularly in what previously had been hf territory. The common fiscal pair wgf also disappeared soon after we first noted aggression on 23 June between it and the 9-member gray-back SK flock (Fig. 1). At that time, pair wgf had fledged two offspring in its territory. The breeding female of the wgf pair and one offspring disappeared in

TABLE 3. Statistical comparisons between the three pitfall trap grids and between seasons. All pairwise comparisons are Wilcoxon's signed rank tests for two groups (Sokal and Rohlf 1981; T_s refers to the test statistic; n refers to the number of pairwise comparisons per category). Comparisons within seasons (wet season: April–August; dry season: January–March and September–November) comparing all three grids and the combined comparison for all grids for 1980 are Friedman rank tests (Brownlee 1965), with the Chi-square approximations listed.

Grid comparison (amount of cover)	Wet season			Dry season			Combined		
	T_s	n	P	T_s	n	P	T_s	n	P
High-intermediate	7.0	8	NS	35.5	12	NS	79.5	20	NS
High-low	20.0	9	NS	4.0	12	<0.01	71.5	21	NS
Intermediate-low	22.0	9	NS	24.5	12	NS	85.5	21	NS
All grids	$\chi^2 = 1.06$ $P > 0.5$			$\chi^2 = 4.40$ $0.1 < P < 0.2$			$\chi^2 = 0.06$ $P > 0.5$		

early August, probably taken by a predator, as the upper mandible of the juvenile was found in the territory about a week later. The widowed male and the remaining juvenile disappeared in late September. By December 1980, only one common fiscal territory not adjacent to the plowed field, wwhf, was present on the study area. No new common fiscal territories were established wholly within the acacia woodland after the above-described events of late 1979.

Prey abundance and vegetational cover.—There was a generally concordant pattern between rainfall and insect abundance (Fig. 2; raw data in Table 2). Data from the three pitfall grids were lumped together to show the seasonal pattern (insect captures from the three grids did not differ significantly overall and thus were combined) (Table 3). There were significant differences (Kruskal-Wallis test, $P < 0.01$), however, between the high- and low-cover areas in edible insect availability during the six driest months of 1980 (January through March and September through November). Other pairwise comparisons between pitfall areas and season (wet months, dry months) showed no significant differences (Table 3). Three significant differences in average prey size (of prey greater than or equal to 1 cm in size) were found in 10 tests [with Bonferroni (1936) adjustment]. The tests were of all pairwise comparisons of the different grids in the two seasons, plus a comparison of overall prey size between the wet and dry months. The average size of prey sampled in the dry months was significantly larger than the average size of prey sampled in the wet months (dry months: mean = 1.146 cm, SD = 0.029, $n = 183$; wet months: mean = 1.137,

SD = 0.009, $n = 1,288$; $F = 1.48$, $P < 0.0005$), but the absolute number of prey differed tremendously between the samples and so this result probably is not biologically meaningful. The two other differences found in average prey size were observed when the low-cover grid was compared with the intermediate-cover grid in the dry season (low cover: mean = 1.188, SD = 0.311, $n = 34$; intermediate cover: mean = 1.130, SD = 0.508, $n = 69$; $F = 2.67$, $P < 0.005$) and when the high-cover grid was compared with the intermediate-cover grid during the wet months (high cover: mean = 1.124, SD = 0.351, $n = 411$; intermediate cover: mean = 1.118, SD = 0.302, $n = 461$; $F = 1.35$, $P < 0.005$). Again, these differences do not appear to be biologically important to the shrikes.

Comparative demography.—Individual survivorship of adult gray-backs was 67% (41/61 birds surviving or staying on the study site) from August 1979 to August 1980 and 64% (34/53 surviving) from August 1980 to August 1981 (note, however, that mortality could not be distinguished from long-distance emigrations). In contrast, survival of adult Common Fiscal Shrikes in the first period was 39% (7/18 surviving). Adult common fiscals were defined as only those birds with bold black-and-white plumage. Thus, dispersing juveniles were not considered. Too few common fiscals were banded in 1981 to evaluate survival in relation to gray-backs. A Mantel-Cox Survival Analysis (Mantel 1966) of the 18-month period from June 1979 to December 1980 by species showed a significant difference in rates of disappearance ($P < 0.001$; Fig. 3). No relationship was found for either species as to when individuals disappeared (wet season vs. dry season in 1980;

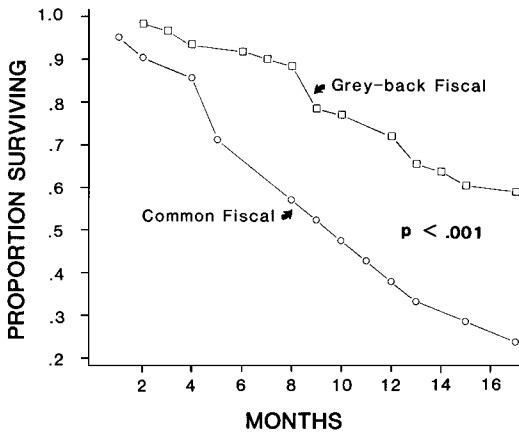


Fig. 3. Survivorship curves for Common Fiscal Shrikes ($n = 21$) and Gray-backed Fiscal Shrikes ($n = 61$) for the period June 1979 to December 1980.

gray-backs: $\chi^2 = 0.39$, $P > 0.50$; common fiscals: $\chi^2 = 0.82$, $P > 0.50$).

Interspecific differences in number of territories lost or vacated during the period from June 1979 to December 1981 were significant ($\chi^2 = 5.76$, $P < 0.025$). Of the gray-back territories recorded in June 1979, 59% (10 of 17) were occupied continuously (although not necessarily by the same individuals) through December 1981. In contrast, only 24% (4 of 17) of the territories of common fiscals were continuously occupied (see Fig. 1).

A few examples for each species will illustrate the dynamics of demographic flux during the study. The gray-back territory NYM (Fig. 1) held 5 birds from June 1979 until sometime between December 1980 and August 1981, when 1 flock member disappeared. No successful breeding occurred in this flock during the study. In contrast, the gray-back flock SK (Fig. 1) had 9 members from June through December 1979. By December 1980, however, considerable flux had occurred. Four adults had died or disappeared, and 4 juveniles had been reared and recruited into the flock. By August 1981, 6 birds had disappeared from this group (including the female breeder, which was replaced by a female helper from the adjacent KM flock); 4 of these 6 had emigrated to nearby flocks. Only 1 was known to have gained breeding status in its new territory, a female hatched in 1980 that attempted unsuccessfully to breed in the FBH territory.

Individual turnover of common fiscals also is readily seen in Fig. 1. The number of fledged young is not indicated for this species, as no offspring became established on the study site after fledging. An indication of the high level of individual and territorial turnover characteristic of this species is shown by the cpwf pair. On 10 March 1980 the female breeder died (directly observed), and she was quickly replaced by a bird from outside the study area. By August 1981, the territory of the pair had shifted or been displaced from the edge of the woodland to entirely within the plowed field, and a new pair of common fiscals occupied the former territory of the cpwf pair. Movement from one territory to another by a breeder was recorded once in the gray-backs and four times in the common fiscals.

Production of young.—A final comparison between species relates to the relative production of young. Brown (1974) predicted that cooperative species would have lower reproductive rates than their noncooperative relatives. Our results do not support this prediction (Table 4). No significant differences were detected when comparing young per pair (here comparing only 2-member gray-back groups with the common fiscals), young per group (comparing production of young per territory, regardless of group size), or young produced per adult (even though only one pair of gray-backs contributes directly genetically to the production of young).

The major reason for these similarities in production of young appears to be the high incidence of nest predation for both species. Eighty-five percent of the nests initiated for both species failed (Zack MS). In the acacia woodland site these two *Lanius* shrikes were among the very few bird species that nested in open cups. (*Turdoides* babblers and the drongo *Dicrurus adsimilis* have nests similar to the shrikes.) Most major groups (weavers, starlings, coraciiforms, sunbirds, old world warblers) nested either in highly cryptic or enclosed nests. Shrike nests appeared to be among the most conspicuous and vulnerable of all species nesting on the study site. Given the similarity in predation rates, it appears that the differences in social structure did not affect a given nest's vulnerability to predation. However, when considering only those nests that successfully fledged young, gray-backs fledged

TABLE 4. Comparison of Common Fiscal and Gray-backed Fiscal shrikes' production of young. Data are combined from 1980 and 1981.

Comparison	Common Fiscal Shrike	Gray-backed Fiscal Shrike	Test	P
Young/pair	1.15	0.78 ^a	$\chi^2 = 0.75$	>0.10
Young/group	1.15	1.39 ^b	$\chi^2 = 1.70$	>0.10
Young/adult	0.58	0.35 ^c	$\chi^2 = 2.83$	0.05 < P < 0.10
Young fledged/ successful nest	1.88	2.65	Wilcoxon two- sample test, z = -1.98	<0.05

^a Pairs only.

^b All groups.

^c Includes helpers.

more young on average than did common fiscals (gray-backs: $n = 17$ nests, mode = 3, mean = 2.64, SD = 0.78; common fiscals: $n = 8$, mode = 1, mean = 1.87, SD = 0.83; Table 1). This result opposes Brown's (1974) prediction. The difference could be due to the presence of helpers in the gray-backs, the occupancy of higher-quality habitat, or a combination of these and other factors.

DISCUSSION

Fry (1972) commented that cooperative breeding systems are a "mixed bag ecologically," and he felt that no common selective agent could account for them. Dow (1980b) even suggested that the observed diversity of cooperative breeders indicates that this phenomenon may be more likely to arise as a consequence of special social rather than strictly ecological factors. Reyer (1980) and Emlen (1982) also observed that attempts to find ecological correlates have been largely unsuccessful. We compared habitat affinities, resource bases, demography, and territory stability of congeneric sympatric species that differ in their social systems (cooperative vs. noncooperative breeding) in an attempt to find meaningful ecological correlates of cooperative breeding (see Brown 1974). Our results strongly implicate habitat stability and saturation in the evolution of cooperative breeding, as has been suggested often (e.g. Selander 1964; Brown 1974, 1978; Emlen 1978; Woolfenden and Fitzpatrick 1978).

The genus *Aphelocoma* of North America is amenable to a similar analysis (Brown 1974), e.g. the Gray-breasted Jay (*A. ultramarina*), a cooperatively breeding species occurring in the southwestern U.S. and Mexico (Brown 1963,

1970), and western populations of the Scrub Jay (e.g. Brown 1974, Atwood 1980). The isolated Florida populations of the Scrub Jay exhibit cooperative breeding in about 50% of the groups (Woolfenden 1975, Woolfenden and Fitzpatrick 1978). Although Brown (1974) outlined several testable predictions for the jays, no comparative measures of habitat and demography have been published. Our comparative study of shrikes agrees with Brown's (1974) predictions of increased survival, diminished dispersal, and occupation of a stable habitat for the cooperatively breeding relative to the noncooperatively breeding species. The diminished dispersal of the Gray-backed Fiscal Shrikes can be readily seen in Fig. 1. All movements were by nonbreeders dispersing to attain breeding status. Most movements were only a few territories in distance. In contrast, no young Common Fiscal Shrikes were seen again on the study site following their presumed dispersal. The occupation of a stable habitat by the cooperatively breeding gray-backs is inferred from the data on insect abundance in the dry season and the relatively higher survivorship. Although our results are in accord with these predictions, it should be emphasized that our environmental measures were collected over a period of time much shorter than the lifetime of the birds. Thus, much of our discussion of the evolution of the social systems of these species must be viewed as tentative.

Habitat quality.—On Morendat Farm, Gray-backed Fiscal Shrikes occur only in relatively dense yellow-barked acacia woodland. High perennial shrub cover is associated with high tree density (Table 1). Areas of high cover have greater availability of insect prey throughout

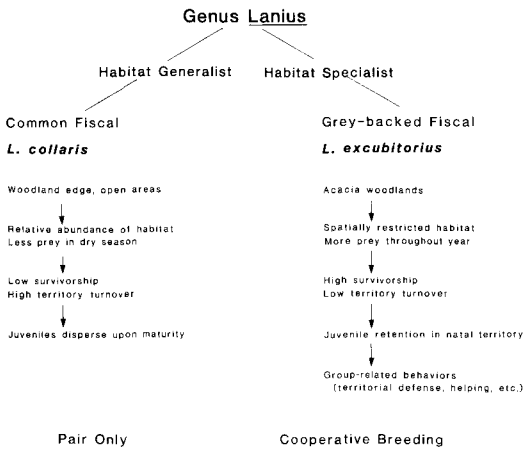


Fig. 4. Hypothetical scenario for the evolution of the social system differences observed in Common Fiscal and Gray-backed Fiscal shrikes.

the annual cycle, but significantly so only during the dry months, when insects are least common (Table 3, Fig. 4). On Morendat Farm, the habitat occupied by gray-backs contrasts with the more open areas used by common fiscals. The latter has significantly fewer available prey in the dry months of the year than do the areas in which gray-backs occur. The presumed higher-quality, but spatially restricted, habitat occupied by the gray-backs may be the critical factor maintaining cooperative breeding in this species. Strong seasonality in rainfall and associated insect availability also have been reported in studies of other cooperative breeders (e.g. Gaston 1978a, Vehrencamp 1978, Emlen 1982).

Because the vegetation characteristic of gray-back territories holds significantly more insects during the dry months, Gray-backed Fiscal Shrikes may benefit from their association with high-cover areas primarily during the dry months. However, since there was no increase in the disappearance rate for either shrike species during the dry months, there was apparently no direct connection between the reduction of the prey base and the disappearance of shrikes.

A relationship between high survivorship and cooperative breeding has been suggested frequently (e.g. Selander 1964; Brown 1974, 1978; Emlen 1978; Gaston 1978b). However, as survivorship in tropical birds is typically high compared to temperate species (e.g. Fry 1980),

a more meaningful comparison is made between similar cooperatively and noncooperatively breeding species in the same environment, as reported here.

Habitat saturation.—One of the most important factors influencing the demographic environment is the degree of habitat saturation, because this may in effect control the dispersal options available to members of the population (Brown 1974, Emlen 1982). If the annual production of young in such a habitat is, on the average, higher than the annual mortality rate of breeders, then the best option for nonbreeding individuals would be to stay in the natal territory and wait for openings (Ricklefs 1975; Brown 1978; Emlen 1978, 1982; Gaston 1978b). If parents allow the young to stay in the breeding territory (Gaston 1978b, Ligon 1981), nonbreeders may attain breeding status by inheriting the territory or part of it (e.g. Woolfenden and Fitzpatrick 1978). Alternatively, nonbreeders may gain allies from within the natal territory to compete as a group against other nonbreeders for territorial vacancies (Ligon and Ligon 1978, 1983; Koenig 1981b).

These complex social strategies appear to be the result of ecological restrictions placed on those populations occupying saturated environments. This saturation is the result of habitat specificity and of a very low ratio of marginal to optimal habitat (Koenig and Pitelka 1981). Habitat saturation is necessarily a relative term. It is not clear from previous works whether "saturated" habitat refers to all suitable habitat, all suitable breeding habitat, or only those areas considered to be of high quality. Most territories of Gray-backed Fiscal Shrikes were occupied continuously throughout the study. These continuously occupied territories tended to have high shrub cover. Those territories that were occupied intermittently contained less cover and were inferior to higher-cover territories in terms of survivorship and fecundity of the occupants (Zack and Ligon 1985).

In contrast, space for immature Common Fiscal Shrikes attempting to enter the breeding population appeared to be frequently available as a result of the high turnover of territorial adults. Upon independence, common fiscals left the parental territory and were not seen again on the study site. On several occasions, we observed immatures of unknown origin on the study area.

For juvenile gray-backs, the ecological and demographic environment poses a much more restricted dispersal option. Gray-backs may remain indefinitely in the natal territory. Several individuals fledged in June 1979 were still in their natal territory in January 1982. The few interflock movements of gray-backs were associated with specific openings for breeding positions or were related to the disruption of a flock due to mortality of one or more key members (Zack and Ligon 1985).

Evolution of Lanius social structure.—The evolutionary backgrounds leading to the habitat specificity of Gray-backed Fiscal Shrikes and the habitat generality of Common Fiscal Shrikes are not known. Part of the differences in habitat affinities may lie in the spatial distribution and quality of the preferred habitat. A basic behavioral difference between common fiscals and gray-backs is the dispersal of young upon maturity in the former and the retention of young in the natal territory in the latter. The cost-benefit relationships of dispersal may be fundamentally different in the two species. The expected benefits of dispersing upon maturity to common fiscal young are much higher (breeding status) than for young gray-backs in the more saturated and more limited habitat of the latter.

The Common Fiscal Shrike, which exhibits the "pair only" pattern typical of laniids, has a wide range of habitats available. Edge and open habitats are utilized throughout its range, and there appears to be little in the way of inherent habitat restriction. With this apparently wide availability of habitat and the high (relative to gray-backs) rate of disappearance, available habitat does not become saturated. Territorial "instability" is simply a function of the disappearance rate of its inhabitants. Adults readily move between territories upon loss of a mate (Fig. 1), and immatures disperse upon independence and are unlikely to interact with their parents again.

The important ecological and demographic differences between the two species are arranged into two hypothetical scenarios that lead to differences in their social structure (Fig. 4). The pathway of gray-backs is determined by their affinity for acacia woodland. Although restricted, this habitat appears to be one of relatively high quality compared to the habitat used by most common fiscals. One presumed effect of higher-quality habitat is higher individual

survivorship. The larger and more numerous gray-backs can dominate common fiscals and hence can exclude the latter from acacia woodland.

Given the low turnover of gray-backs, juveniles can be retained indefinitely in their parent's territory, as the option to disperse and search for a territorial vacancy is unlikely to succeed. A proximate concern of parents that allow juveniles to stay in the natal territory is the ability of the territory to provide resources for all members of the developing flock. Presumably, intraflock competition for food resources is less critical to the breeding pair and the supernumeraries than interflock competition for space. This presumption follows from the intensity of interflock territorial interactions and the absence of data suggesting that flock members are expelled unless there is a replacement of a breeder. As flocks develop in such a setting, selection should favor the evolution of group cohesiveness and group cooperation (e.g. defending the territory).

Once group-living has developed, individuals are subject to social as well as ecological limitations. Social limitations are those placed on individuals (e.g. breeding opportunity) by the local social environment rather than by ecological factors *per se*. Social limitations can be a function of an individual's dominance rank within a flock, which is often related to its age and sex. Social limitation also may be related to an individual's ability to form alliances to compete successfully with other groups for breeding positions (e.g. Koenig 1981b, Ligon 1983).

In such a setting, ecological and social limitations may covary, as ecological limitation can determine much of the form of social structure in a population (e.g. the amount of available habitat, available nesting structures). The social environment, however, can change independently of the ecological environment, as in the death of one or more key flock members. This dynamic interplay between ecological and demographic limitations presumably has affected the diversity of cooperative breeding systems observed (see also Ligon 1983).

Our results suggest that habitat restriction and habitat saturation are critical factors in the maintenance of cooperative breeding in *Lanius excubitorius*. Ecological restrictions appear to form the underlying basis of cooperative breeding in many bird species (Brown 1974;

Emlen 1982, 1984). The great diversity in avian cooperative breeding systems reflects adaptations both to ecological restrictions and to widely differing demographic environments.

ACKNOWLEDGMENTS

We thank T. L. George, P. B. Stacey, L. W. Oring, W. D. Koenig, C. H. Fry, J. A. Wiens, and an anonymous reviewer for constructive criticisms of earlier drafts of this paper. S. H. Ligon and D. Schmitt ably assisted us in the field. R. E. Leakey and G. R. Cunningham-van Someren and their staff at the National Museums of Kenya made our research possible. E. K. Ruchiami, of the Office of the President of Kenya, kindly granted research permits. Dr. H.-U. Reyer kindly loaned us color bands and snap-traps early in the study. The R. Terry family, the W. Hillyar family, and Lakamia Bulinda provided friendship and logistical support. This project was supported by NSF Grant DEB-7905866 to J. D. and S. H. Ligon. We thank all these individuals and institutions.

LITERATURE CITED

- ATWOOD, J. L. 1980. Social interactions in the Santa Cruz Island Scrub Jay. *Condor* 82: 440-448.
- BATCHELLER, C. L., & D. J. BELL. 1971. Experiments in estimating density from joint point- and nearest-neighbour distance samples. *Proc. New Zealand Ecol. Soc.* 17: 111-117.
- BONFERRONI, C. E. 1936. Publ. 1st Sup. Sci. Econ. Commun. Firenze 8: 1-62.
- BRITTON, P. L. (Ed.). 1980. Birds of East Africa, their habitat, status and distribution. Nairobi, East African Natural History Soc.
- BROWN, J. L. 1963. Social organization and behavior of the Mexican Jay. *Condor* 65: 126-153.
- . 1970. Cooperative breeding and altruistic behavior in the Mexican Jay, *Aphelocoma ultramarina*. *Anim. Behav.* 18: 366-378.
- . 1974. Alternate routes to sociality in jays with a theory for the evolution of altruism and communal breeding. *Amer. Zool.* 14: 63-80.
- . 1978. Avian communal breeding systems. *Ann. Rev. Ecol. Syst.* 9: 123-155.
- , & R. P. BALDA. 1977. The relationship of habitat quality to group size in Hall's Babbler (*Pomatostomus halli*). *Condor* 79: 312-320.
- , D. D. DOW, E. R. BROWN, & S. D. BROWN. 1983. Socio-ecology of the Grey-crowned Babbler: population structure, unit size and vegetation correlates. *Behav. Ecol. Sociobiol.* 13: 115-124.
- BROWNLIE, K. A. 1965. Statistical theory and methodology, 2nd ed. New York, John Wiley and Sons.
- COTTAM, G., & J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451-460.
- CRAIG, J. L. 1979. Habitat variation in the social organization of a common gallinule, the Pukeko, *Porphyrio porphyrio melanotis*. *Behav. Ecol. Sociobiol.* 5: 331-358.
- DOW, D. D. 1980a. Communally breeding Australian birds with an analysis of distributional and environmental factors. *Emu* 80: 121-140.
- . 1980b. Systems and strategies of communal breeding in Australian birds. *Proc. 17th Intern. Ornithol. Congr.*: 875-881.
- EMLEN, S. T. 1978. The evolution of cooperative breeding in birds. Pp. 245-281 in *Behavioural ecology* (J. R. Krebs and N. B. Davies, Eds.). Oxford, Blackwell Sci. Publ.
- . 1982. The evolution of helping. I. An ecological constraints model. *Amer. Natur.* 119: 29-39.
- . 1984. Cooperative breeding in birds and mammals. Pp. 305-339 in *Behavioural ecology*, 2nd ed. (J. R. Krebs and N. B. Davies, Eds.). Oxford, Blackwell Sci. Publ.
- FRY, C. H. 1972. The social organization of bee-eaters (Meropidae) and co-operative breeding in hot-climate birds. *Ibis* 114: 1-14.
- . 1980. Survival and longevity among tropical land birds. *Proc. 4th Pan-African Ornithol. Congr.* 4: 333-343.
- GASTON, A. J. 1978a. Demography of the Jungle Babbler, *Turdoides striatus*. *J. Anim. Ecol.* 47: 845-870.
- . 1978b. Factors affecting the evolution of group territorial behavior and co-operative breeding in birds. *Amer. Natur.* 112: 1091-1100.
- GRIMES, L. G. 1979. Sexual dimorphism in the Yellow-billed Shrike *Corvinella corvina* and in the other African shrikes (subfamily Laniinae). *Bull. Brit. Ornithol. Club* 99: 33-36.
- . 1980. Observations of group behaviour and breeding biology of the Yellow-billed Shrike *Corvinella corvina*. *Ibis* 122: 166-192.
- HALL, B. P., & R. E. MOREAU. 1970. An atlas of speciation in African passerine birds. London, Brit. Mus. (Nat. Hist.).
- HOPKINS, B., & J. G. SKELLAM. 1954. A new method for determining the type of distribution of plant individuals. *Ann. Bot. London N.S.* 18: 213-227.
- KOENIG, W. D. 1981a. Reproductive success, group size, and the evolution of cooperative breeding in the Acorn Woodpecker. *Amer. Natur.* 117: 421-443.
- . 1981b. Space competition in the Acorn Woodpecker: power struggles in a cooperative breeder. *Anim. Behav.* 29: 396-409.
- , & F. A. PITELKA. 1981. Ecological factors and kin selection in the evolution of cooperative breeding in birds. Pp. 261-280 in *Natural selection*

- tion and social behavior (D. Tinkle and R. Alexander, Eds.). New York, Chiron Press.
- LIGON, J. D. 1981. Demographic patterns and communal breeding in the Green Woodhoopoe, *Phoeniculus purpureus*. Pp. 231-243 in Natural selection and social behavior (D. Tinkle and R. Alexander, Eds.). New York, Chiron Press.
- . 1983. Cooperation and reciprocity in avian social systems. *Amer. Natur.* 121: 366-384.
- , & S. H. LIGON. 1978. The communal social system of the Green Woodhoopoe in Kenya. *Living Bird* 17: 159-197.
- , & ———. 1983. Reciprocity in the Green Woodhoopoe (*Phoeniculus purpureus*). *Anim. Behav.* 31: 480-489.
- MACKWORTH-PRAED, C. W., & C. H. B. GRANT. 1960. Birds of eastern and northeastern Africa, vol. 2. New York, Longman, Inc.
- MANTEL, N. 1966. Evaluation of survival data and two new rank order statistics arising in its consideration. *Cancer Chemotherapy Repts.* 50: 163-170.
- REYER, H.-U. 1980. Flexible helper structure as an ecological adaptation in the Pied Kingfisher (*Ceryle rudis rudis* L.). *Behav. Ecol. Sociobiol.* 6: 219-227.
- RICKLEFS, R. E. 1975. The evolution of co-operative breeding in birds. *Ibis* 117: 531-534.
- SELANDER, R. K. 1964. Speciation in wrens of the genus *Campylorhynchus*. *Univ. California Publ. Zool.* 74: 1-305.
- SOKAL, R. R., & F. J. ROHLF. 1981. *Biometry*, 2nd ed. San Francisco, W. H. Freeman.
- STACEY, P. B. 1979. Habitat saturation and communal breeding in the Acorn Woodpecker. *Anim. Behav.* 27: 1153-1166.
- TRAIL, P. W. 1980. Ecological correlates of social organization in a communally breeding bird, the Acorn Woodpecker *Melanerpes californicus*. *Behav. Ecol. Sociobiol.* 7: 83-92.
- VEHRENCAMP, S. L. 1978. The adaptive significance of communal nesting in Groove-billed Anis (*Crotophaga sulcirostris*). *Behav. Ecol. Sociobiol.* 4: 1-33.
- WOOLFENDEN, G. E. 1975. Florida Scrub Jay helpers at the nest. *Auk* 92: 1-15.
- , & J. W. FITZPATRICK. 1978. The inheritance of territory in group-breeding birds. *BioScience* 28: 104-108.
- ZACK, S., & J. D. LIGON. 1985. Cooperative breeding in *Lanius* shrikes. II. Maintenance of group-living in a nonsaturated habitat. *Auk* 102: 766-773.