COOPERATIVE BREEDING IN *LANIUS* SHRIKES. II. MAINTENANCE OF GROUP-LIVING IN A NONSATURATED HABITAT

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ABSTRACT.—We studied the cooperatively breeding Gray-backed Fiscal Shrike (*Lanius excubitorius*) near Naivasha, Kenya, to explore the roles of social and ecological factors in the maintenance of group-living. Gray-backs occurred in groups of 2–9 or more individuals, with only one breeding pair per group. Supernumeraries act as helpers to the breeders. Habitat of this species varied in the amount of perennial shrub cover. In the dry months high-cover areas had significantly more prey items than did low-cover areas. Group size was significantly positively correlated with shrub cover at 3 of the 4 times tested during the 3-yr study, and mean group size over an 18-month period also was correlated with shrub cover. Both individual survivorship and production of young increased with increasing cover. Group size also was correlated with survivorship and production of young. Partial correlation analysis could not separate the influences of group size and cover on survivorship. However, cover was significantly associated with the production of young when group size was held constant, and not vice versa. Pairs or small groups occasionally colonized low-cover areas; typically, however, the birds immigrating into these areas disappeared without having bred successfully. In contrast, high-cover areas held a constant number of breeding pairs and a varying number of supernumeraries. Supernumerary birds appeared to have a choice between dispersal and natal-territory fidelity, with the decision to disperse apparently weighed against the probability of eventual attainment of breeding status within or near the natal territory. *Received 5 October 1984, accepted 12 April 1985.*

PREVIOUSLY, Zack and Ligon (1985) compared the habitat and demography of two sympatric, congeneric shrikes to find potentially important differences that may have led to their distinctly different social systems. We argued that habitat was a focal difference between the group-living species, the Gray-backed Fiscal Shrike (*Lanius excubitorius*), and the Common Fiscal Shrike (*L. collaris*). Here, we explore further the role of "habitat saturation" in the maintenance of cooperative breeding in the gray-backs, focusing on the role of microhabitat. Microhabitat, specifically perennial shrub cover, is evaluated in terms of its effects on the demography and dispersal of gray-backs. Although much speculation has been directed at the ecological bases of cooperative breeding systems (e.g. Selander 1964; Brown 1974, 1978, 1983; Ricklefs 1975; Emlen 1978, 1982, 1984; Gaston 1978b; Koenig and Pitelka 1981; Emlen and Vehrencamp 1983), little effort has been made to investigate directly the role of habitat in the maintenance of cooperative social systems.

Selander (1964) first suggested a causal relationship between "saturation" of a habitat and the development of cooperative breeding. A saturated habitat is one in which breeding vacancies occur only rarely, generally as a result of low adult mortality rates. In the 20 yr following this widely accepted suggestion, however, few measurements have been made of the degree of habitat saturation for cooperatively breeding species (see Rowley 1965, Stacey 1979, Emlen and Vehrencamp 1983). Rather, most field and theoretical work on such species has dealt with the evolutionary rather than the ecological bases of cooperative breeding, focusing on the pros and cons of kin selection theory (Hamilton 1964). Habitat has been considered important, but in seemingly contradictory ways (Emlen 1982). Workers in the New World originally stressed the importance of relatively stable and predictable environments as an important correlate of the social system (Selander 1964, Brown 1974, Woolfenden 1975, Ricklefs 1975), whereas some workers in the Old World felt that cooperative breeding is as-

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sociated with unpredictable and harsh environments (e.g. Rowley 1965, Fry 1972). Koenig and Pitelka (1981) and Emlen (1982, 1984) focused on the limitations of some aspect of habitat (spatial limitations, resources or breeding openings), rather than habitat quality or stability of the habitat *per se.* This approach emphasizes individual strategies (e.g. disperse vs. stay at home) in relation to the limitations imposed by habitat (but see Dow 1980 for a dissenting view).

Koenig and Pitelka (1981) refined the basic habitat saturation model and postulated that a relative scarcity of marginal habitat is important in the establishment of cooperative breeding. Marginal habitats are those good enough to allow successful reproduction, but of lesser quality than other occupied habitats. Because of the absence of marginal habitats, surplus young are expected to remain in the natal territory and wait for vacancies in areas of high quality. Emlen and Vehrencamp (1983) considered two additional ecological constraints on the habitat saturation hypothesis: mate shortage (Rowley 1965) and erratic changes in carrying capacity [e.g. rainfall patterns and associated prey abundance in White-fronted Bee-eaters (*Merops bullockoides;* Emlen 1982)]. For three cooperatively breeding species [Superb Blue Wrens (*Malurus cyaneus*), White-fronted Bee-eaters, and Acorn Woodpeckers (*Melanerpes formicivorus*)], Emlen and Vehrencamp (1983) found correlations between the constraints upon independent breeding of supernumeraries and breeding group size, even though the proximate factors responsible for the constraints differed between species.

It is not altogether clear how much or how little marginal habitat (Koenig and Pitelka 1981) is necessary for cooperative breeding to develop, nor is it clear if these models can account for species that may not occupy saturated environments. Carrick (1963), Fry (1972), Stacey (1979), and Dow (1980) discuss other factors that may promote cooperative breeding.

Perhaps the most important points to consider in the maintenance of cooperatively breeding social systems are assessments of the behavioral options available to nonbreeding adults. Brown (1983) outlined the possible dispersal pathways available to nonbreeders in the socially restricted setting of group-living species. These options include delayed breeding within the natal territory, individual or social (group) dispersal to another established territory, floating (constant movement from territory to territory in an attempt to find a vacancy), and mate or nest sharing. However, as discussed below, some mature individuals may remain indefinitely in the natal territory even in apparently unsaturated habitats.

We now present ecological and demographic data gathered in Kenya on a cooperatively breeding laniid shrike, the Gray-backed Fiscal Shrike, and address the question of maintenance of group-living in an apparently nonsaturated habitat. In Part I, we reported that 59% of the territories occupied at the outset of the study were still occupied by gray-backs at the end of the study, 30 months later. Gray-backs are mostly insectivorous but occasionally prey on small vertebrates (frogs, lizards, rodents, and, rarely, birds). Only one breeding pair occurs per group, with all other members (up to 7 or more) of the flock aiding in feeding and defending the young and in performing group displays that serve in territory defense (Banage 1969). Gray-backs begin nesting with the onset of the rainy season. During our study (1979–1981) gray-backs nested between June and November.

METHODS

Methodology for the assessment of vegetation, annual prey abundance and distribution, and seasonality is described by Zack and Ligon (1985). Here we consider only Gray-backed Fiscal Shrikes and their interterritory differences in group size, individual survivorship, and production of young.

Gray-backs were captured and individually color-marked, sexed, weighed, and released. Groups were assessed for breeding status and flock size at least once per month. Fledged young were used as the measure of reproductive success. Composition of groups was best tallied during the elaborate territorial group displays. We periodically checked for marked birds in territories beyond the boundaries of the study site. Special attention was given to marked birds that moved from one territory to another.

Perennial shrub cover is the vegetational measure of interest here as it is associated with many important measures of demography (see below). All regressions between perennial shrub cover and various demographic measures were compared by nonparametric Spearman rank tests.

RESULTS

Prey abundance and vegetational cover.—A significant difference in the abundance of edible

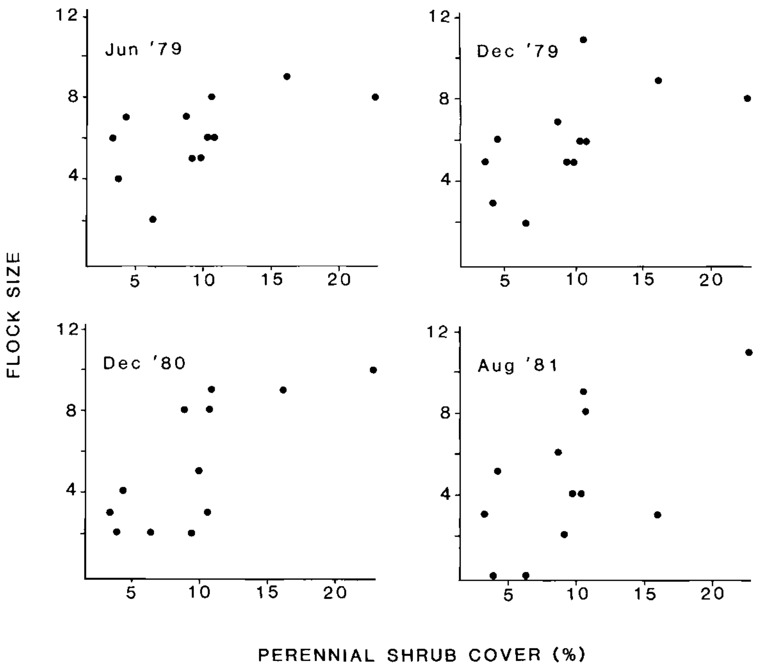

Fig. 1. The relationship between Gray-backed Fiscal Shrike group size and perennial shrub cover at four times during the study. The tests are Spearman rank tests.

insects (≥ 1 cm) between areas of high cover (tree and perennial shrubs) and low-cover areas existed in the 6 driest months of 1980 (Zack and Ligon 1985). This difference was important in that gray-back territories often occur in both kinds of habitat.

Group size and habitat.—Group size of gray-backs was significantly positively correlated with perennial shrub cover 3 of the 4 times tested during the study. It was significant in December 1979 ($r_s = 0.695$, $P < 0.05$), December 1980 ($r_s = 0.764$, $P < 0.05$), and August 1981 ($r_s = 0.587$, $P < 0.05$), and approached significance in June 1979 ($r_s = 0.573$, $0.05 < P < 0.10$; Fig. 1). We also averaged flock sizes by month between June 1979 and December 1980 (Table 1) and found that mean group size also was significantly correlated with shrub cover (Spearman rank test, $r_s = 0.713$, $P < 0.01$).

Shrub cover and territory occupancy.—Perennial shrub cover in the 12 territories varied from 3.3% to 22.7% (Table 1). Eight of these territories had greater than 6.5% cover and were occupied continuously by gray-backs. Two of the 4 territories with less than 6.5% cover were not occupied continuously. One territory of 6.3% cover was unoccupied for 2 months of study, and another with a cover of 3.45% was vacant for 7 of the 18 months. Several unmeasured territories also were unoccupied for various portions of the study. In all of these, it was subjectively apparent that perennial shrub cover was low. Conversely, several unmeasured territories with high cover always contained gray-backs. The duration of an individual adult shrike's occupancy of a territory also was a function of that territory's perennial shrub cover ($n = 71$ over 18 months, $r_s = 0.348$, $P < 0.05$; Fig. 2). In other words, an adult was more likely to persist in a territory of high perennial shrub cover than in a territory of lesser cover. As mortality usually cannot be distinguished from emigration, this is not solely a measure of survivorship, but in many ways the implications are the same for the demographic dynamics we consider (see Discussion). Mean group size also was correlated with duration of occupancy (here expressed in mean months present on the territory out of the 18 months measured; Spearman rank test, $r_s = 0.671$, $P < 0.05$). We found no significant correlation with duration of occupancy when perennial shrub cover and mean group size were held constant in separate tests of partial correlation ($P > 0.20$ for

TABLE 1. Group size parameters, breeding attempts, and total number of fledged young for 12 Gray-backed Fiscal Shrike territories on Morendat Farm, Kenya from June 1979 to January 1982. Territory name designations follow Zack and Ligon (1985).

Territory	Percent shrub cover	Mean group size (1979–1980)	Range	Aug. 1981 group size	Breeding attempts/ successes	No. of birds fledged
RM	9.24	3.89	2–5	2	2/0	0
NWW	10.52	8.42	8–9	9	6/3	7
RYU	10.40	4.84	3–6	4	2/0	0
BM	8.71	6.74	6–8	6	5/2	4
CW	3.88	2.21	0–4	2	4/0	0
KM	10.67	6.58	5–9	8	2/2	7
MN	4.27	5.10	3–7	2	6/2	4
NYM	9.76	5.00	5	4	5/0	0
PYM/NS	6.30	2.05	2–3	0	4/0	0
SK	16.00	9.11	7–10	3	3/2	6
MYN	22.67	8.32	7–10	11	4/2	6
HKK	3.30	4.37	3–6	3	7/0	0

both). Thus, it is not possible to evaluate the effects of shrub cover and group size independently when addressing duration of occupancy.

Breeding success.—The number of young fledged in each territory was related to its cover (Fig. 3). More young fledged in high- than in low-cover areas during the study (largely driven by the success of the SK and MYN territories; $r_s = 0.348$, $P < 0.05$). To compare the possible effects of flock size on production of young, it was necessary to make two separate analyses. We recorded no fledglings or juveniles in June or July 1981, but in early August several broods fledged; thus, we assumed that this represented the first successful breeding effort of 1981. The first analysis includes flocks that fledged young in August 1981 (Table 1), while the second considers only nesting attempts while one of us (SZ) was on the study site. Thus, the first analysis assumes no nesting failures before August, and the second analysis considers only those times when all flocks were monitored as to success and failure. Both analyses consider the data from June 1979 to December 1980. For each of the 12 flocks with known cover values, we recorded every nesting attempt during the entire study. With the inclusion of the early August fledglings, flock size was not quite significantly correlated with the number of young fledged ($n = 51$, $r_s = 0.247$, $P = 0.081$). When considering only those nesting attempts initiated during the study period, the relationship between flock size and the number of young produced was again nearly significant (Spearman rank test, $n = 45$, $r_s = 0.282$, $P = 0.061$). When analyzing the effects of shrub cover in terms of nesting success (number of times any young were fledged, as opposed to simply number of young fledged), both of the tests were significant (with early August 1981 included, $n = 49$, $r_s = 0.463$, $P < 0.001$; without early August 1981, $n = 43$, $r_s = 0.391$, $P < 0.01$).

Partial correlation tests also were conducted on both data sets in an attempt to explain more variance between flock size and perennial shrub cover. When considering all nesting attempts including the early August 1981 successes, flock size was not significant when holding shrub cover constant (df = 46, $r = -0.071$, $P = 0.633$), but shrub cover was still correlated with the number of young fledged when flock size was held constant (df = 46, $r = 0.344$, $P = 0.017$). When considering only nesting attempts observed during the study and with shrub cover held constant, flock size again was not significantly associated with the production of young (df = 40, $r = 0.011$, $P = 0.945$). Shrub cover in this case was nearly significant when flock size was held constant (df = 40, $r = 0.268$, $P = 0.086$). Thus, it appears that shrub cover is more important than flock size *per se* when considering the number of young produced in a given territory. All nest failures appeared to be the result of predation rather than the inability of a group to feed nestlings. For example, the rate at which nestlings were fed did not differ between flocks of different sizes or of different perennial shrub cover measures (Zack MS).

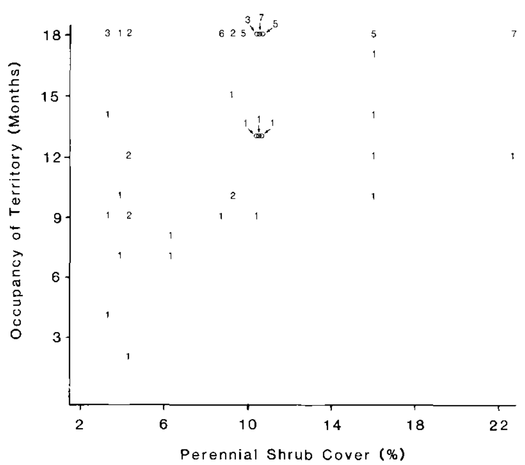

Fig. 2. The relationship between individual survivorship (persistence on a territory) as a function of a perennial shrub cover in 12 territories during the period June 1979 to December 1980. The numbers in the graph refer to individuals persisting for a given number of months.

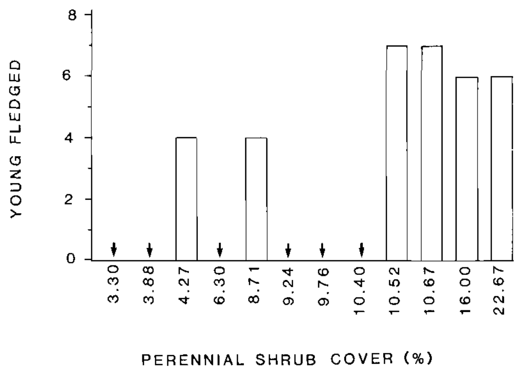

Fig. 3. The relationship between total number of young fledged and perennial shrub cover for 12 territories during the period June 1979 to December 1980. Arrows indicate territories that failed to produce young.

Many failed nests showed external evidence of disturbance. Of the diurnal nest predators, the Gabar Goshawk (*Melierax gabar*) appeared to be most important. Upon the appearance of this hawk, all shrikes quickly disappeared, so it is unlikely that shrike group size would deter the goshawk from preying on nestlings.

DISCUSSION

The role of habitat in fostering the demographic setting that leads to cooperative breeding in many species is widely recognized (e.g. Brown 1974, 1978; Koenig and Pitelka 1981; Emlen 1982; Emlen and Vehrencamp 1983). Our study indicates further that microhabitat differences within occupied habitat can be associated with the dynamics of group size, breeding success, and individual mortality or disappearance. For the ground-foraging Gray-backed Fiscal Shrikes, percent shrub cover is a good predictor of insect abundance in the dry season and may be the most important variable of microhabitat. It is not clear exactly how shrub cover relates to nesting success. As high shrub cover usually is related to high tree density (see Zack and Ligon 1985), it may be that nests in high-cover areas are more difficult for predators to detect. Similarly, we do not know how much of the variance in reproductive success is the result of nest failures vs. the failure to nest.

Several investigators have found a correlation between flock or group size and vegetation variables, and in many of these studies shrub cover is an important correlate (e.g. Brown and Balda 1977, Gaston 1978a, Vehrencamp 1978, Craig 1979, Brown et al. 1983). The ability to escape predators may be related to cover. Bird hawks are a conspicuous element of the avifauna on the study site. Along with the Gabar Goshawk, Lanner Falcons (*Falco biarmicus*) and especially Augur Buzzards (*Buteo rufofuscus*) were observed almost daily on the study site. All of these species, plus others less frequently seen, prey on birds and probably prey on shrikes. Finally, cover could be important in creating a greater number of perch sites for the gray-backs. Gray-backed fiscals, like other *Lanius* shrikes, forage from conspicuous perches, sallying out to capture a prey item and returning to a perch above the ground (Zack in prep.). It is likely that with increased cover in a given territory, gray-backs would have greater opportunity to use perch sites throughout the territory. Conversely, low-cover territories probably limit this foraging technique, in addition to having fewer insects during part of the year. These trends should be viewed with caution, however, because of the relatively short duration (1 yr) of environmental measures.

Our results suggest that the critical driving force in the population dynamics of these shrikes is territory-to-territory variation in habitat quality rather than presence or absence of occupiable habitat or scarcity of marginal habitat (cf. Koenig and Pitelka 1981). Although all the habitat did not hold breeding pairs or groups (some low-cover areas were always available), territories with high perennial shrub cover continuously contained shrikes throughout the study. High-cover territories apparently conferred higher survival for all flock members and higher fecundity for the breeding pair, and, as a result of these factors, they typically held larger groups. Breeding vacancies rarely occurred in these territories. Competition to fill such vacancies probably was high, for two reasons. First, above-average group sizes probably cause intense competition among supernumeraries within the territory. Second, supernumeraries in adjacent territories are likely to compete for any breeding position in high-cover territories. The "winner" not only gains breeding status in a high-quality area, but also acquires a helping group. The potential acquisition of helpers in a high-quality territory may increase the probability that a nonbreeder will remain home when dispersal to a breeding vacancy in a lesser-quality territory is possible.

An example of a single shrike's dispersal and the resulting consequences illustrates this point. Female O/R-L, hatched in the SK territory (16% cover), remained on the natal territory for at least 6 months (from July 1980 until we left Kenya in December 1980). In August 1981, this female was found two territories away in the CW territory (3.4% cover) with an unbanded adult male. (The CW territory had a previous history of high turnover of individuals. Four birds had resided in, and subsequently disappeared from, this territory during the 18-month period, June 1979 to December 1980. In addition, the territory was occupied for only 12 of the 18 months.) This pair nested in September 1981, but the nest failed before the eggs hatched. The male partner disappeared soon thereafter, and female O/R-L returned to her natal territory and became a helper to the mated pair there.

Possibly associated with this female's initial dispersal to the CW territory was considerable flux within her natal territory: (1) her mother disappeared in December 1980 and was replaced by a nonbreeding helper from an adjacent territory (KM); (2) her father died before she fledged, and his breeding position was taken by a male from within the flock; (3) three flock mates also moved to new areas in 1981 (to two previously unoccupied areas of the study site); and (4) three other flock mates disappeared during our absence. This dispersal by O/R-L from, and return to, her natal territory is not convincingly accounted for by considerations of kin, as she returned to help distant relatives at best. Rather, we feel that her initial dispersal was to attain breeding status. In the low-quality territory she occupied, however, our data suggest that O/R-L had a high probability of dying without successfully breeding. Following the failure of the nest and the loss of her mate, who possibly deserted this territory, female O/R-L returned to her high-quality natal territory, possibly gaining an increased probability of surviving. Why she was allowed to return to her natal territory and why she helped is not known. Gaston (1978a) suggested that helping may be a means of payment for residing in a territory, and Ligon and Ligon (1983) discussed helping behavior by birds not related to the nestlings in another cooperatively breeding species and described some benefits to such helpers.

We have no other observations of a bird that left and later returned to its natal territory. Most other dispersals resulted in the acquisition of breeding status (known from at least two other banded females). Possible exceptions to this were the flockmates of O/R-L mentioned above. One female, G/Y-L, a member of the flock since birth in 1979, was found in a newly formed flock (6 members) adjacent to her natal territory, but of lower cover (5.7%). Whether she held breeding status was not determined. Two other females (R/B-L and R/W-R) defended a previously unoccupied territory with low cover at the edge of the study site. No males joined them during our observations. In three cases male helpers ascended to breeding status within their flocks.

In a study of Yellow-billed Shrikes (*Corvinella corvina*), another cooperatively breeding laniid shrike, Grimes (1980) noted one instance in which a male emigrated and later returned to his original group. Grimes also reported one instance of 3 females and another of 2 males emigrating together. Grimes made no measures of vegetational cover, so whether or not ecological and demographic patterns of Yellow-billed and Gray-backed Fiscal shrikes are similar is not known.

The fact that gray-backs maintain large

groups in high-cover habitat when some openings are available in occupiable habitat provides a subtle but important difference to the model presented by Koenig and Pitelka (1981). Koenig and Pitelka postulated that areas of marginal quality are very rare among cooperative breeders. Apparently, marginal habitat does exist for nonbreeding gray-backs, but occupying it potentially entails high costs, including a reduced probability of survival and a low probability of producing young. These costs must be weighed against the probability of eventual attainment of breeding status within the natal territory. If the natal territory is one of high shrub cover, then it is likely that (1) many flock members potentially are waiting for the same opening, (2) all will have relatively high survivorship, and (3) birds in adjacent flocks also would compete for any breeding opening in the territory. These conditions together create a highly competitive and restrictive setting for nonbreeders attempting to gain breeding status in a territory of high cover.

It appears that the costs of dispersing to a low-cover territory generally exceed the benefits, since breeding vacancies in areas of low cover frequently are not taken by supernumeraries occupying higher-cover areas. This last point supports Koenig and Pitelka's (1981) model of the shift in the cost/benefit assessments of dispersal in a habitat with highly restricted openings. Occasionally, however, dispersal to areas of low cover pays off. In 1981, four new territories were established in areas of low cover. Three of these social units originally consisted of simple pairs, and 2 pairs successfully fledged young. Part of the reason for this success may lie in the fact that 1981 was a wetter than normal year; prey resource levels may have been above average. It is tempting to speculate that the "costs" of immigration into low-cover areas may decrease when rainfall is abundant just prior to the next breeding period.

This "dispersal dilemma," where supernumerary birds are confronted with both ecological and social constraints, is not restricted to cooperatively breeding birds. Examples include Rufous-collared Sparrows (*Zonotrichia capensis;* Smith 1978), in which 50% of the population are floaters that move constantly through breeding territories in anticipation of a vacancy; yearling male Blue Grouse (*Dendragapus obscurus;* Jamieson and Zwickel 1983), which appear to choose between high- and low-quality areas that offer tradeoffs between survival and potential fecundity; and Black-capped Chickadees (*Parus atricapillus;* Smith 1984), in which young birds choose between becoming a member of a low-ranked pair and becoming a flock switcher chancing replacement of a high-ranked breeder. In all of these systems the interplay of social and ecological constraints molds the possibilities for young birds attempting to attain reproductive status and success.

Assessment of the roles of ecological and social constraints in the maintenance of complex social systems requires recognition and measurement of both the costs and benefits of alternative strategies by nonbreeding individuals. Further work is warranted in all avian social systems on the interplay of such constraints.

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