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Sociality of grassland birds during winter

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Summary. Sociality of granivorous passerine birds occupying open grassland habitats of the south-central United States was evaluated during winter in relation to habitat cover, seed density and bird density. Habitat height and habitat density, measures of exposure to potential predation, are associated with the major distinction of social pattern between the two granivore subgroups; sparrows, which tend to be more solitary, occupy the taller and denser grasslands, while horned larks (*Eremophila alpestris*) and longspurs (*Calcarius* spp.), which tend to be gregarious, occupy sparse and open habitats.

Group size increased with increasing seed density for sparrows and for longspurs, but not for both horned larks and longspurs or for all granivores taken together. For sparrows, group size increased less in relation to seed density than for longspurs. For granivores in total and for sparrows, bird density increased with increasing seed density. However, this association did not exist for longspurs.

The interaction of ecological variables may synergistically influence granivore group sizes. Habitat cover, in combination with other variables, appears to polarize the two granivore subtypes towards primarily gregarious or solitary strategies. Potential mechanisms leading to gregarious or solitary behavior are discussed in relation to hypotheses of predator avoidance and risk-sensitivity.

Introduction

Social relations of birds are the result of responses by individuals to various features of the environment, including other individuals of the species (Brown and Orians 1970). Spacing patterns and gregariousness can aid in predator avoidance and afford protection (Murton et al. 1963; Pulliam 1973; Bertram 1978; Kenward 1978; Lazarus 1979). Flocking may enhance the efficiency of food exploitation (Crook 1965; Cody 1971; Krebs 1973). Pulliam (1973) and Powell (1974) suggested that advantages of enhanced food exploitation and predator detection may interact in foraging flocks. Environmental features, such as nesting or roosting sites, or the amount of cover, can also influence sociality and use of space (Davis 1973; Post 1974; Snapp 1976; Pulliam and Mills 1977). However, Goss-Custard (1970) and Caraco (1979a) pointed out that group membership may have disadvantages, such as increasing susceptibility to disease or parasites, foraging interference, and increasing costs associated with intraspecific aggression. Thus, sociality of birds reflects a balance of selective forces acting both to draw organisms together and spread them apart (Wilson 1975).

Studies concentrating on the within group interactions in foraging flocks are prevalent (e.g., Goss-Custard 1970; Krebs 1973; Davies 1976). These studies focus on the proximate factors affecting foraging group size (usually for one species); i.e., the internal and external factors which motivate the behavior of individuals. A few studies evaluate social groups within populations (Caraco 1979a, b; Barnard 1980), but these studies dwell primarily on the dynamics of foraging flock size. At the community level, however, little attention has been given to evaluating factors which settle species into particular social strategies – viewing the ultimate impacts of various environmental factors on spatial and social organization.

A number of general factors affecting spatial relations of birds emerge from earlier studies (Brown and Orians 1970; Morse 1980). Among these are food abundance, exposure to predation and bird density. In this paper, I evaluate sociality

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Table 1. Social and ecological characteristics of horned larks and longspurs (flyers) and sparrows. See text for definitions of variables. Habitat density is given in vegetation contacts (see text); bird density as birds/100 ha.; seed density as cu. mm. of seeds/sq. m. (see text). Standard deviations (SD) are given in parentheses; *n* is the sample size

Species	Treatment[a] type	Region[b]	Social		Ecological			
			Group size	% of individuals solitary	Habitat density	Habitat height (cm)	Bird density	Seed density
Flyers								
Horned Lark (*Eremophila alpestris*)	CU	Okla	$n=317$ 6.1 (5.2)	3	$n=109$ 0.8 (1.1)	$n=109$ 0.8 (1.7)	$n=4$ 102.3 (80.8)	$n=1$ 512.9 (–)
	LG	WTex	$n=204$ 8.5 (6.2)	3	$n=24$ 30.8 (11.2)	$n=24$ 21.6 (3.8)	$n=2$ 132.0 (186.7)	$n=2$ 1.3 (0.3)
	HG	WTex	$n=136$ 8.1 (7.3)	2	$n=42$ 10.0 (9.1)	$n=42$ 7.5 (8.3)	$n=1$ 102.0 (–)	$n=2$ 4.6 (0.7)
	PD	WTex	$n=557$ 15.0 (29.8)	1	$n=1091$ 4.5 (7.6)	$n=1091$ 3.5 (5.7)	$n=1$ 734.0 (–)	$n=2$ 120.2 (116.0)
Lapland Longspur (*Calcarius lapponicus*)	CU	Okla	$n=291$ 147.9 (434.7)	0	$n=5729$ 0.6 (1.1)	$n=5729$ 1.0 (1.3)	$n=5$ 118.8 (47.9)	$n=1$ 512.9 (–)
Smith's Longspur (*Calcarius pictus*)	MG	Okla	$n=178$ 11.6 (11.7)	2	$n=12$ 33.5 (20.5)	$n=12$ 39.0 (5.7)	$n=14$ 139.7 (212.4)	$n=2$ 38.9 (10.3)
	HG	Okla	$n=224$ 12.8 (13.3)	1	$n=1030$ 37.7 (25.5)	$n=1030$ 21.2 (8.8)	$n=5$ 297.8 (244.1)	$n=2$ 28.8 (2.3)
Chestnut-collared Longspur (*Calcarius ornatus*)	MG	Okla	$n=107$ 8.6 (4.1)	1	$n=130$ 29.3 (13.2)	$n=130$ 38.7 (14.3)	$n=5$ 26.8 (44.6)	$n=2$ 38.9 (10.3)
	HG	Okla	$n=215$ 5.4 (4.6)	5	$n=110$ 25.5 (16.2)	$n=110$ 17.3 (9.1)	$n=2$ 40.5 (7.8)	$n=2$ 28.8 (2.3)
	HG	WTex	$n=33$ 2.6 (3.1)	15	$n=5$ 15.5 (2.1)	$n=5$ 14.5 (7.8)	$n=2$ 28.5 (9.2)	$n=1$ 4.1 (–)
	HG[c]	WTex	$n=48$ 5.1 (6.3)	4	$n=30$ 17.6 (9.4)	$n=30$ 14.5 (7.2)	$n=1$ 122.0 (–)	$n=1$ 5.1 (–)

of granivorous passerine birds occupying open grasslands in temperate regions during winter in relation to these factors, and propose mechanisms for the interaction of ecological variables in creating patterns of sociality. Grasslands provide structurally simple habitats which often occur in large homogeneous tracts. During winter, granivory is the primary and almost exclusive foraging mode of grassland birds, further simplifying the system. Climatic severity and reduced winter daylength necessitate effective exploitation of food resources. While most grassland passerines are territorial during the breeding season, the constraints of reproductive activity are not present during winter.

Materials and methods

Grasslands of varied grazing pressure or cultivation practices in several regions of Oklahoma and Texas were used. Data were collected at 14 sites from the winters of 1975–1976 through 1978–1979. The sampling period began 15 November and ended 15 February for each season. The sites included seven in central Oklahoma (Cleveland, Grady, and McClain counties), three in western Texas (Muleshoe National Wildlife Refuge, Bailey County), and four on the Rob and Bessie Welder Wildlife Refuge (San Patricio County) in southern coastal Texas. The sizes of sites ranged from about 30 ha on the smallest sites in southern Texas to greater than 100 ha. Sites were characterized by their uniformity and large size, thus minimizing edge effect with other habitats. Two of the southern Texas sites contained about 5% shrub cover. Otherwise tree or shrub cover was absent

Table 1 (continued)

Species	Treatment[a] type	Region[b]	Social		Ecological			
			Group size	% of individuals solitary	Habitat density	Habitat height (cm)	Bird density	Seed density
Sparrows								
Savannah Sparrow (*Passerculus sandwichensis*)	LG	Okla	$n=362$ 1.2 (0.4)	74	$n=93$ 47.5 (29.4)	$n=93$ 45.1 (26.4)	$n=1$ 46.0 (–)	$n=2$ 28.7 (12.8)
	MG	Okla	$n=58$ 1.1 (0.3)	92	$n=12$ 32.3 (15.4)	$n=12$ 40.6 (24.3)	$n=7$ 12.3 (7.6)	$n=2$ 12.9 (6.9)
	HG	Okla	$n=278$ 1.2 (0.7)	70	$n=131$ 38.6 (22.4)	$n=131$ 23.8 (9.5)	$n=3$ 38.3 (16.6)	$n=2$ 32.3 (19.0)
	LG	STex	$n=197$ 4.2 (2.5)	8	$n=48$ 52.0 (17.4)	$n=48$ 60.1 (19.9)	$n=1$ 1,228.0 (–)	–
	MG	STex	$n=155$ 2.8 (2.1)	16	$n=48$ 52.0 (17.4)	$n=48$ 60.1 (19.9)	$n=4$ 786.2 (129.9)	$n=2$ 25,704 (10,181)
	HG	STex	$n=52$ 1.3 (0.7)	57	$n=7$ 28.4 (17.7)	$n=7$ 23.3 (14.3)	$n=5$ 84.2 (36.6)	$n=3$ 2.0 (1.9)
Grasshopper Sparrow (*Ammodramus savannarum*)	MG	STex	$n=79$ 1.0 (0.0)	100	$n=37$ 68.8 (18.8)	$n=37$ 63.6 (16.3)	$n=3$ 71.0 (24.0)	$n=2$ 12.6 (4.6)
Baird's Sparrow (*Ammodramus bairdii*)	LG	WTex	$n=14$ 1.0 (0.0)	100	$n=5$ 30.0 (9.1)	$n=5$ 21.6 (4.9)	$n=2$ 25.5 (4.2)	$n=2$ 1.3 (0.3)
LeConte's Sparrow (*Ammodramus leconteii*)	LG	Okla	$n=147$ 1.0 (0.0)	100	$n=64$ 66.4 (22.7)	$n=65$ 63.2 (21.6)	$n=2$ 32.5 (14.9)	$n=2$ 2.7 (1.2)
	LG	STex	$n=112$ 1.0 (0.0)	100	–	–	$n=1$ 1,888.0 (–)	–
	MG	STex	$n=336$ 1.0 (0.0)	100	$n=32$ 64.0 (15.6)	$n=32$ 63.2 (16.2)	$n=5$ 141.8 (100.7)	$n=2$ 12.6 (4.6)
Vesper Sparrow (*Pooecetes gramineus*)	MG	STex	$n=98$ 3.0 (1.8)	10	$n=13$ 37.7 (23.3)	$n=13$ 24.6 (25.1)	$n=3$ 122.7 (88.6)	$n=2$ 832.1 (78.7)

[a] CU = cultivated; HG = heavily grazed; LG = lightly grazed; MG = moderately grazed; PD = prairie dog (*Cynomys* sp.) town

[b] Okla = Oklahoma; STex = southern Texas; WTex = western Texas

[c] Means from January 1979 when the site was recovering from being heavily grazed

or comprised less than 0.5% cover, consisting of isolated individual plants less than 3 m in height.

Sites were classified on the basis of grazing pressure or cultivation practices. A site was considered a lightly grazed grassland (LG) when the dominant palatable grasses had uniformly grown to heights approaching their maximum potential heights. For LGs in Oklahoma and southern Texas, maximum vegetation heights ranged from 1 to 2 m. In western Texas, maximum grass heights of LGs were about 0.5 m. When dominant palatable grasses occurred in distinct clumps, the site was designated a moderately grazed grassland (MG). Vegetation heights of MGs were up to 1 m in Oklahoma, and 1.5 m in southern Texas. When the dominant palatable grasses were absent or present only in widely scattered clumps and/or grazed to near ground level, the site was considered a heavily grazed grassland (HG). Vegetation heights in HGs were less than 0.5 m on all sites. The cultivated sites were planted with winter wheat (*Triticum aestivum*); these sites had been harvested of a sorghum (*Sorghum bicolor*) crop in fall. More detailed site descriptions are given in Grzybowski (1980, 1982).

Habitat height (HHT) and habitat density (HDEN) provide a measure of potential exposure to predation. They represent the primary habitat gradients present in the grasslands studied (Grzybowski 1980). Vegetation height for a 15 meter-square block was the average of four point samples about 1 m apart, and measured to the nearest centimeter. HDEN is:

$$\mathrm{HDEN} = \sum_{m=1}^{4} \sum_{k=1}^{25} x_{km} \tag{1}$$

where x_{km} is the number of vegetation contacts made with the tip of a wire passed through the vegetation for 30 cm at the kth height (at 10-cm intervals from 5 to 245 cm), and mth point (of four).

Habitat use was determined in the 1975–1976 and 1976–1977 seasons for each species on each specific grazing treatment (Grzybowski 1980). Strips 1,000 × 60 m were established on each site, and these divided into 15 meter-square blocks. Frequency occurrence of bird species in the blocks was recorded during 16–20 visits to each treatment type. The habitat values for a species on a given site were determined by averaging the HHTs and HDENs of blocks in which the species was observed. Each block used by a bird species was weighted by the frequency occurrence of that species in the block.

Seed samples were obtained in January of 1978 and 1979 on 9 of the 14 sites. Areas occupied by a species, as characterized through the space-use data (Grzybowski 1980) and general impressions of occupied habitat, were sampled. Seeds samples within these habitats were obtained by brushing debris from the surface of 15 to 30 randomly selected points (15 m or more apart), each 10 × 10 cm, into a container. Seeds from these samples were sorted into size classes and counted. A volume estimate for seed density (SDEN) on each site was calculated (to cubic millimeters of seeds per square meter). This provided a relative index of seed availability (Pulliam 1975) among the habitats in mid-winter.

Estimates of bird densities (BDEN) were obtained for sites from November through February by the Emlen (1971) strip method. January population estimates (December 1976 on southern Texas sites) for each species were used in the analysis; these estimates represent a mid-winter period when species composition appeared most stable (unpubl. data). One extremely high estimate of LeConte's sparrow is treated separately; this density estimate was more than seven times higher than the next highest estimate (Grzybowski 1982). Late November estimates for horned larks were used to avoid the beginning of the reproductive period (Bent 1942).

The basic measure of sociality used for each species was group size (GSIZ). The GSIZ was the number of individuals of a species that responded similarly to disturbance by the observer, or were observed foraging or resting together as a unit distinct from other individuals. Only observations made on the first pass through a site on each visit were used. The GSIZ of individuals known to be moving ahead of the observer (and of birds which these individuals joined) were recorded only once in any site visit. From data on GSIZs, the percent of solitary individuals (SOL) of a species was calculated. This variable estimates the proportion of individuals acting independently of any other individuals of their own or other species. Data on GSIZ were collected from 0.5 h after sunrise to 1.5 h before sunset to avoid effects of behavior associated with roosting.

Measures of sociality and bird density were averaged over winter seasons and within grazing treatments to provide a value for each species. Seed densities obtained on sites during the 1977–1978 and 1978–1979 seasons were averaged among similar site types and used to characterize seed availability in habitats.

Two behavioral subsets of granivores were analyzed: 1) flyers, which included those species regularly observed moving between grasslands, and 2) sparrows, which included more sedentary species never observed flying high over grasslands. Of the flyers, longspurs were dealt with separately. These distinctions are shown in Table 1.

Pearson product-moment correlation coefficients were calculated using Statistical Analysis Procedures (SAS; SAS Institute, Inc. 1979). Partial and multiple correlations were computed through a program procedure BMDP-PROG 6R developed by Dixon and Brown (1977).

Results

Mean values of social and ecological variables for each species by grazing treatment and region are given in Table 1. GSIZ (group size) and SOL (% of solitary individuals) were significantly correlated with each other ($P<0.001$) for all granivores ($r=-0.81$). The ecological measures of HDEN (habitat density) and HHT (habitat height) were also significantly correlated ($r=0.94$; $P<0.001$). SDEN (seed density) was significantly correlated with BDEN (bird density) ($P<0.05$) for granivores ($r=0.53$) and sparrows ($r=0.75$), but not for flyers ($r=0.23$; $P>0.05$).

Simple correlation coefficients of ecological variables with GSIZ and SOL are given in Table 2. For granivores, GSIZ and SOL were significantly correlated with HDEN and HHT ($P<0.01$). As HDEN (or HHT) increases, GSIZ decreases and SOL increases. SOL also decreases with increases in BDEN ($P<0.05$). Densities of LeConte's sparrows on one site in southern Texas (December

Table 2. Correlations of social and ecological characteristics for grassland birds. See Table 1 and text for definitions of variables. n = number of mean values of variables for characteristics of species on specific treatment types and regions (from Table 1). * indicates $P<0.05$; ** indicates $P<0.01$; *** indicates $P<0.001$

Variables[a]	Granivores ($n=22$)	Sparrows ($n=11$)	Flyers ($n=11$)	Longspurs ($n=7$)
log GSIZ-HDEN	−0.65***	−0.07	−0.29	−0.45
log GSIZ-HHT	−0.57**	−0.08	−0.24	−0.36
log GSIZ-log BDEN	0.39	0.82**	0.39	0.44
log GSIZ-log SDEN	0.34[b]	0.88***[c]	0.58	0.94**
SOL-HDEN	0.63**	0.20	−0.02	−0.19
SOL-HHT	0.56**	0.09	−0.03	−0.20
SOL-log BDEN	−0.48*	−0.76**	−0.53	−0.54
SOL-log SDEN	−0.37[b]	−0.80**[c]	−0.44	−0.70

[a] BDEN = bird density; GSIZ = group size; HDEN = habitat density; HHT = habitat height; SDEN = seed density; SOL = percent of solitary individuals

[b] $n=21$

[c] $n=10$

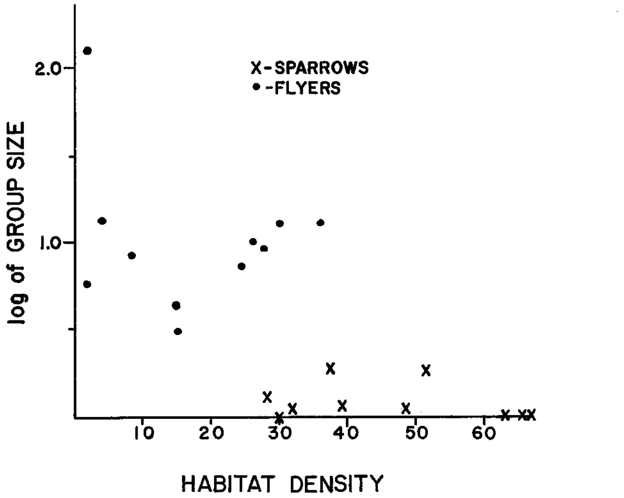

Fig. 1. Relation of group size to habitat density for sparrows and flyers (horned larks and longspurs)

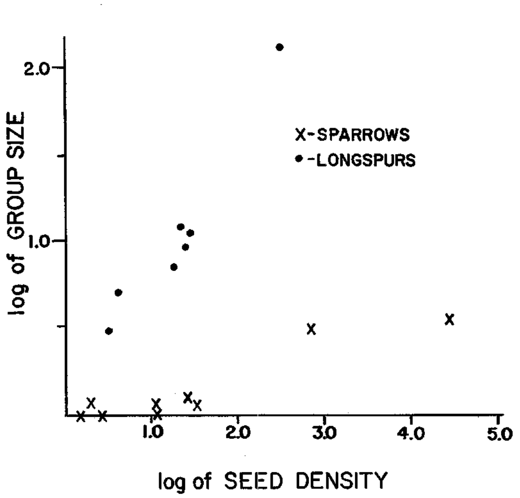

Fig. 2. Relation of group size to seed density for sparrows and longspurs

1976) were very high. With this observation included, the correlation of SOL with BDEN for granivores is non-significant ($r = -0.35$; $P > 0.05$).

However, when the two granivore subgroups (i.e., sparrows and flyers) were analyzed separately, the correlations of GSIZ or SOL with HDEN and HHT became non-significant ($P > 0.05$; Table 2). Among the sparrows, mean GSIZ never exceeded 4.2 individuals, and was 3.0 or less in all other cases (Table 1). The highest mean GSIZ values for sparrows occurred for savannah sparrows at very high densities (1,228 birds/100 ha). Mean HDEN was never below 28 vegetation contacts per grid sample for sparrow habitats. However, longspurs and horned larks usually occurred in groups of greater than five individuals, and almost always occurred at vegetation densities of less than 30 vegetation contacts. Inspection of data points for GSIZ with HDEN (Fig. 1) reveals this separation of granivore types; flyers which tend to be gregarious and occupy sparse open habitats, and sparrows which tend to be more solitary and occupy the taller and denser grasslands.

GSIZ was correlated with SDEN for sparrows ($r = 0.88$; $P < 0.001$) but not for flyers ($r = 0.58$; $P > 0.05$), or for both taken together (Table 2). The correlation of GSIZ with SDEN for longspurs, however, was significant ($r = 0.94$; $P < 0.01$). The divergence of pattern for these subgroups is shown in Fig. 2; for sparrows, GSIZ increased less in relation to SDEN than for longspurs.

For sparrows, SOL was inversely correlated with SDEN ($r = -0.80$; $P < 0.01$), and BDEN ($r = -0.76$; $P < 0.01$). Three of the five sparrow species (LeConte's sparrow, grasshopper sparrow, and Baird's sparrow) were always solitary and occurred in relatively seed-poor habitats (Table 1).

Since interactions between variables may occur, partial correlations were employed to statistically hold one or more variables constant while testing the relations between others. For sparrows, BDEN was significantly correlated ($P < 0.05$) with SDEN ($r = 0.75$), and both were significantly correlated with GSIZ and SOL (Table 2). When controlling for SDEN, the partial correlation of GSIZ with BDEN dropped precipitously ($r = 0.10$; $P > 0.05$); controlling for BDEN, however, only slightly reduced the association of GSIZ with SDEN ($r = 0.76$; $P < 0.05$). Thus, in sparrows, the correlation of GSIZ with BDEN appears to be the result of an intervening variable – SDEN.

For flyers, patterns were erratic and no ecological factors were significantly correlated with GSIZ and SOL. However, when horned larks (which initiate breeding activities during winter) were removed, the correlation of GSIZ with SDEN was highly significant ($r = 0.94$; $P < 0.01$) for the remaining longspur observations. The relation of SDEN with BDEN for longspurs was low ($r = 0.26$; $P > 0.05$), unlike the relations for sparrows. When controlling for SDEN, the relation of GSIZ with BDEN improved, in contrast to sparrows, but remained non-significant ($r = 0.60$; $P < 0.20$).

SDEN and GSIZ were highly associated within granivore subgroups, yet SDEN must act through intermediary mechanisms to influence GSIZ. Gregariousness may aid individuals in avoiding possible predation. SDEN was significantly correlated

($P<0.05$) with BDEN for granivores. Higher BDEN may attract more predators. Indices of potential exposure to predation are HHT and HDEN. Partial correlations of GSIZ with these habitat variables improved substantially over simple correlations when controlling for SDEN and BDEN; to -0.72 ($P<0.05$) and -0.66 ($P>0.05$) with HHT and HDEN, respectively, for sparrows, and to -0.64 ($P>0.05$) and -0.89 ($P<0.05$) with HHT and HDEN, respectively, for longspurs. This analysis implicates that, within granivore subgroups, the effects of SDEN and BDEN masked the relation of GSIZ with habitat variables.

Discussion

The results indicate that ecological factors interact in influencing patterns of sociality, but that exposure of habitat appears to play an important role for grassland birds. Habitat density and height are measures of exposure to potential predation. Applying the concept that birds in flocks gain foraging time by decreasing time needed in vigilance over that of solitary individuals (Pulliam 1973; Caraco 1979a, b), a conceptual time-budget model can be constructed to help evaluate the interactions of exposure, seed density and bird density. The model, graphically depicted in Fig. 3A for a set of potential predator-risk conditions, assesses the tendency to be gregarious or solitary based upon risk of potential predation. For a set of predator-risk conditions, birds are expected to remain solitary as long as vigilance time needed by a solitary bird to maintain a minimally acceptable risk of predation, *Ps*, is less than the free time (when solitary), *Fs*, available to birds after foraging or other non-vigilance activities; i.e., $Fs-Ps>0$. When $Fs-Ps<0$, birds should form into small groups to reduce vigilance time by *Gi*; but they also incur the costs of grouping (*Ci*; Fig. 3A). A switching threshold (*S*) occurs when $Fs-Ps=0$.

Sociality can change with changes in exposure to predation, but also with predation pressure (equivalent to raising *Ps*) and with free time available to individuals when solitary (lowering *Fs*). Increasing bird density may increase predation pressure for a solitary individual by attracting more predators, and also increase interaction time with other individuals, thus reducing free time. Caraco (1980), studying the dynamics of foraging flock size in yellow-eyed juncos (*Junco phaeonotos*), indicated that the arrival rate of individuals into groups increases under conditions of cold weather when time becomes limiting. Increasing seed density should increase free time. However, the interaction of ecological factors may produce results differing from those expected by changes in any single factor alone.

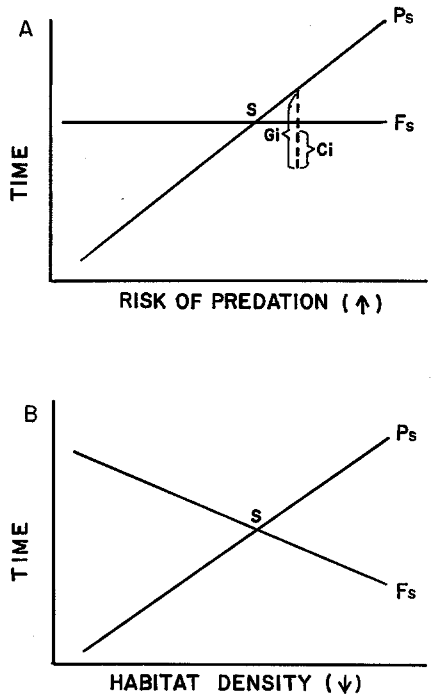

Fig. 3A, B. Conceptual model of the relation of free-time after foraging or other non-vigilance activities when solitary (*Fs*) and vigilance time when solitary (*Ps*) for a set of increasing (↑) predator-risk conditions. A switching threshold (*S*) occurs where $Fs-Ps=0$. **A** General case showing gain in vigilance time per individual in a group (*Gi*) minus cost of grouping (*Ci*) when $Fs-Ps<0$. **B** Case for grassland birds where predator-risk condition is decreasing (↓) habitat density. See text

Using habitat height and density as measures of risk to predation, the model can be applied to grassland birds during winter (Fig. 3B). In this case, time needed for foraging is expected to increase with increasing energetic costs of greater exposure to climatic factors associated with less cover; thus *Fs* declines as exposure increases. A number of possible mechanisms placing birds on one side or the other of the switching threshold are shown in Fig. 4. Simply increasing exposure to predators may enhance gregariousness (Pathway I). Free time and vigilance time can easily be stressed in exposed habitats; gregariousness is prevalent (Pathway II). In all but one case for longspurs, the % of solitary individuals was 5% or less. The exception occurred for chestnut-collared longspurs in a habitat with low seed density and low bird density. When bird density which can attract predators is low, vigilance time could be lowered, allowing these longspurs to utilize seed-poor environments (Fig. 4; Pathway III).

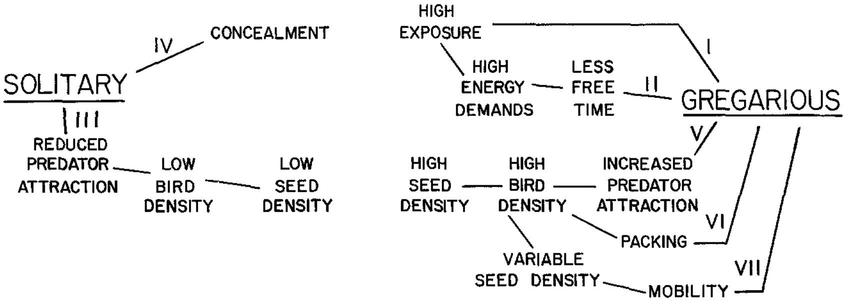

Fig. 4. Potential mechanisms (I–VII) encouraging solitary or gregarious behavior for grassland birds

Three of the five grassland sparrow species studied were always solitary and occurred in the densest and tallest habitats available where concealment was high (Fig. 4; Pathway IV). Grouping for these species may raise their risk of predation, since groups may be more easily detected and the cover which can conceal them can also act as a screen for approaching predators. Seed production on lightly grazed tall-grass areas in Oklahoma is less than on more disturbed and exposed sites (Risser 1981; Grzybowski 1982). The potential costs of foraging interference, aggression and communication between individuals on these sites may further favor solitary behavior.

Savannah sparrows were primarily solitary except when at high densities. Just as seed density was correlated with bird density, so might the density of predators increase with bird density. In addition, interactions with greater numbers of individuals can reduce free time. Thus, *Ps* could exceed *Fs* (Fig. 4; Pathway V). However, grouping at high bird densities in this case may be the result of packing the environment and clumping otherwise solitary individuals on a variably distributed food source (Pathway VI); but, see Grzybowski (MS) and discussion below.

Vesper sparrows formed small groups on a relatively seed-rich site with good cover (Table 1), but the distribution of values for the habitats occupied was bimodal (Grzybowski 1980). The sparrows occurred on and along mowed fire breaks and often foraged in exposed sections near the taller and denser grasses (Fig. 4; Pathway I).

Barnard (1980) demonstrated that vigilance time increases with increasing distance from cover for house sparrows (*Passer domesticus*). In grasslands, the habitat can be considerably more homogeneous than that for juncos (Caraco 1980) or house sparrows, and the options of finding cover in shorter grasslands more limited. Birds in these habitats may not have better cover to move to when not foraging. Risk of predation may be more constant, and gregariousness for species in very open habitats may be necessary.

Bird density was significantly correlated with seed density for sparrows but not for longspurs. This may indicate that sparrows track their environments more closely than longspurs. However, longspurs were often seen flying over sites. Because longspurs forage over large areas, and could easily have utilized sites nearby, calculations of birds per area, or birds per seed density would not be valid. Longspurs may very closely track seed density.

Thompson et al. (1974) constructed a simulation model of flocking on patchily distributed food resources. They concluded that flocking decreased the risk of doing badly on a patchily distributed food source, and that, for small birds, this risk may be more important than maximizing foraging success. Caraco et al. (1980) and Caraco (1981) developed and tested a risk-sensitivity model demonstrating that risk-aversion in a variable food environment promotes flocking. Raitt and Pimm (1976) presented the argument that flocking is a response to the concentration of food resources by desert rains. Flocks search for the seed bonanzas.

Dispersion of seeds was not considered in my study. However, lapland longspurs occurred in flocks of 1,000 or more at times; other longspur species were often observed in flocks of 50 to 500 during migratory periods (unpublished data), a time of uncertainty in finding food. These longspur flocks were larger than might be expected if flocking simply aided in predator detection. Habitats occupied by longspurs contained moderate to high seed densities compared to other habitats, attracting larger numbers of birds in flocks which can quickly deplete food resources at a patch or on a site. Patchiness at these levels in more open habitats may promote risk-aversion flocking induced by large numbers of longspurs responding to and creating variability in seed density (Fig. 4; Pathway VII). The low association of bird density with seed density for longspurs could be expected in this situation. However, these longspurs also occurred in more open habitats, including plowed fields (unpublished data for chestnut-collared longspurs), where exposure to both weather and potential predation was greater. Large flocks in open terrain may also be useful in flocking maneuvers which evade avian predators or increase the predator's risk of collision with non-target birds (Treisman 1975).

Increasing seed density should increase free time and decrease the propensity of individuals to flock. Caraco (1979b) artificially increased seed density; juncos responded by increasing aggression thus decreasing group size. At the community level, however, birds occupying habitats with higher seed densities formed larger groups. Seed density was associated with bird density. Myers et al. (1979) found that Sanderlings (*Calidris alba*) could not maintain territories over areas with high prey density because attraction of intruders to these areas made them too costly to defend. Grassland birds may be faced with a similar situation when high seed densities attract high bird densities.

The theory for flocking behavior often considers groups as discrete units. However, the practical aspects of determining group size impose constraints on its definition which may be artificial to the perceptions of the animals involved. Space-use patterns for savannah sparrows implicate grouping at a different level than that defined in this study. Savannah sparrows, occurring on sites at moderate to high bird densities, exhibited spacing patterns which clustered them in only part of their habitat-use areas at any time with interindividual distances of 12–14 m (Grzybowski MS). Individuals would join each other when first disturbed by the observer, but, by the definition used here, were solitary upon first encounter. Among the grassland birds studied, this behavior appears as a compromise between the potential costs and benefits of gregariousness. The group size reported here at high bird densities may merely reflect the packing of individuals with reduced individual distances.

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