Habitat distributions of wintering sparrows along an elevational gradient: tests of the food, predation and microhabitat structure hypotheses

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Summary

1. Sage sparrows [*Amphispiza belli* (Cassin)], black-throated sparrows [*A. bilineata* (Cassin)] and dark-eyed juncos [*Junco hyemalis* (L.)] winter in different habitats along an elevational gradient in the Sonoran Desert of southern California, USA. Such species replacements along environmental gradients are commonly attributed to interspecific competition. We tested the alternative hypotheses that food, predation and microhabitat structure might shape species distributions.

2. Species abundances were unrelated to food availability. Species were missing from habitats in which food standing crop was no less abundant than in the habitats they occupied. A second measure of food availability, predicted food intake rate, also failed to explain the distributions. The profitabilities of seed species ranked similarly among the three species of sparrows suggesting that the sparrows should prefer the same foods and should have similar habitat distributions if habitat distributions were shaped by food.

3. All three species escape predators by fleeing to woody cover and all prefer to feed near cover. Hence, if predation risk determined sparrow distributions, all species should be most abundant in the habitat with the most escape cover; this was not observed.

4. Foraging microhabitats used by individual species were more widely distributed than the species themselves, suggesting that species' distributions are not limited by microhabitat structure. Also, although species occupy different habitats, they overlap extensively in the types of microhabitats that they occupy

5. Although predictions of the competition hypothesis were not tested, species distributions and the results above are consistent with the hypothesis that interspecific competition is responsible for habitat partitioning by the species. Direct tests of this hypothesis are warranted.

Key-words: food, habitat distribution, habitat structure, predation, sparrow.

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Introduction

Closely-related bird species often have abutting distributions along environmental gradients. They probably use similar food and it is possible that their distributions are restricted by competition (Lack 1944; Svärdson 1949; Terborgh 1971; MacArthur 1972). This statement is supported by evidence that species often have broader distributions in areas where presumed competitors are absent (e.g. Cody 1974; Terborgh & Weske 1975; Noon 1981). Indeed, such evidence indicates that two-thirds of 91 bird species along an elevational gradient in the Andes appear to be limited by competition (Terborgh 1971, 1985).

Abutting species distributions may be explained in other ways. There may be a factor in the environment whereby a species well suited to one range of values of the factor is necessarily poorly suited to others (see Levins 1968). If so, there is only a limited potential for current competition to influence distributions. Possible factors include food, predation and abiotic factors. For example, ground finches (*Geospiza* spp.) differing in size appear to be best suited to eat different sizes of seeds (Grant 1986, p. 134), and food, not

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competition, appears to be the major factor determining their distributions along an elevational gradient (Schluter 1982). Despite the strong possibility that food determines species distributions, the food hypothesis has been tested directly in only a few studies (e.g. Abbott, Abbott & Grant 1977; Schluter 1982; Schluter & Grant 1982; Price 1991).

Hypotheses regarding species distributions can be tested using predictions stemming from them (e.g. Terborgh 1971; Schluter 1982). Species' distributions can be compared to distributions predicted from environmental factors (Schluter 1982). The predictions themselves are based on knowledge of species biology and how the factors being considered affect species abundances. By testing several factors in this way, strong inferences (Platt 1964) can be made about the factors that limit species distributions. Although such tests are weaker than direct experimentation, they nevertheless provide important information that is essential for planning experiments.

In the present study, we ask what factors shape the habitat distributions of sparrows wintering along an elevational gradient in the Sonoran Desert of California. Sage sparrows [*Amphispiza belli* (Cassin)], black-throated sparrows [*A. bilineata* (Cassin)] and dark-eyed juncos [*Junco hyemalis* (L.)] winter in different vegetation types (Weathers 1983). We tested several hypotheses that might determine the distributions, including food, predation and microhabitat structure.

Factors and predictions

In testing which factors might limit distributions, we ask whether factors vary along the elevational gradient in ways that are consistent with the hypothesis that they limit distributions. We acknowledge that single factors rarely, if ever, limit species abundances to the exclusion of all others and that factors may act simultaneously or interact. For example, food and predation are linked through the time budget if foraging places a bird at greater risk of predation than do other activities (McNamara & Houston 1987). Our tests eliminate factors that vary along the elevational gradient in ways that are inconsistent with the hypothesis that they limit species distributions. For example, if two factors vary along a gradient, one becoming more favourable for a species and the other less favourable, only the factor becoming less favourable can restrict the species' distribution. We emphasize factors that might limit distributions in such a way that they predict species occur one per habitat. Here, we outline the specific factors and predictions stemming from them. The strength of our predictions is that they afford opportunities to falsify hypotheses. Corroborative evidence would support hypotheses only weakly because observational evidence is always subject to alternate interpretations.

FOOD

Food alone could shape the habitat distributions of species if there is little overlap in the type of food different species can eat and species' foods occur in different habitats (Schluter 1982). This hypothesis predicts that species do indeed consume different foods, that sharp discontinuities in the types of food available occur between habitats and that species abundances along the elevational gradient should be proportional to food availability.

PREDATION

Foraging birds avoid areas of high predation risk (e.g. Lima 1990; Watts 1990, 1991) suggesting that predation could influence species' distributions. Predation could shape habitat distributions if species differ in the habitat in which they are safest from predators. If each species is very safe in a unique habitat and very much at risk in others, then there is little opportunity for cohabitation. Species differences in the safety of habitats may be rooted in methods used to escape from predators. Pulliam & Mills (1977) observed three different techniques of escape used by granivorous birds. One set of species foraged close to woody vegetation and fled to it when disturbed. Another set foraged solitarily farther from shrubby cover and crouched when disturbed, apparently relying on crypsis. The third set foraged in flocks at long distances from cover and flew away when threatened. Species that flush to cover suffer high predation rates away from cover (Watts 1990), and those that tend to feed far from cover and fly off are reluctant to forage close to cover (Lima 1990).

The predation hypothesis predicts that each species should be most abundant in the habitat where it is safest and less abundant in habitats of greater risk. All three of the sparrow species that we studied flush to cover to escape predation, suggesting that all should be safest and most abundant in the habitat with the most cover. Clearly, this prediction is discordant with the observation that species live in different habitats. We tested the predation hypothesis by asking whether all three species foraged closer to cover than expected by chance. The predation hypothesis would be supported if some species prefer to forage close to cover whereas other species avoid cover. It would be falsified if all species forage closer to cover than expected by chance because that result suggests that all species are safest from predators while foraging close to cover.

Although predation is unlikely to explain habitat partitioning because species respond similarly to avian predators, predation can affect our expectations of the relation between bird distributions, abundance and food supply (Schluter & Repasky 1991). For example, the risk of predation could be strong enough to reverse the predicted distributions of species from

those expected from food alone. Therefore, we test a joint predation–food hypothesis by comparing species' distributions and abundances to food abundance discounted by the risk of predation.

MICROHABITAT STRUCTURE

Habitats can be defined in terms of their structural features and those features are obvious factors that could determine species distributions. This hypothesis is not exclusive of others, because the effects of habitat should be mediated by food, abiotic factors, competition and/or predation. Yet, structural features of habitat could influence the foraging abilities of birds or predation rates in ways that are not captured by our measures of food availability and safety from predators. For example, soil texture, leaf litter and herbaceous plants may affect a species' ability to search the ground for food and they are not reflected in measures of food standing crop.

If microhabitat structure determines distributions, it should be possible to identify components of habitat structure that are relevant to foraging and ask two questions:

1. Are the microhabitats used by species themselves restricted in distribution?
2. Do species forage in different microhabitats?

If foraging activity is restricted to particular microhabitats and those microhabitats are absent outside of species' preferred habitats, some feature of microhabitat structure would then be implicated. Ready availability of suitable foraging microhabitats outside of preferred habitats suggests that microhabitat structure *per se* is unlikely to account for distributions. Also, species should forage in different microhabitats; otherwise, they should be distributed similarly among habitats.

Methods

STUDY SITE AND SPECIES

The elevational gradient was located in the Sonoran Desert of southern California, USA. It ran from sea level in the Coachella Valley in the vicinity of Palm Desert up the side of Santa Rosa Mountain to 2660 m. Vegetation varied from very open desert scrub habitat on the valley floor to coniferous forest at the upper elevations (see Zabriskie 1979; Weathers 1983). Between these two habitats lie rocky creosote scrub, a yucca–galleta grass community, pinyon pine–juniper woodland and chaparral.

We studied three common species of sparrows wintering in different habitats along the gradient: sage sparrow, black-throated sparrow and the dark-eyed junco. Their distributions have been described by Weathers (1983 and unpublished data). Briefly, sage sparrows are largely winter migrants, common on

the valley floor and rare in chaparral. Black-throated sparrows are permanent residents occupying the rocky creosote scrub up through pinyon–juniper woodland. During winter, they are uncommon in pinyon–juniper. The dark-eyed junco population is a mixture of permanent residents that migrate along the elevation gradient and winter migrants from other areas. Juncos breed in coniferous forest and winter in chaparral and pinyon–juniper. The exact boundaries of species' distributions and the extent to which species distributions overlap are imprecisely known because Weathers' study sites and our own were located far apart and in the interiors of habitats. Nevertheless, species distributions are stable: (i) they are consistent with observations made at a variety of sites while exploring for study plots; and (ii) fluctuations of species' distributions over seven winters [Weathers (1983)—3 years, this study, 2 years, subsequent winter; (R. R. Repasky & D. Schluter, R. R. Repaky (unpublished manuscript)—2 years] were insufficient to place species deep inside of habitats that they do not usually occupy.

We worked in three habitat types along the gradient: valley floor, alluvial fan and pinyon–juniper. The valley floor is bare sand or hard-packed sediments vegetated with widely spaced shrubs (e.g. *Larrea tridentata*, *Atriplex* spp.) and patches of herbs (e.g. *Schismus barbatus*, *Cryptantha* spp., and *Erodium cicutarium*). Alluvial fans are located in the lower ends of valleys opening into the Coachella Valley. They are rocky and sparsely vegetated with shrubs (e.g. *Larrea tridentata*, *Beloperone californica*, *Hymenoclea salsola*, *Ambrosia dumosa*, *Bebbia juncea*), trees (*Prosopis glandulosa*, *Cercidium floridum*) and patches of herbs (e.g. *Bromus rubens*, *Schismus barbatus*, *Cryptantha* spp., *Plantago insularis*). Pinyon–juniper woodland exists on a plateau at about 1200 m elevation. The trees (*Pinus monophyla*) and large shrubs (up to 2 m) (*Juniperus californicus*, *Quercus* spp., *Rhus ovata*) are widely spaced. Common herbs include *Bromus* spp., *Bouteloua aristidoides*, *Erioneuron pulchellum* and *Stipa speciosa*.

We conducted the study during autumn and winter months, after migrant sparrows had arrived on the study site and before spring seed crops began to set. Sage sparrows and dark-eyed juncos arrive in the study area by early November. Rains occurring from November through January may result in germination and the production of a spring seed crop in some years. Seed may ripen as early as late February (R. Repasky, personal observation) or March (Burk 1982). A second rainy period during the summer months July through September may result in a winter crop of seeds that sets during December and January (Burk 1982), although crops of this type were not observed during either of the two winters of the present study or during the following two winters. The frequency of years in which summer rains produce winter seed crops is unknown.

DATA COLLECTION

Study plots were located along a transect of representative vegetation types maintained by Deep Canyon Desert Research Center and the Coachella Valley Preserve. One study plot was located in each habitat type during the first winter (1985–86). A second plot, not less than 1 mile from the first, was added in each habitat type during the second winter (1986–87). Because study plots were few and limited to a single mountain range, inferences drawn about species distributions are restricted to the elevational gradient that we studied. Study plots were located away from habitat boundaries to provide a clear test of the hypothesis that species can live in habitats that they do not normally occupy. For example, the availability of food in a habitat should be better characterized by plots located in its interior than by plots near its edge. Each plot was a 2-ha rectangle measuring 40 m × 500 m marked with flagging tape. Plots were visited twice during each winter. Visits were made during December, January and February of the first winter. They were advanced to November, December and January of the second winter because a crop of seeds began to ripen late in February of the first winter.

During a visit to a study plot, we censused bird abundance, sampled seed abundance, determined food habits and measured the structural characteristics of the habitat, as well as the sites where birds foraged.

Bird census

We carried out one to four censuses per visit to each plot during the first field season ($\bar{x} = 2.5$). Estimates of population density were quite variable (standard error approximately equal to the mean), and so in the second field season we conducted four censuses per visit to each habitat. A census consisted of a count of the number of birds feeding on the study plot during a 2 h period beginning at sunrise. An observer walked the length of the study plot by advancing 20 m at 5-min intervals. Only actively foraging birds were counted. We recorded every individual and noted whether it was 0–10 m or 10–20 m from the line of travel.

Bird density was estimated from census data using Emlen's (1971) transect method. That method adjusts for differences in the probability of observing birds at different distances from the census path. The number of birds in each 10-m band of the census plot was enumerated, and the count in the 10–20-m bands was calculated as a fraction of that in the inner and then adjusted upward by the reciprocal of this fraction. We made this correction because differences in habitat structure along the gradient might affect the probability of observing birds at longer distances from the observer.

Seed standing crop

Seed abundance was estimated during each plot visit by counting seeds present on 30 quadrats, each 0·125

m². Quadrats were randomly chosen from a grid coordinate system describing the study plot. Seeds on plants and on the ground were counted *in situ* because regulations at Deep Canyon at the time prevented us from removing soil. Seeds on the ground were counted by systematically picking through the surface soil with a pair of forceps to a maximum depth of 1 cm, depending on soil hardness. Although this method undoubtedly underestimated the abundances of small seeds, none of the seeds eaten by birds was too small to be seen in the soil. Whatever bias was introduced should be consistent among habitats, and comparisons made among habitats are meaningful. We identified seeds by comparing them with a seed collection maintained by Deep Canyon Desert Research Center as well as our own reference collection.

Standing crop was estimated by multiplying seed abundance by mean seed mass. Masses were determined for seeds in our reference collection by weighing them after they had been oven dried for 24 h.

Microhabitat structure

Habitat characteristics were measured at each sampling quadrat. Distance to cover was measured from the quadrat centre to the nearest shrub at least 50 cm tall. Shrubs of that size were readily used as cover by startled birds. Other characteristics were estimated visually within a 1-m square plot surrounding each 0·125-m² quadrat, including the percentage of the ground surface covered by rock, barren soil and either leaf litter or sprouting herbs. We also estimated by eye the percentage volume of the air column occupied by vegetation at the heights: 0–10, 10–20, 20–40 and 40–60 cm, 0·6–1·0, 1·0–2·0, 2·0–5·0 and more than 5·0 m.

Feeding habits

Observations of foraging birds were made whenever possible. We recorded the location of each bird (ground, plant) and measured the habitat characteristics at the spot as described above.

To determine diets, we captured birds using mist nets and we administered to them the emetic apomorphine hydrochloride (Sigma Chemical Co.; see Schluter 1988; Esteban 1989). Vomit samples were preserved in alcohol to arrest digestion. In the laboratory, seeds were identified by comparing them with the reference collection and counted.

Seed handling times

Time taken to handle seeds was recorded from captive birds during the winter of 1988–89. Observations were made after the birds had been held in captivity between 1 and 2 months. Birds were housed and observed singly. We videotaped them as they ate seeds from a dish, after they had been fasted for an hour.

Handling time began when a bird picked up a seed and ended when movement of the lower mandible ceased. We measured it by counting the number of frames elapsed and multiplying by the rate at which frames were recorded. Handling time for each individual bird on a seed type was taken to be the median handling time for that seed type because a few seeds appeared to be handled for inordinately long periods. Handling time on a seed type by a species was taken to be the mean of the medians of individual birds. Unfortunately, we were unable to measure handling times of all three bird species on all seeds types eaten by any species. However, our data include the principal foods eaten by each species with one exception. *Perityle emoryi*, a common food of black-throated sparrows during the first field season, simply could not be found when we collected seeds.

HYPOTHESIS TESTING

Here we outline the methods used to predict distributions of species from the alternative hypotheses.

Species' distributions and abundances should be proportional to the availability of their foods if distributions are determined by food abundance. We quantified food availability in two ways: standing crop and estimated food intake rate. Standing crop is a simple measure that is readily estimated, although it does not necessarily represent the amount of food available to foraging birds. Intake rate is a more realistic measure, but it is more difficult to estimate. We estimated it from its component variables: value of food items, handling time, and encounter rate.

Food itself had to be defined for each species. Not all species were found in all habitats so we had to decide what a species would eat if it occurred in habitats outside of its distribution. This problem was tempered by a few vomit samples collected from birds foraging outside of their typical habitats during a transplant experiment (R. R. Repasky & D. Schluter, unpublished manuscript). We defined food for a species as any seed type falling within the range of seed morphologies observed in vomit samples. Seed morphology was described in terms of the first two principal components of the variables seed mass, seed length (longest dimension), seed depth and seed width (shortest dimension). The two principal components represented overall seed size and seed shape. Shape described the lengths of seeds of a given mass. To define food for a species, we plotted all seed types against the principal component axes and constructed a convex polygon around those seed types consumed by a species. All seed types within the polygon were classified as food.

We used rarefaction methods (see Schluter 1988) to determine whether the number of birds captured was adequate to characterise species' diets for the purpose of estimating food availability. Food standing crop was plotted against sample size and inspected for the presence of an asymptote. Each point represented mean food standing crop calculated from 200 random subsamples of a given size. All three species exhibited a clear asymptote in estimated food standing crop (Fig. 1), indicating that the number of birds captured was sufficient to characterize species' diets.

Our estimate of food intake rate was based on Holling's (1959) disc equation,

$$R = \frac{\Sigma \lambda_i e_i}{1 + \Sigma \lambda_i h_i}$$

where R is intake rate in milligrammes per second, λ_i is encounter rate of seed type i in seeds per s, e_i is mass of seed type i in milligrammes, and h_i is handling time for seed type i in s. Seed masses (e_i) were measured from the seed reference collection. Handling times (h_i) were measured in the laboratory. Only encounter rates (λ_i) were unknown. We assumed them to be linearly related to seed abundance: $\lambda_i = k d_i$ where d_i is the density of seeds of type i in seeds per square meter and k is a constant representing search rate in square metres per second. Intake rate was calculated as a function of k. With this formulation, we compared food availability between habitats by calculating intake rates using a range of reasonable values of k.

The food hypothesis also predicts that species should overlap little if at all in the types of foods that they eat. Overlap in diet composition was calculated in two ways. First, we calculated proportional similarity (see Hurlbert 1978) in seed species composition of diets. This measure provides a limited measure of the extent to which fundamental niches overlap because not all seed species were found in all habitats. Overlap in fundamental niches can be described by comparing the profitabilities of foods among species (Pulliam 1985). Profitability is seed mass divided by the amount
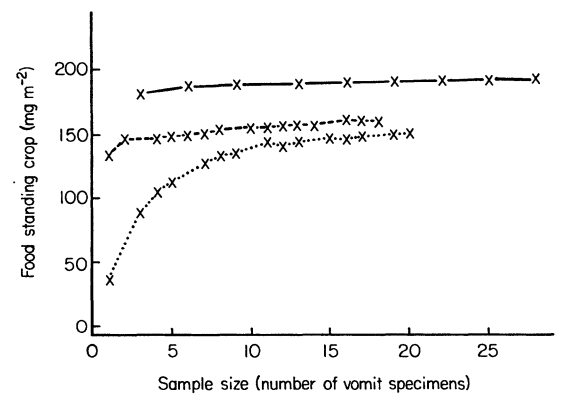

Fig. 1. Estimated food standing crop as a function of the number of vomit specimens obtained from sage sparrows (——), black-throated sparrows (- - - -) and dark-eyed juncos (– – –). Any seed species falling within the range of seed morphology within a sample of vomit specimens was used in the calculation of food standing crop. Curves were generated by randomly resampling different sample sizes from the collected sample (see Schluter 1988).

of time required to handle the seed. Intake rates are maximized by consuming the most profitable foods and ignoring others. If foods rank similarly in profitability among species, species share preferences for the same foods and food is unlikely to be responsible for lack of overlap in species distributions. We calculated profitabilities of seeds from seed masses taken from our reference collection and from handling times measured in the laboratory. We calculated rank correlations of food profitabilities among species and plotted profitabilities to determine whether differences in profitability were on high or low ranking seed types.

The three species escape from predators by flying to cover, suggesting that each is safest in the habitat with the most cover. If this interpretation is correct, the three species should forage closer to cover than expected by chance. We compared distances of feeding birds to cover to distances of randomly located quadrats to cover using one-tailed comparisons. Wilcoxon two-sample tests were used because the data were not normally distributed. To determine whether birds forage closer to cover than expected from food availability, we visually compared the distribution of foraging birds with the distribution of food in each habitat. The relative frequency distribution of foraging birds was described as the probability density curve of foraging distance from cover (Becker, Chambers & Wilks 1988). The distribution of food was estimated in three steps. First, we estimated the probability density curve of the distance from randomly located quadrats to cover. Secondly, we estimated mean food standing crop as a function of distance from cover using non-parametric regression (lowess; Becker *et al.* 1988), at the default parameters. Finally, the distribution of food relative to cover was calculated by multiplying the probability density curve by food standing crop. The resulting distribution was standardized by rescaling it to have an area underneath it of 1. This frequency distribution of available food in relation to cover was compared to the frequency distribution of foraging birds.

We calculated food abundance discounted by the risk of predation to test the hypothesis that food and predation together account for species distributions. For each habitat, we calculated an index ranging from 0 to 1 that described the relative value of food as a function of distance from cover. The index is based on the assumption that predation risk at a given distance from cover is linearly related to the degree of disparity between the relative frequency of birds foraging at that distance and the relative frequency of food there. Food value was calculated as $(O-E)/E$ where O is the observed probability density of birds foraging at a distance and E is the probability density of food at that distance. The largest positive deviation was assumed to occur at the safest distance from cover and was ascribed the value 1. The most extreme negative deviation was assumed to occur at the most dangerous distance from cover and was ascribed relative value 0.

Other deviations were linearly scaled between the 0 and 1. Adjusted food standing crop was calculated by multiplying food standing crop at each sampling quadrat by the index describing relative food value at that distance from cover.

To determine whether species' distributions correspond with the availability of their foraging microhabitats, we characterized habitats in terms of the first three principal components of habitat variables. Data from all habitats were combined, and the percentage cover variables were arcsin-square root transformed prior to analysis. The axes represented, first, variation in total cover; secondly, a gradient from shrub cover to tree cover; and, thirdly, variation in rockiness (Table 1). Habitats were described as polygons plotted against pairs of axes from the principal components analysis. Each polygon contained the central 75% of the sampling quadrats in the bivariate distribution. Briefly, the density of points within the neighbourhood of each data point was calculated using a scatter plot sharpening algorithm (Chambers *et al.* 1983) and we eliminated points below the 25th percentile of neighbourhood density. Finally, we projected the habitat structure at birds' foraging sites on to the principal component axes characterizing habitats.

Overlap in the use of microhabitats was calculated using a discriminant function in which individual birds were classified to species based on the structural characteristics of foraging sites. This method was used because measures such as proportional similarity are difficult when niches are defined in terms of several variables. The success of a discriminant function at classification increases as the amount of overlap in species' foraging habits declines. Error rates are zero in the absence of overlap between species, and they

Table 1. Principal components analysis of habitat structure. All variables other than distance to cover are arcsin square root transformed measures of percentage cover

	Principal component axis		
	1	2	3
Eigenvalue	5·90	2·01	1·03
Proportion of variance explained	0·49	0·17	0·08
Eigenvectors:			
Distance to cover	−0·26	0·04	−0·22
Bare ground	−0·30	−0·16	−0·15
Rock	0·01	−0·13	0·94
Cover (cm above ground):			
0–10	0·31	−0·33	−0·12
10–20	0·33	−0·34	−0·09
20–40	0·36	−0·26	−0·07
40–60	0·38	−0·15	−0·03
60–100	0·37	0·00	−0·02
100–150	0·31	0·29	0·04
150–200	0·28	0·37	−0·05
200–500	0·21	0·49	−0·01
>500	0·09	0·42	0·05

tend toward $(s-1)/s$ when overlap is complete, where s is the number of species. The error rate when overlap is perfect is actually biased below $(s-1)/s$ because of sampling error. An index of overlap can be calculated by dividing the observed rate of error by that expected by chance if overlap is perfect. Error rates were simply the proportion of observations misclassified by the function. Expected rates of error if species overlap perfectly were calculated by randomization. Foraging sites were randomly assigned to species, and a discriminant analysis was carried out. This process was repeated 1000 times, and the mean error rate among randomized analyses was used as the expected error rate. Calculations were performed using Procedure DISCRIM (SAS Institute 1988). Habitat variables were arcsin-square-root transformed prior to the analysis.

Results

DISTRIBUTIONS OF BIRDS

The sparrows were distributed nearly one species per habitat with little overlap between species in habitat use (Table 2). Sage sparrows were observed only on the valley floor and juncos occurred only in pinyon–juniper. Black-throated sparrows were most common on the alluvial fan and uncommon in pinyon–juniper. These results are consistent with earlier census data from the study area collected during the three winters 1977–78 through 1979–80 (Weathers 1983, Weathers, unpublished data).

TESTS OF HYPOTHESES

Food

Distributions of species were unrelated to food supply. Foods of all species were most abundant in a single habitat in the first year of study and they were nearly equally abundant in all three habitats in the second year (Fig. 2). In the first year, food standing crop in pinyon–juniper was greater than that in the other two habitats, although the differences could not be tested because of the absence of replication. Differences in food standing crop were slight during the second year and were not statistically significant (ANOVA—sage sparrow: $F = 0.19$, df = 2, 3, $P = 0.84$; black-throated sparrow: $F = 0.22$, df = 2, 3, $P = 0.82$; dark-eyed junco: $F = 0.22$, df = 2, 3, $P = 0.81$). Clearly, food abundance alone does not explain species distributions.

Estimated food intake rates showed a similar pattern. All three species experience similar estimated intake rates in any one habitat and the habitats rank similarly for all three species, regardless of the value of the search rate constant (Fig. 3). Pinyon–juniper stood out as having markedly higher predicted intake rates than the other habitats in the first year. Predicted intake rates in the second year were higher on the valley floor than in the other habitats.

The reason that sparrow abundance is not shown to be closely related to food abundances is that the different sparrow species consume similar foods. Species diets overlapped in both the seed species present and in seed morphology. Proportional similarity in seed species present was moderately high between sage sparrows and black-throated sparrows, and it was low between each of these two species and dark-eyed juncos (Table 3). Seed profitability was highly correlated among species (Table 4) suggesting that fundamental niches overlap broadly. The rank order of profitabilities was similar among species with only two exceptions that were due to more than minor differences in profitability (Fig. 4). One of those exceptions (*Phacelia* spp.) was rare in the environment. Clearly, species share preferences for the same foods.

Predation

The predation hypothesis predicts that species differ in habitat use because they are safest in different habi-

Table 2. Sparrow species abundances (birds ha^{-1} h^{-1}) in three habitats during two winters. The upper entry for a species in a habitat is mean abundance on a single census plot during the winter of 1985–86. The lower entry is mean abundance on two census plots during the winter of 1986–87. Standard errors (in parentheses) listed for the first year are calculated from individual census on study plots (three to eight censuses per plot) because there was only one study plot per habitat. Those for the second year are calculated from the means of the two study plots in each habitat (eight censuses per plot). A zero indicates that the species was never observed in the habitat during censuses

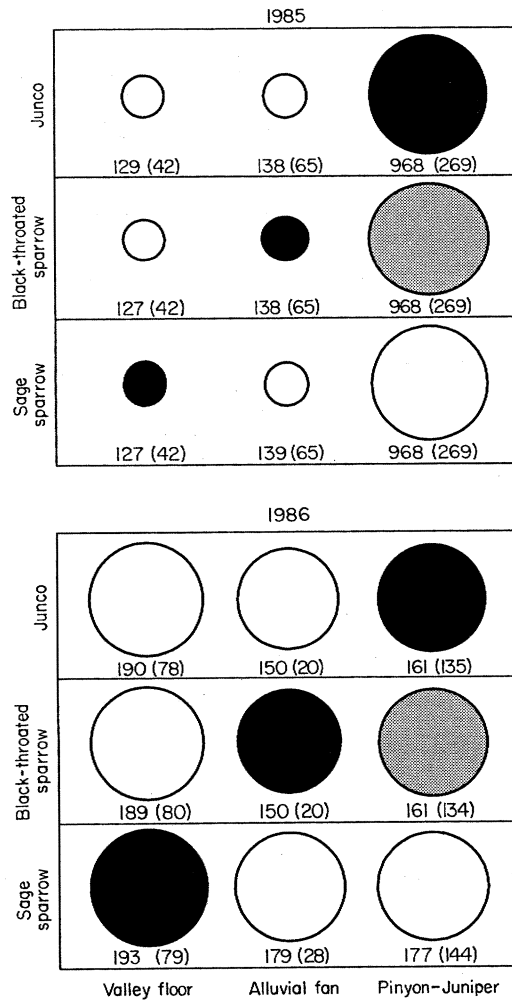|	Bird density (birds ha^{-1} h^{-1})		
	Valley floor	Alluvial fan	Pinyon–juniper
Dark-eyed junco	0	0	4·28 (2·91)
	0	0	0·57 (0·37)
Black-throated sparrow	0	0·65 (0·49)	0·04 (0·05)
	0	0·49 (0·02)	0·06 (0·06)
Sage sparrow	0·10 (0·10)	0	0
	0·78 (0·23)	0	0

Fig. 2. Food standing crop (mg m^{-2}) for three species of sparrows and sparrow population densities in three habitats over two winters. Circle area reflects food standing crop, years scaled separately. Actual means and standard errors are listed just below each circle. Standard errors for 1985–86 data are based on variation in standing crop within study plots because only one study plot existed per habitat. Standard errors for the second year are based on variation among replicate study plots. Circle colour depicts bird population density: ●, common; ◉, uncommon; ○, absent.

Fig. 3. Estimated food intake rates of three species of sparrows in three habitats in 2 years of study. Intake rates were calculated from the variables mass of food item, handling time, and seed density times the unknown constant search rate for seeds that were considered or were likely to be consumed by species (see text). Predicted intake rates for the first year of study are in (a) and those for the second in (b). The species are: sage sparrow (——), black-throated sparrow (- - - -) and dark-eyed junco (– – –).

Table 3. Diet overlap among species calculated as proportional similarity (see Hurlbert 1978) in seed species composition. Standard errors given in parentheses were calculated using a bootstrap technique (see Methods)

	Proportional similarity in diet (SE)	
	Black-throated sparrow	Dark-eyed junco
Sage sparrow	0·362 (0·101)	0·049 (0·026)
Black-throated sparrow	—	0·059 (0·026)

Table 4. Similarity in relative profitability of seed types among sage sparrows, black-throated sparrows and dark-eyed juncos. Profitability was calculated as seed mass divided by seed handling time. Similarity was calculated as the rank correlation between species. $n = 11$ in each case

	Rank correlation (probability)	
	Black-throated sparrow	Dark-eyed junco
Sage sparrow	0·91 (0·0001)	0·90 (0·0002)
Black-throated sparrow	—	0·84 (0·0010)

tats. Counter to the hypothesis, the three species use the same method to escape predators, suggesting that they should have similar habitat preferences. Because the three species escape to shrubby cover, they should forage as close to cover as possible. Both sage sparrows and black-throated sparrows foraged significantly closer to cover than expected by chance (Fig. 5; one-tailed Wilcoxon two-sample tests—sage sparrow: $S = 2220$, $n = 121$, 50, $P < 0·001$; black-throated sparrow: $S = 1407$, $n = 117$, 28, $P < 0·001$). Dark-eyed juncos did not do so and actually foraged farther from cover than expected by chance (Fig. 5; two-tailed Wilcoxon two-sample test, $S = 6538$, $n = 112$, 64, $P = 0·008$). Food could be responsible
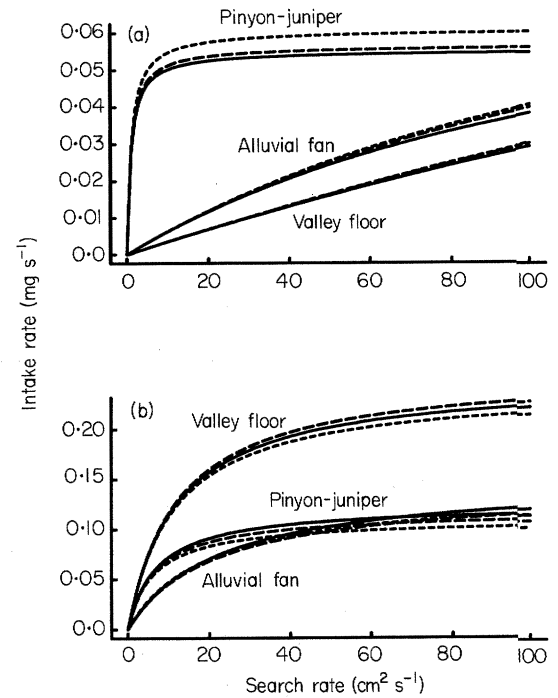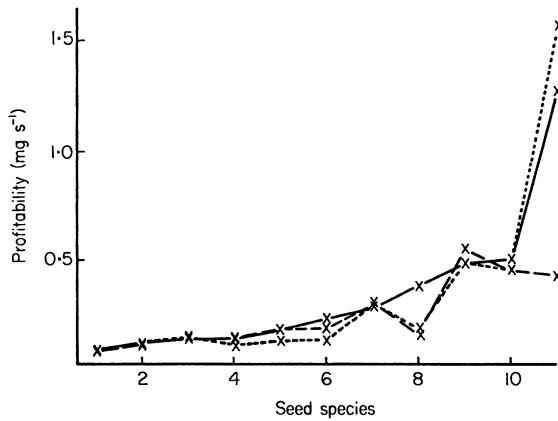
Fig. 4. Profitability (seed mass·handling time⁻¹) of seed foods to sage sparrows (——), black-throated sparrows (----) and dark-eyed juncos (– – –). Seed types: (1) *Bouteloua aristidoides*; (2) *Aristida adscensionis*; (3) *Schismus barbatus* that must be extracted from floret; (4) *Festuca octoflora*; (5) *Cryptantha* spp. that must be extracted from remnant calyx; (6) *Eriogonum fasciculatum*; (7) *Schismus barbatus* bare seed; (8) *Cryptantha barbigera*; (9) *Amaranthus albus*; (10) *Cryptantha* spp. bare seed; (11) *Phacelia* spp. either *P. crenulata* or *P. distans*.

Fig. 5. Distribution of distances from cover of foraging birds (----) and randomly located points (——). Dark-eyed juncos in pinyon-juniper, black-throated sparrows on the alluvial fan, and sage sparrows on the valley floor. Probability density curves were estimated using the density function of Becker *et al.* (1988). The solid fine line in the top frame (——) shows the distribution of foods eaten by juncos relative to cover (see Methods—Hypothesis testing for methods). Distributions of the foods of black-throated sparrows and sage sparrows relative to cover were identical to the distributions of randomly located points.

for the tendency of dark-eyed juncos to feed farther from cover than expected: food standing crop close to cover in pinyon-juniper was approximately half of the standing crop farther from cover (Fig. 6). Indeed, dark-eyed juncos foraged as far from cover as expected from the availability of food when bird distributions are compared to food distributions (Fig. 5). Sage sparrows and black-throated sparrows foraged slightly closer to cover than expected from food availability (not shown). In fact, these two comparisons were identical to the comparisons of foraging distances to chance expectations, because food was randomly distributed relative to cover on the valley floor and the alluvial fan (Fig. 6).

The similar preferences of sage sparrows and black-throated sparrows for foraging close to cover suggests that the predation hypothesis alone is unable to account for the distributions of species along the elevational gradient. Both species should prefer pinyon-juniper, the habitat with the greatest amount of cover and the habitat occupied by dark-eyed juncos. Additionally, if birds avoid foraging far from cover then food availability may be inadequately measured by food standing crop. Food in a habitat with little cover is not equivalent to the same amount of food in a safer habitat. Hence, weighting food by distance to cover may yield different predictions about habitat distributions than those derived from food alone.

Adjusting estimates of food standing crop by the distance from cover changed the predictions of species distributions from food availability (Fig. 7). Differences in adjusted standing crop between habitats were marginally significant (ANOVA—sage sparrow: $F = 9.91$, df $= 2, 3$, $P = 0.048$; black-throated spar-
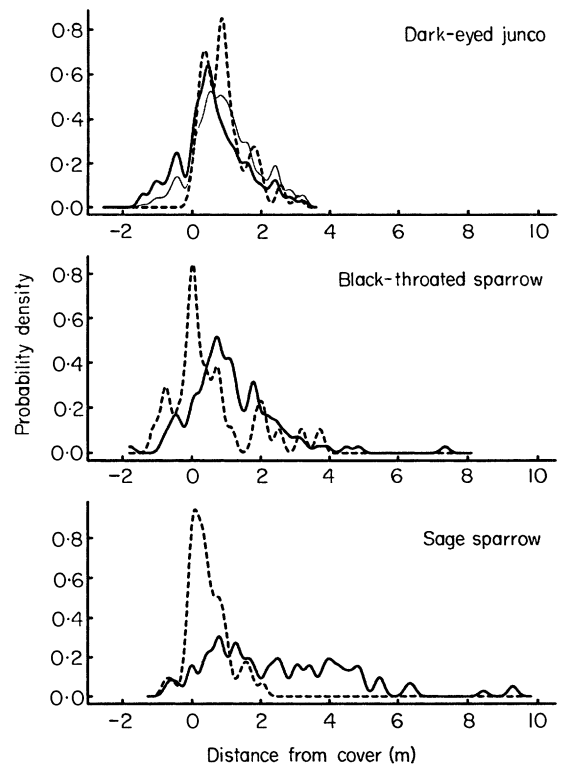
row and dark-eyed junco: $F = 8.93$, df $= 2, 3$, $P = 0.055$), and habitats ranked similarly for all species. Adjusted food standing crop was greatest in pinyon-juniper woodland for all three species in both years. Yet, only one species of sparrow is abundant there. Hence, food and predation jointly fail to explain species distributions along the elevational gradient.

Microhabitat structure

Structural features of habitat might be responsible for species distributions if they influence the foraging abilities of birds in ways that are not captured by the simple measures of food and predation that we used. To accommodate this possibility, we asked if the microhabitats used by foraging birds were themselves restricted in distribution and might limit the distributions of species.

Foraging microhabitats used by a given species were not restricted to the habitat in which the species is found (Fig. 8). The only habitat variable that might
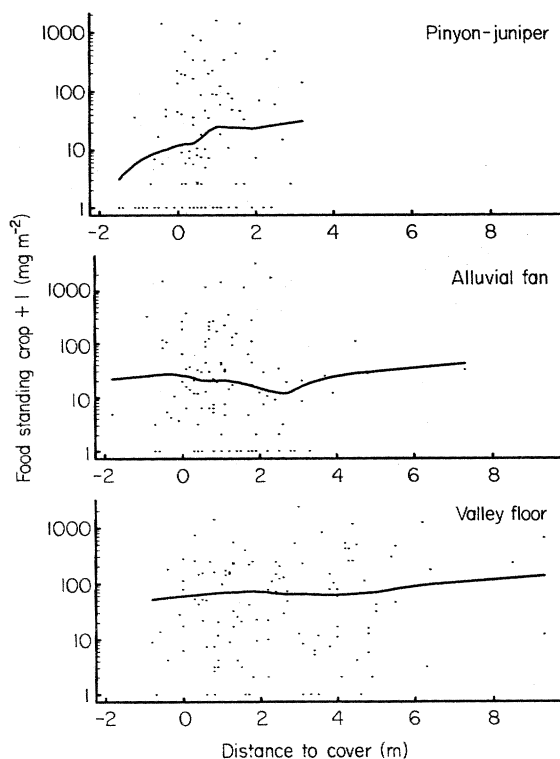
Fig. 6. Food density as a function of distance to cover for: dark-eyed juncos in pinyon–juniper, black-throated sparrows on the alluvial fan, and sage sparrows on the valley floor. The curves in the figures were fit using the scatter plot smoothing algorithm lowess (Becker *et al.* 1988) at the default parameter settings.
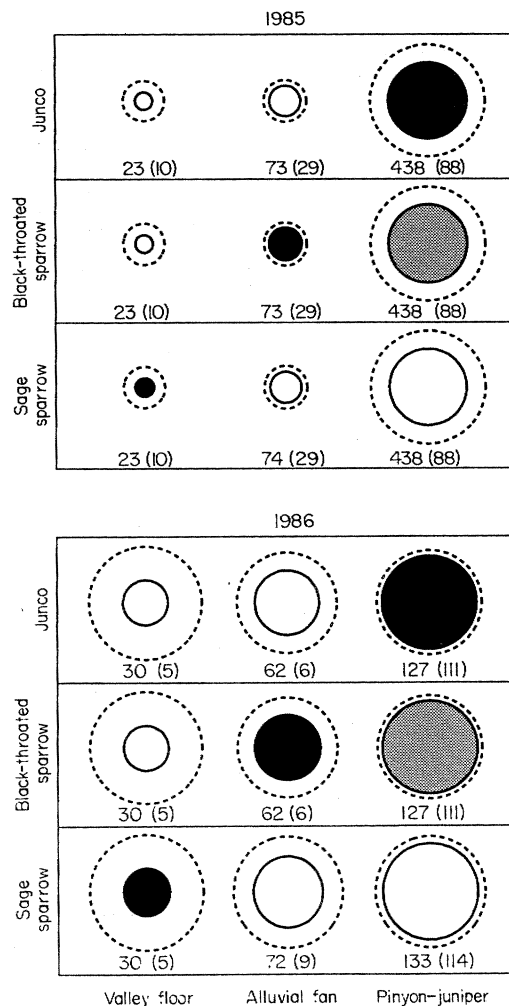

Fig. 7. Food standing crop discounted by risk of predation for three species of sparrow and sparrow population density in three habitats over two winters. The outer dashed circles represent raw food standing crop, and the inner circles discounted standing crop. The statistics below the circles are mean discounted standing crop and standard error as in Fig. 3. Circle colouration reflects population density as in Fig. 3.

limit distributions was rockiness, the third principal component axis. Sage sparrows and juncos both live in habitats with few rocks and hence there appears to be relatively little foraging habitat for them in alluvial fan habitat where rocky substrate is common (Fig. 8b, 8f). However, neither species is restricted to its usual habitat by peculiar habitat structure, nor is habitat structure likely to exclude sage sparrows or black-throated sparrows from pinyon–juniper where food availability may be highest.

The three species also overlap in their use of foraging microhabitats. There was significant overlap in the polygons depicting microhabitat use (Fig. 9). Error rates in the classification of foraging observations using a discriminant function of microhabitat characteristics also suggested that there was significant overlap in microhabitat use (Table 5). The overall error rate in discriminating species on the basis of microhabitat characteristics was 24% or 45% of that expected if overlap in microhabitat use was complete. Clearly, the structural features of habitat that we measured are unlikely to account for species' habitat distributions.

Discussion

What shapes bird species distributions along environmental gradients? We tested several hypotheses that

might account for abutting habitat distributions of sparrows, including food, predation, and microhabitat structure. Food was abundant outside of species' usual habitats suggesting that it is not responsible for species' distributions. Predation is also an unlikely explanation of the distributions because all species appear to be safest from predators while foraging close to cover and they should be safest in the same habitat. The microhabitat structure hypothesis was rejected: species used foraging microhabitats that were more widely distributed than the species themselves, and species forage in similar microhabitat suggesting that they should have similar habitat distributions.

Our inferences are based on observation rather than experiment and, thus, they are less convincing than experimental results might be. Here, we discuss other evidence that supports our conclusions and alter-
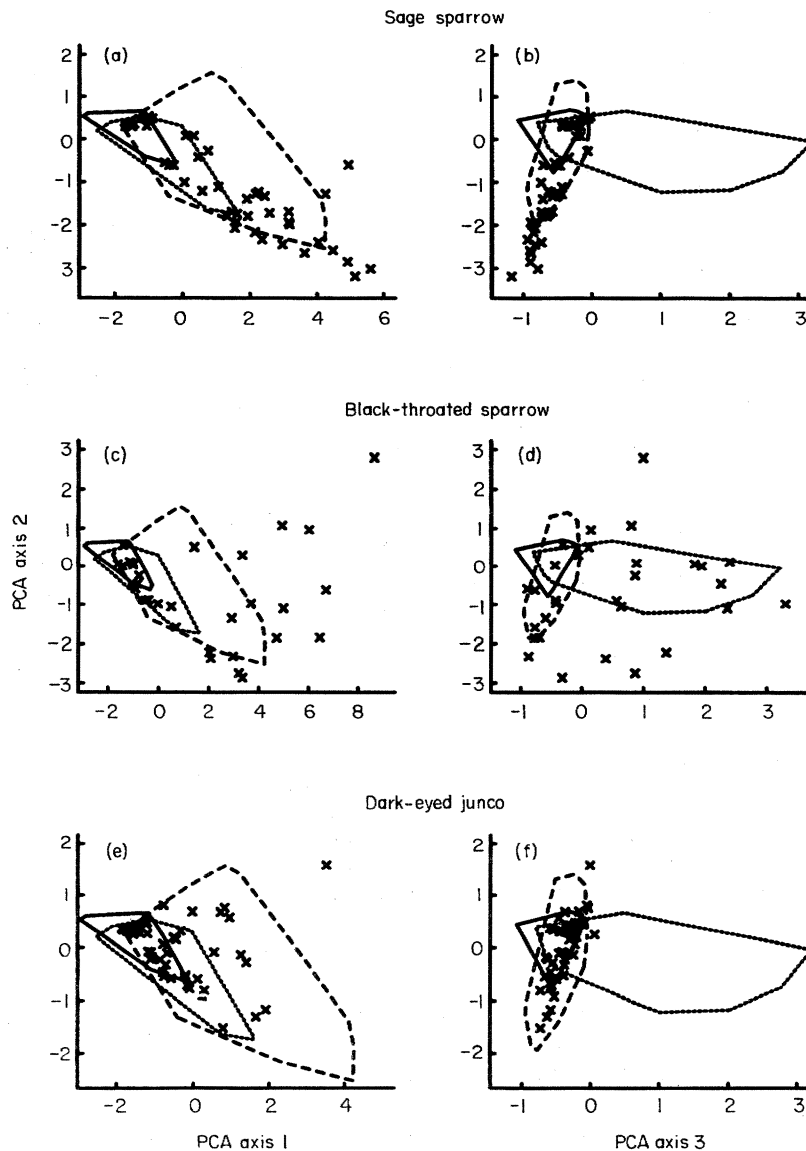
R.R. Repasky &
D. Schluter

Fig. 8. Foraging locations of species plotted over polygons describing the availability of microhabitats within habitats. The first principal component is an axis of increasing total cover; the second one represents increasing tree cover and decreasing shrub cover; the third represents increasing rockiness. Habitats are: valley floor (———), alluvial fan (- - - -) and pinyon–juniper (— — —). The polygons enclose the central 75% of each bivariate distribution (see text).

native hypotheses that might account for species' distributions. We also reconsider the competition hypothesis and suggest that it is worth testing directly.

OTHER EVIDENCE

The results of an introduction experiment (R. R. Repasky & D. Schluter, unpublished manuscript) support our conclusion that food is unlikely to restrict species distributions because food is readily available outside of species' typical habitats. Each species was forced to forage in each habitat for naturally occurring seeds. Only dark-eyed juncos achieved food intake rates in the habitat that they occupy that were significantly higher than in other habitats. Sage

sparrows and black-throated sparrows experienced smaller trade-offs in feeding ability between habitats. Those species also achieved food intake rates in the habitats that they occupy that were slightly less than in unoccupied habitats. Although the differences were small, they suggest that differences in foraging ability among habitats are minor and that sage sparrows and black-throated sparrows are more narrowly distributed than they would be if food were responsible for their distributions.

The introduction experiment also supported our conclusion that species differences in predation risk are unlikely to be responsible for shaping the species' habitat distributions (R. R. Repasky, unpublished manuscript). Sage sparrows and black-throated spar-
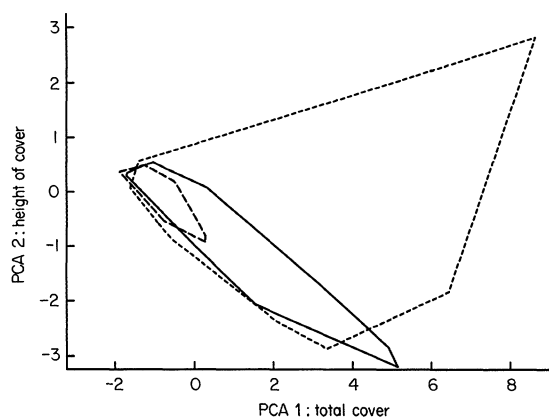
Fig. 9. Overlap in the foraging microhabitats of sage sparrows (——), black-throated sparrows (- - - -) and dark-eyed juncos (— — —). Axes represent principal components of habitat structure. Polygons enclose the central 75% of the bivariate distribution (see Methods—Hypothesis testing).

Table 5. Overlap in use of microhabitats quantified as the rate at which observations were misclassified by a discriminant function used to categorize foraging observations according to species on the basis of microhabitat characteristics. Zero error rates are expected if species do not overlap. Error rates of 53.1% are expected if mean microhabitat characteristics are identical

Species	Misclassification rate	
	Percentage of observations	Percentage of maximum
Sage sparrow	40·8	76·8
Black-throated sparrow	30·0	56·5
Dark-eyed junco	7·9	14·9
Species combined	23·9	45·0

rows transported between habitats exhibited similar changes in the amount of time that they spent scanning the environment suggesting that they experience similar changes in predation risk between habitats and that they are likely to be safest in the same habitat. Vigilance data from dark-eyed juncos, unfortunately, could not be compared.

Evidence from the introduction experiment also weighs against the microhabitat structure hypothesis. The means by which structural features of habitat affect species' distributions are likely to be through their influence on feeding ability and predation risk. The net effects of these factors were captured in feeding rates and vigilance levels of birds foraging in the introduction experiment. Those effects were small and appeared to be insufficient to restrict species to single habitats.

OTHER POSSIBILITIES

We considered several biotic factors that might be responsible for habitat partitioning among species.

Factors were considered singly with one exception, food and predation together. Species distributions might be explained by other combinations of the factors that we considered or by abiotic factors which were not considered. Complex interactions among factors are outside the scope of this paper. Here we explain why abiotic factors are unlikely to explain habitat partitioning. Temperature and water are both relevant to the present study, temperature because the habitats lie along an elevation gradient and water because the lower habitats in our study area are in a desert. Also, we consider the possibility that winter habitat preferences simply reflect preferences for breeding habitats and are themselves uninteresting. This hypothesis is pertinent because each of the three sparrow species occupies that habitat in the study area that most closely resembles its breeding habitat.

Neither the temperature hypothesis nor the water hypothesis yields the prediction that species are restricted to different habitats. Rather than forming absolute bounds to species distributions, temperature interacts with food and predation to limit distributions (Repasky 1991), modulating food requirements and hence the risks of starvation and predation (McNamara & Houston 1990). Each species should be most abundant in the habitat where the least amount of energy is needed to maintain body temperature. Species actually overlap broadly in the range of temperature over which energy expenditure is least (Fig. 10), and all species should be most abundant in the same habitat and less abundant elsewhere. Like temperature, the water hypothesis fails because it predicts that species should share preferences for habitats. The primary adaptation to aridity by North American passerines appears to be small body sizes favourable for dissipating heat and conserving water (MacMillen 1990). Because passerines lack peculiar adaptations that might restrict desert-dwelling species such as sage sparrows and black-throated sparrows to arid areas, all species should be best suited to the presence of water.

Winter habitat distributions could be by-products of breeding habitat distributions if species possess stereotyped habitat preferences that reflect their breeding habitats. Although this hypothesis is worth testing, there is no reason to expect that choice of winter habitat is constrained by breeding habitat preferences, especially if winter habitat choice affects survival. Although some species exhibit inherent habitat preferences (e.g. Klopfer 1963; Greenberg 1984), other species forage flexibly (see Klopfer & Ganzhorn 1985) and change their habitat preferences seasonally. For example, dark-eyed juncos in eastern North America breed at the margins of northern coniferous forests of spruce (*Picea* spp.) and fir (*Abies* spp.) and spend the winter in openings of hardwood and pine (*Pinus* spp.) forests. Juncos prefer their winter habitat over their breeding habitat when they are exposed to winter photoperiods, but that preference can be
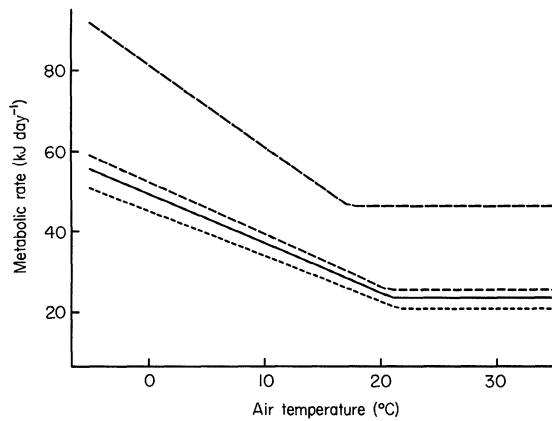
Fig. 10. Maintenance metabolism as a function of ambient temperature: black-throated sparrows (13 g, - - - -), sage sparrows (17 g, ——), dark-eyed juncos (19 g, – – –) and, for comparison, rufous-sided towhees (42 g, — —). Note that species overlap broadly in the range of temperatures that are most favourable to them. Estimates were based on allometric relationships in the literature: basal metabolic rate (the flat portion of each relationship) was calculated as $3 \cdot 19 \ M^{0 \cdot 73}$, where M is body mass (in g) (Aschoff & Pohl 1970); the threshold ambient temperature below which additional energy must be spent to maintain body temperature was $T_b - 11 \cdot 5 \ M^{0 \cdot 19}$ where T_b is body temperature (in °C) and M is body mass (in g) (Weathers & van Riper 1982); the rate at which energy expenditure increases as ambient temperature declines below the threshold temperature is $0 \cdot 28 \ M^{0 \cdot 54}$ (in kJ day^{-1} per °C) where M is body mass (Aschoff 1981).

reversed by experimentally lengthening photoperiod (Roberts & Weigel 1984). In the wild, sparrow habitat distributions vary in response to changes in food abundance (Pulliam 1986).

THE COMPETITION HYPOTHESIS REVISITED

Although we did not test the competition hypothesis itself, we wish to point out that our results are consistent with the hypothesis that on-going interspecific competition is responsible for the habitat distributions of sage sparrows, black-throated sparrows and dark-eyed juncos along the elevational gradient. The presence of potential competitors in habitats unoccupied by a species is the most conspicuous factor that might limit species distributions. Our data clearly indicate that species share some foods and forage in similar microhabitats. Does food limit population abundance as it must if competition is indeed responsible for species distributions? Two sources of evidence suggest that food is limiting. First, a short-term food addition experiment (R. R. Repasky, unpublished manuscript) showed that birds recruited to food addition plots where food standing crop was increased with millet seed. Hence, birds readily switch their feeding to areas of greater food abundance if they are available. Such a response must be seen if food is limiting, although it is not sufficient evidence of food

limitation because a change in survival was not demonstrated directly. Nevertheless, the absence of a response would have suggested that food was not limiting (e.g. Pulliam & Dunning 1987).

Secondly, food limitation appears to be a general phenomenon among granivorous birds in arid lands. Sparrows in the arid grasslands of Arizona appear to be food limited in years of low seed production, but not in years of higher seed production: there is a positive relationship between sparrow abundance and food abundance among years of low food availability (Pulliam & Parker 1979); predictions of species composition that are derived from competition theory tend to be upheld in years of poor seed production, but not in years of good seed production (Pulliam 1983); and birds failed to recruit to a food addition plot when the experiment was in a year of moderate food availability (Pulliam & Dunning 1987). Also, there is a positive correlation between the abundance of finches (broadly defined as small granivores in several avian families) and food abundance among the arid areas of the world suggesting that food limitation is widespread (Schluter & Repasky 1991). Although the worldwide study included data from the present study site, the pattern is clearly present without those data.

On the basis of the evidence above, we suggest that the competition hypothesis is a plausible explanation of habitat partitioning by sparrows, more plausible than the food, predation or habitat structure hypotheses. Tests of the competition hypothesis are needed.

Acknowledgements

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