

HABITAT PARTITIONING BY SPARROWS
ALONG AN ELEVATIONAL GRADIENT

by

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ABSTRACT

Although species replacements along environmental gradients are commonly attributed to interspecific competition, predictions of what species distributions would be in the absence of competition are usually lacking. I tested alternative hypotheses that might account for species distributions including: food, predation, and habitat structure. These factors were unable to account for the distributions of sparrows wintering along an elevational gradient in the Sonoran Desert of southern California, USA.

Sage sparrows (*Amphispiza belli*), black-throated sparrows (*A. bilineata*) and dark-eyed juncos (*Junco hyemalis*) inhabit different vegetation types. Under the food hypothesis, species occupy different habitats because they eat foods that occur in different habitats. Species ate seeds of the same species of plants, and the profitability of seeds (seed mass ingested / handling time) ranked similarly among sparrow species suggesting that species should have similar distributions. Also, species can apparently forage profitably outside of their customary habitats. Several measures of food availability suggested that two species are missing from habitats in which food is at least as available as in occupied habitats. The measures included: food standing crop; food intake rate estimated from seed abundance, seed size, and handling time; and food intake rates observed in an "introduction" experiment in which individuals of each species were placed in an aviary and allowed to forage in each habitat. Observed differences in food intake rate between habitats were small suggesting that species would be more broadly distributed if food shaped their distributions.

Predation could be responsible for habitat distributions if species are safest from predation in different habitats and predation risk is severe. Alternatively, predation can not be responsible for habitat partitioning if all species rank habitats similarly by safety. Data support the latter alternative. All species escape predators by fleeing to woody cover and feed near cover. Hence, they are likely to be safest in the habitat

with the greatest amount of cover. Also, I recorded the rate at which birds scanned the environment while they foraged in an aviary to test two predictions: (1) if species experience similar changes in risk between habitats and if the same level of vigilance yields the same probability of detecting predators, species should exhibit similar changes in vigilance level between habitats; (2) if some species experience increased risk when moved from one habitat to another whereas other species experience decreased risk, species should exhibit dissimilar changes in vigilance levels. Two species for which comparisons were possible exhibited similar changes in vigilance between habitats.

I also considered structural features of habitat that might affect foraging ability or the risk of predation. Foraging microhabitats used by individual species were more widely distributed than the species themselves, suggesting that species' distributions are not limited by habitat structure.

I addressed the competition hypothesis by testing two conditions necessary for competition: species must share limiting resources and they must deplete the amount of food available to one another. Species overlapped in the kinds of foods that they ate and in the types of microhabitats where they foraged. To test the food limitation hypothesis, I carried out a short-term food addition experiment. Bird densities increased as the result of the food addition, supporting the hypothesis of food limitation in the short term. The chronology and magnitude of recruitment to experimental plots illuminated the existence and dynamics of depletion. Initially less common, yet mobile species (mourning doves and house finches) recruited fastest and in the greatest numbers to experimental plots, removing up to 72 percent of the total amount of seeds available to birds. The initially more common yet least mobile species (white-crowned sparrows, black-throated sparrows) recruited more slowly and in lower numbers. Much less food was available to these later species than would have been in the absence of the earlier species.

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GENERAL INTRODUCTION

Species replacements along environmental gradients are striking. A number of species occur in sequence, sometimes with little or no overlap between their distributions (e.g., Terborgh 1971, MacArthur 1972, Wolcott 1973, Adams and Bernard 1977). Early explanations of this pattern invoked competition. Darwin (1859) argued that competition is responsible for species replacements along elevational gradients and latitudinal gradients. He reasoned that minor differences between species put each species at a competitive advantage under different environmental conditions along gradients. The first explicit statement of the competitive exclusion principle was by Grinnell (1904) in a discussion of the habitat distribution of the chestnut-backed chickadee (Lack 1971). Closely related species of temperate birds often dwell in adjacent habitats, and Lack (1944) argued that this pattern of distribution was the result of interspecific competition. He reasoned that closely related species consumed similar foods and that differences in species' morphology were too small to restrict their distributions. He supported his view with natural experiments in which the distributions of species were observed in areas in which supposed competitors were absent. MacArthur (1972) provided theoretical insight into how competition might result in species replacements. The hypothesis that competition is responsible for elevational distributions has been tested frequently (e.g., Terborgh 1971, Terborgh and Weske 1975, Noon 1981, Schluter 1982, Price 1991).

The makings of an alternative view also began early. Grinnell (1904) suggested that species distributions might be restricted by habitat itself. The distribution of a species might expand until it reached habitats having characteristics that were insurmountable. Gleason (1926) proposed that species are distributed independently of one another according to the favorability of the environment to individual species. His hypothesis was supported by the absence of pattern in the distributions of large

numbers of plant species along elevational gradients (Whittaker 1951, 1956). Bowman (1961) suggested that species' food requirements might account for the distributions of Galápagos ground finches (*Geospiza* spp.) among islands. He reasoned that each species is adapted to different foods and that species distributions were shaped by the distributions of their foods among islands rather than by interspecific competition as Lack (1947) had argued (see Abbott et al. 1977 and Schluter and Grant 1982 for a vindication of Lack). The suggestion that species distributions are shaped independently by environmental factors has been raised (e.g., Sweeney and Vannote 1978, Vannote and Sweeney 1980, Wiens and Rotenberry 1981, Strong 1983), but it has rarely been tested (e.g., Abbott et al. 1977, Schluter 1982, Price 1991). A reasonable test would compare species' actual distributions with distributions predicted from environmental factors.

In this thesis, I ask what factors are responsible for the habitat distributions of three sparrows along an elevational gradient in the Sonoran Desert of southern California. Sage sparrows (*Amphispiza belli*), black-throated sparrows (*A. bilineata*), and dark-eyed juncos (*Junco hyemalis*) inhabit different vegetation types along the gradient (Weathers 1983). Present-day competition for food is an obvious factor that might be responsible for the distributions of these species. However, I have emphasized factors other than competition that might account for the distributions and tested the competition hypothesis only indirectly. I considered the alternatives that food, predation and habitat structure account for species distributions. In each case, I test the hypothesis that species specialize on single habitats because each species is so well adapted to a factor in one habitat and so poorly adapted to it in other habitats that the factor restricts its distribution. Under the food hypothesis, for example, species are suited to different types of foods, and their distributions are determined by the distribution of food types among habitats. I tested the competition hypothesis by evaluating the conditions that are necessary for competition to occur. Competition is

unlikely to explain species distributions if there is no sign that it operates, whereas it could shape distributions if the necessary conditions are present.

I tested hypotheses using both observational and experimental data. Observational data presented in Chapter 1 provide an initial test of each hypothesis. The food hypothesis is investigated by determining what is food for each species and by comparing species' distributions with the distributions of their foods. The predation hypothesis is tested by comparing species' use of shrubby vegetative cover that can be used to escape predators. Predation is unlikely to be responsible for habitat partitioning if species have similar preferences for cover. The habitat structure hypothesis is investigated by describing the microhabitats that each species uses in its usual habitat and asking if sites of that type are available in other habitats. Finally, the competition hypothesis is tested by determining whether species use similar resources or would do so if they occupied the same habitats. Also, I tested the competition hypothesis by testing one of its major premises: food limits population abundance. Food limitation is evaluated by measuring the relationship between bird abundance and food supply.

Each of the three following chapters (i.e., 2-4) presents experimental evidence dealing with one of the hypotheses. The food hypothesis is pursued in Chapter 2. An introduction experiment measured foraging abilities of all three species in each of the three habitats. These data were used to test whether each species achieves its highest food intake in the habitat that it typically occupies, and whether significant tradeoffs in foraging ability exist between habitats. The introduction also tested the vegetation structure hypothesis: any feature of habitat structure that affects foraging ability strongly enough to result in habitat specialization should be reflected in food intake rates.

In Chapter 3, data from the introduction experiment are analyzed to test the predation hypothesis. If predation is responsible for habitat specialization, species

ought to perceive different changes in risk between habitats and exhibit dissimilar changes in vigilance. The predation hypothesis is tested against the alternative that all species experience similar changes in risk between habitats and the prediction that species exhibit similar changes in vigilance between habitats.

The competition hypothesis is treated in Chapter 4. A short-term food addition experiment was carried out to see if food was indeed limiting. Food must be limiting if competition is to be responsible for species distributions. Additionally, the experiment provides evidence on whether species are capable of depleting the amounts of food available to one another.

Finally in the general discussion, I integrate the results of the individual chapters.

Chapter I

HABITAT DISTRIBUTIONS OF WINTERING SPARROWS

ALONG AN ELEVATIONAL GRADIENT:

NO RELATION TO FOOD, HABITAT STRUCTURE OR ESCAPE COVER

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, Svärðson 1949, Terborgh 1971, MacArthur 1972). This reasoning is supported by evidence that species often have broader distributions in areas where presumed competitors are absent (e.g., Cody 1974, Terborgh and 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 1986:134), and food, not 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 et al. 1977, Schluter 1982, Schluter and 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, I ask what factors shape the habitat distributions of sparrows wintering along an elevational gradient in the Sonoran Desert of California. Sage sparrows (*Amphispiza belli*), black-throated sparrows (*A. bilineata*) and dark-eyed juncos (*Junco hyemalis*) winter in different vegetation types (Weathers 1983). I tested alternative hypotheses that might determine the distributions, including food, predation and habitat structure and current interspecific competition for food.

Factors and predictions

In testing which factors might limit distributions, I ask whether factors vary along the elevational gradient in ways that are consistent with the hypothesis that they limit distributions. I 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 and Houston 1987). My 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 favorable for a species and the other less favorable, only the factor becoming less favorable can restrict the species' distribution. I emphasize factors that might limit distributions in such a way that they predict species occur one per habitat. Here, I outline the specific factors and predictions stemming from them.

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 abundances along the elevational gradient should be proportional to food availability and that sharp discontinuities in the types of food available occur between habitats.

Predation

Foraging birds avoid areas of high predation risk (e.g., Lima 1990, Watts 1990, Watts 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 one 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 and 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 I 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. I 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 my expectations of the relation between bird distributions, abundance and food supply (Schluter and 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, I test a joint predation-food hypothesis by comparing species' distributions and abundances to food abundance discounted by the risk of predation.

Habitat 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 the 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 my 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 habitat structure determines distributions, it should be possible to identify microhabitat components of habitat structure that are relevant to foraging and ask if the microhabitats used by foraging birds are themselves restricted in distribution. If foraging activity is restricted to particular microhabitats and those microhabitats are absent outside of species' preferred habitat, some feature of habitat structure would then be implicated. Ready availability of suitable foraging microhabitats outside of preferred habitats suggests that habitat structure *per se* is unlikely to account for distributions.

Competition

Habitat partitioning is consistent with the hypothesis that interspecific competition has shaped species distributions. I explored the competition hypothesis by testing for the conditions that are necessary for competition. Species compete when they reduce the availability of shared resources that limit population abundance. I asked whether species share resources and whether food might be limiting. Failure to observe either of these conditions suggests that competition is unlikely, whereas both conditions must hold true if species compete. First, I asked whether species share food types and forage in similar microhabitats. Second, I tested for food limitation by plotting the abundance of all sparrows with food density across habitats. A positive relationship is predicted if food is limiting. Birds in different habitats are different species in my study area, and hence, a positive relationship is likely to represent food limitation rather than simply the local aggregations of birds that have moved to areas of abundant food (Schluter and Repasky 1991).

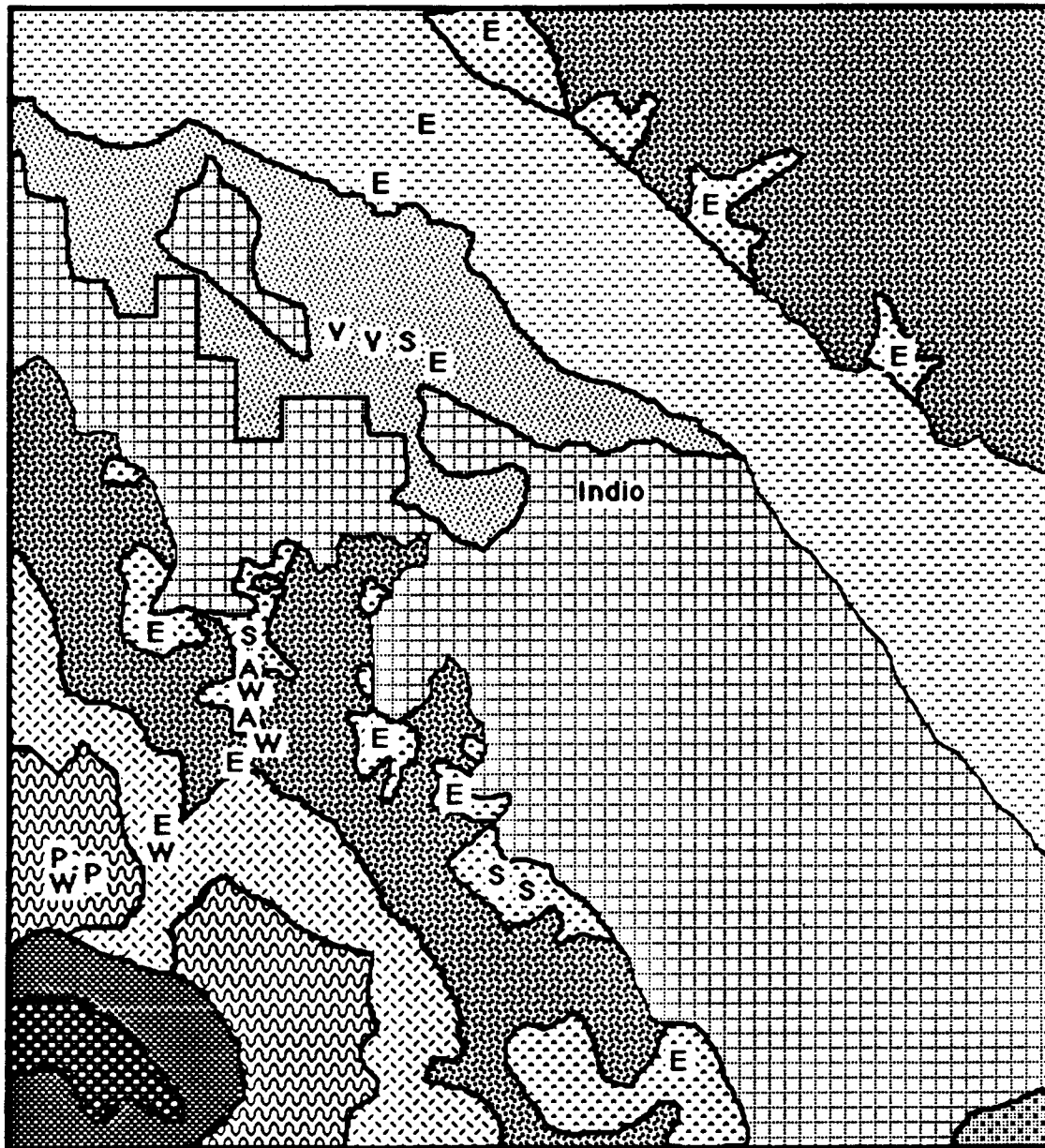
Methods

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 (Figure 1 see Zabriskie 1979 and Weathers 1983). Between these two habitats lie rocky creosote scrub, a yucca-galleta grass community, pinyon pine-juniper woodland, and chaparral.

I studied three common species of sparrows wintering in different habitats along the gradient: sage sparrow (*Amphispiza belli*), black-throated sparrow (*Amphispiza bilineata*) and the dark-eyed junco (*Junco hyemalis*). 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

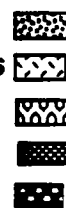
Figure 1. Locations of study plots in the lower Coachella Valley, California. “V” - study plot on valley floor, “A” - study plot on alluvial fan, “P” - study plot in pinyon pine, “S” - study plot used in other portions of the project (Chapters 2 through 4), “E” - area explored as potential study sites or used as a source of birds for captive studies, “W” - study plot of Weathers (1983). Vegetative features taken from topographic maps are broad scale: small islands of developed land may occur within natural habitat types and *vice versa*. Residential/agricultural lands occupy sites that would be either valley floor habitat or alluvial fan habitat. Indio, California is marked.



Salton Sea
Valley floor
Residential/Agricultural
Bajada
Alluvial fan



Rocky slope
Yucca - galleta grass
Pinyon pine
Chaparral
Pine forest



5 km

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 my own were located far apart and in the interiors of habitats (Figure 1). Nevertheless, species distributions are stable: (1) they are consistent with observations made at a variety of sites while exploring for study plots (see Figure 1), and (2) fluctuations of species' distributions over 7 winters (Weathers [1983] – 3, this study – 2, subsequent winters [Chapter 2, Chapter 4] – 2) were insufficient to place species deep inside of habitats that they do not usually occupy.

I 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 monophylla*) 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*.

I conducted the study during fall 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 (Figure 1). One study plot was located in each habitat type during the first winter (1985-86). A second plot, not less than one 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 I 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 by 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, I 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.— I carried out 1 to 4 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 I conducted 4 censuses per visit to each habitat. A census consisted of a count of the number of birds feeding on the study plot during a two-hour period beginning at sunrise. An observer walked the length of the study plot by advancing 20 m at 5-minute intervals. Only actively foraging birds were counted. I 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. I 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 me 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. I identified seeds by comparing them with a seed collection maintained by Deep Canyon Desert Research Center as well as my own reference collection.

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

Habitat Structure.— Habitat characteristics were measured at each sampling quadrat. Distance to cover was measured from the quadrat center 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. I also estimated by eye the percent volume of the air column occupied by vegetation at the heights: 0-10 cm, 10-20 cm, 20-40 cm, 40-60 cm, 0.6-1.0 m, 1.0-2.0 m, 2.0-5.0 m, and more than 5.0 m.

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

To determine diets, I captured birds using mist nets, and I administered to them the emetic apomorphine hydrochloride (Sigma Chemical Co.; see Schluter 1988b, Esteban 1989). Vomit samples were preserved in alcohol to arrest digestion. In the lab, 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. I 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. I 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, I was unable to measure handling times of all three bird species on all seeds types eaten by any species. However, my 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 I collected seeds.

Hypothesis testing

Here I 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. I 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. I 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 I 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 (Chapter 2). I 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, I 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.

I used rarefaction methods (see Schluter 1988b) to determine whether the number of birds captured was adequate to characterize species' diets. Diet breadth, measured as area of diet polygon, was plotted against sample size and inspected for the presence of an asymptote. Each point represented mean polygon area calculated from 200 random subsamples of a given size. Although none of the species exhibited a clear asymptote in polygon size (Figure 2), I concluded that the sample sizes were sufficient because the final polygons included the most abundant seed types and further increases in diet breadth only slightly affected estimated food standing crop. For example, a 20 percent increase in final polygon area increased estimated food standing crop by more than 1 percent for only one species.

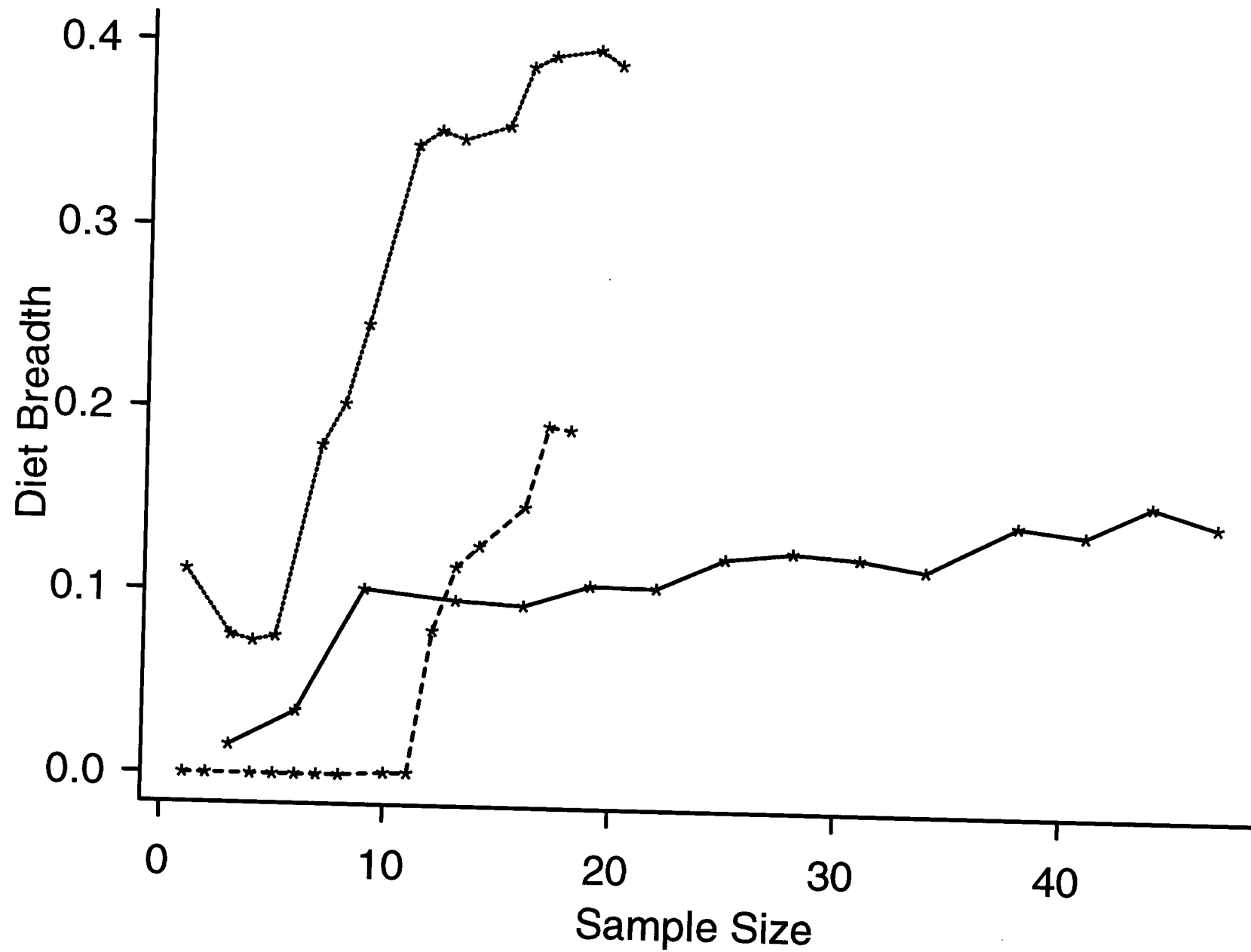
My estimate of food intake rate was based on Holling's (1959) disc equation,

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

where R is intake rate in milligrams per second, λ_i is encounter rate of seed type i in seeds per second, e_i is mass of seed type i in milligrams, and h_i is handling time for seed type i in seconds. Seed masses (e_i) were measured from the seed reference collection. Handling times (h_i) were measured in the lab. Only encounter rates (λ_i) were unknown. I assumed them to be linearly related to seed abundance: $\lambda_i = kd_i$ 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 meters per second. Intake rate was calculated as a function of k . With this formulation, I compared food availability between habitats by calculating intake rates using a range of reasonable values of k .

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

Figure 2. Diet breadth as a function of number of individual birds sampled of sage sparrow (—————), black-throated sparrow (-----), and dark-eyed junco (-----). Breadth is the area of the polygon defining food in terms of principal components axes describing seed size and seed shape. The curves were generated by randomly resampling different sample sizes from the collected sample (see Schluter 1988b).



species should forage closer to cover than expected by chance. I compared distances of feeding birds to cover to distances of randomly located quadrats to cover using one-tailed comparisons. Wilcoxon 2-sample tests were used because the data were not normally distributed. To determine whether birds forage closer to cover than expected from food availability, I 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 et al. 1988). The distribution of food was estimated in three steps. First, I estimated the probability density curve of the distance from randomly located quadrats to cover. Second, I 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 foraging birds in relation to cover was compared to the frequency distribution of available food.

I 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, I 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 $\frac{O-E}{E}$ 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, I characterized habitats in terms of the first three principal components of habitat variables. Data from all habitats were combined, and the percent cover variables were arcsin-square root transformed prior to analysis. The axes represented, first, variation in total cover, second, a gradient from shrub cover to tree cover, and, third, 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 percent of the sampling quadrats in the bivariate distribution. Briefly, the density of points within the neighborhood of each data point was calculated using a scatter plot sharpening algorithm (Chambers et al. 1983), and I eliminated points below the 25th percentile of neighborhood density. Finally, I projected the habitat structure at birds' foraging sites on to the principal component axes characterizing habitats.

To test the competition hypothesis, I tested to see whether species share limiting resources. I examined two aspects of overlap in resource use: food itself and foraging microhabitat. Overlap in diet composition was calculated in two ways. First, I 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 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

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

	Principal Component Axis		
	1	2	3
<hr/>			
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 (above ground):			
0-10 cm	0.31	-0.33	-0.12
10-20 cm	0.33	-0.34	-0.09
20-40 cm	0.36	-0.26	-0.07
40-60 cm	0.38	-0.15	-0.03
60-100 cm	0.37	0.00	-0.02
100-150 cm	0.31	0.29	0.04
150-200 cm	0.28	0.37	-0.05
200-500 cm	0.21	0.49	-0.01
> 500 cm	0.09	0.42	0.05

species, species share preferences for the same foods, and they are likely to compete. I calculated profitabilities of seeds from seed masses taken from my reference collection and from handling times measured in the lab. I 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.

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' diets declines. Error rates are zero in the absence of overlap between species, and they tend toward $\frac{s-1}{s}$ when overlap is complete, where s is the number of species. The error rate when overlap is perfect is actually biased below $\frac{s-1}{s}$ 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. Diet observations 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.

I tested the hypothesis that food is limiting by plotting bird abundance against food supply. If food is limiting, bird abundance should be positively related to food supply. I had six data points that could be considered to be independent: one point from each habitat in each year. Total sparrow standing crop was used because it incorporates differences in body mass among species and because the less common

species within a habitat contribute to resource limitation if it exists. Food was defined to be any seed 1 mg or less in mass.

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). Sage sparrows were present exclusively on the valley floor. Black-throated sparrows were present on the alluvial fan and in pinyon-juniper. In Pinyon-juniper, black-throated sparrows were present in low numbers during autumn (September through November) but absent during winter (December through February). Dark-eyed juncos were present only in pinyon-juniper.

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 3 habitats in the second year (Figure 3). 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.

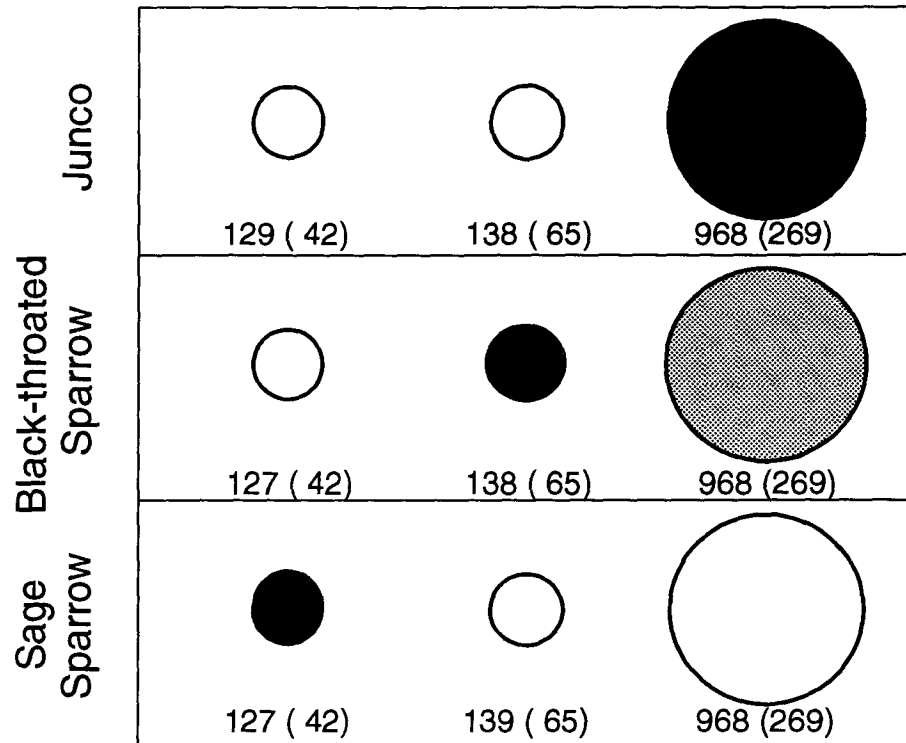
Estimated food intake rates showed a similar pattern. All three species experience similar estimated intake rates in any one habitat, and the habitats rank similarly for all

Table 2. Sparrow species abundances (birds / ha / hr) 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 (3 - 8 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 (8 censuses per plot). A zero indicates that the species was never observed in the habitat during censuses.

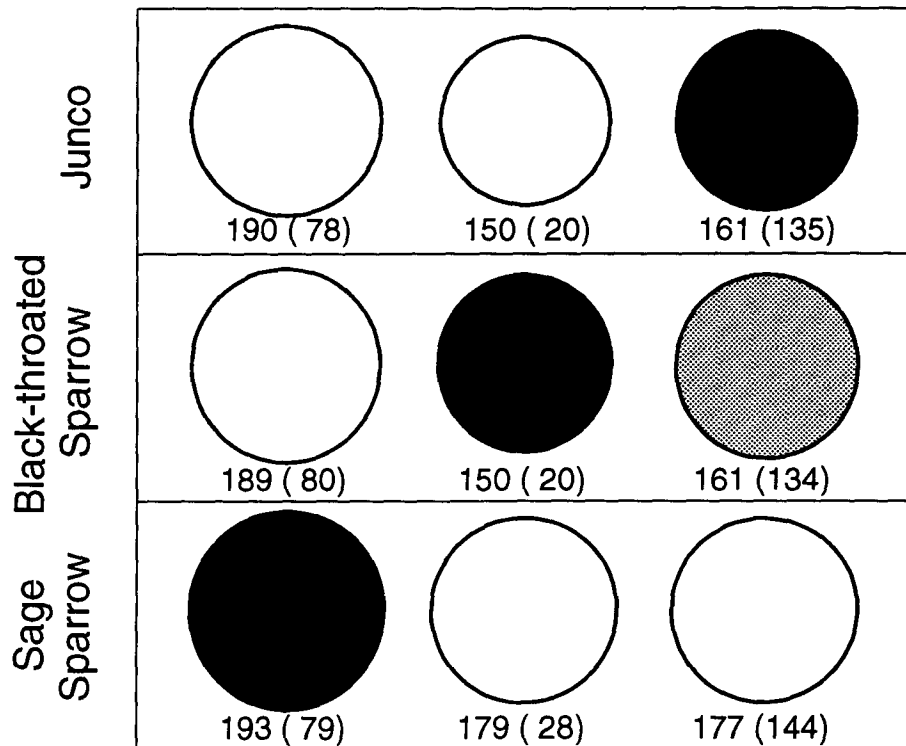
	Bird Density (birds / ha / hr)		
	Valley Floor	Alluvial Fan	Pinyon-juniper
Dark-eyed junco	0	0	4.28(2.91)
	0	0	0.57(0.37)
Black-throated Sparrow	0	0.65(.49)	0.04(0.05)
	0	0.49(.02)	0.06(0.06)
Sage sparrow	0.10(0.10)	0	0
	0.78(0.23)	0	0

Figure 3. Food standing crop (mg /m^2) for three species of sparrows and sparrow population densities in three habitats over 2 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 color depicts bird population density: black – common, stippled – uncommon, white – absent.

1985



1986



Valley Floor Alluvial Fan Pinyon-Juniper

three species, regardless of the value of the search rate constant (Figure 4). 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.

Predation.— The predation hypothesis predicts that species differ in habitat use because they are safest in different habitats. 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 (Figure 5; one-tailed Wilcoxon 2-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 (Figure 5; two-tailed Wilcoxon 2-sample test, $S = 6538$, $n = 112,64$, $P = 0.008$). Food could be responsible 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 (Figure 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 (Figure 7). Sage sparrows and black-throated sparrows foraged slightly closer to cover than expected from food availability.

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,

Figure 4. Estimated food intake rates of three species of sparrows in three habitats in two 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 did 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 (- - - - -).

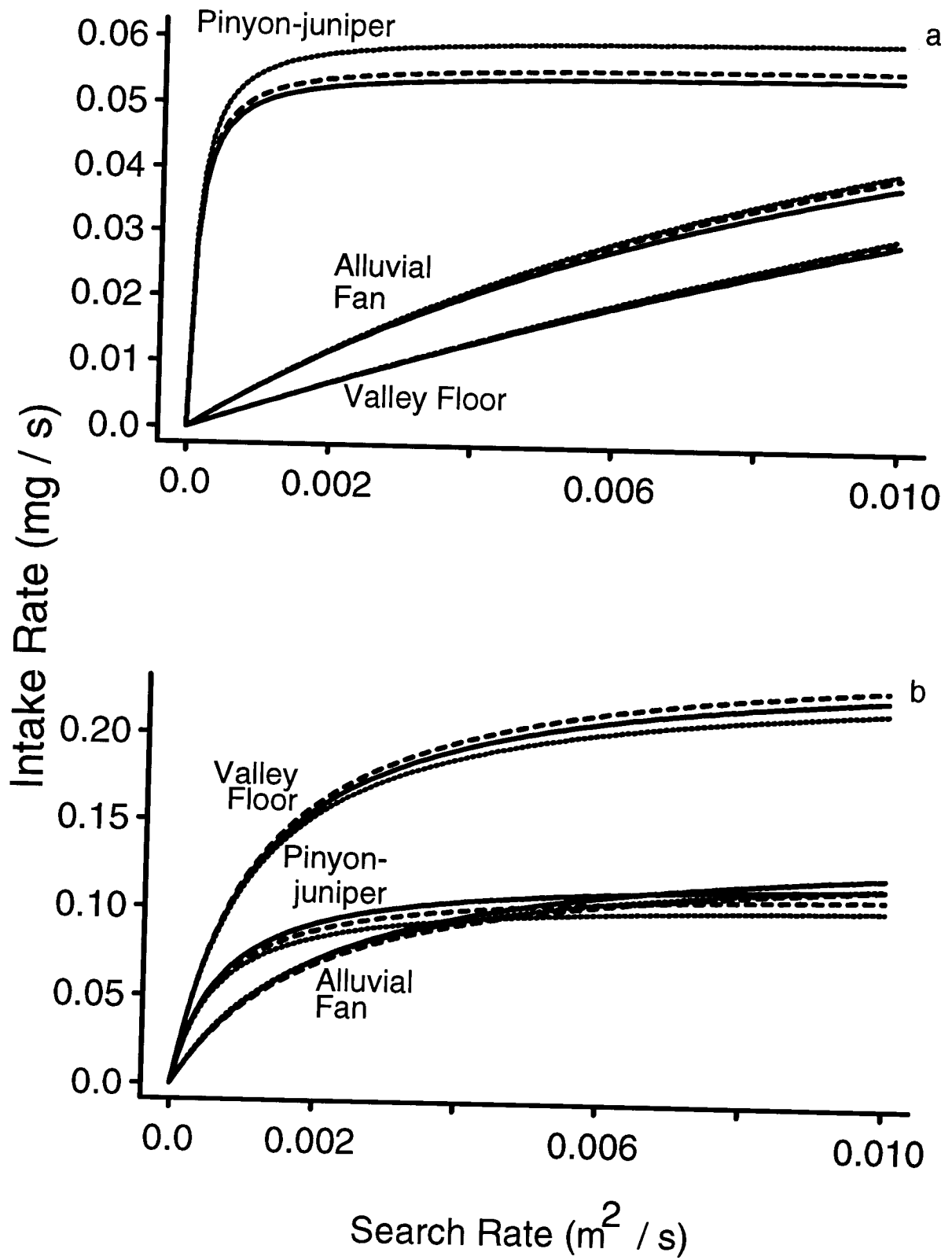


Figure 5. Distribution of distances from cover of foraging birds (- - - - -) and randomly located points (—————). Dark-eyed juncos in pinyon-juniper, black-throated sparrows on the alluvial fan, and sage sparrows on the valley floor. Probability density curves were estimated using the density function of Becker et al. (1988).

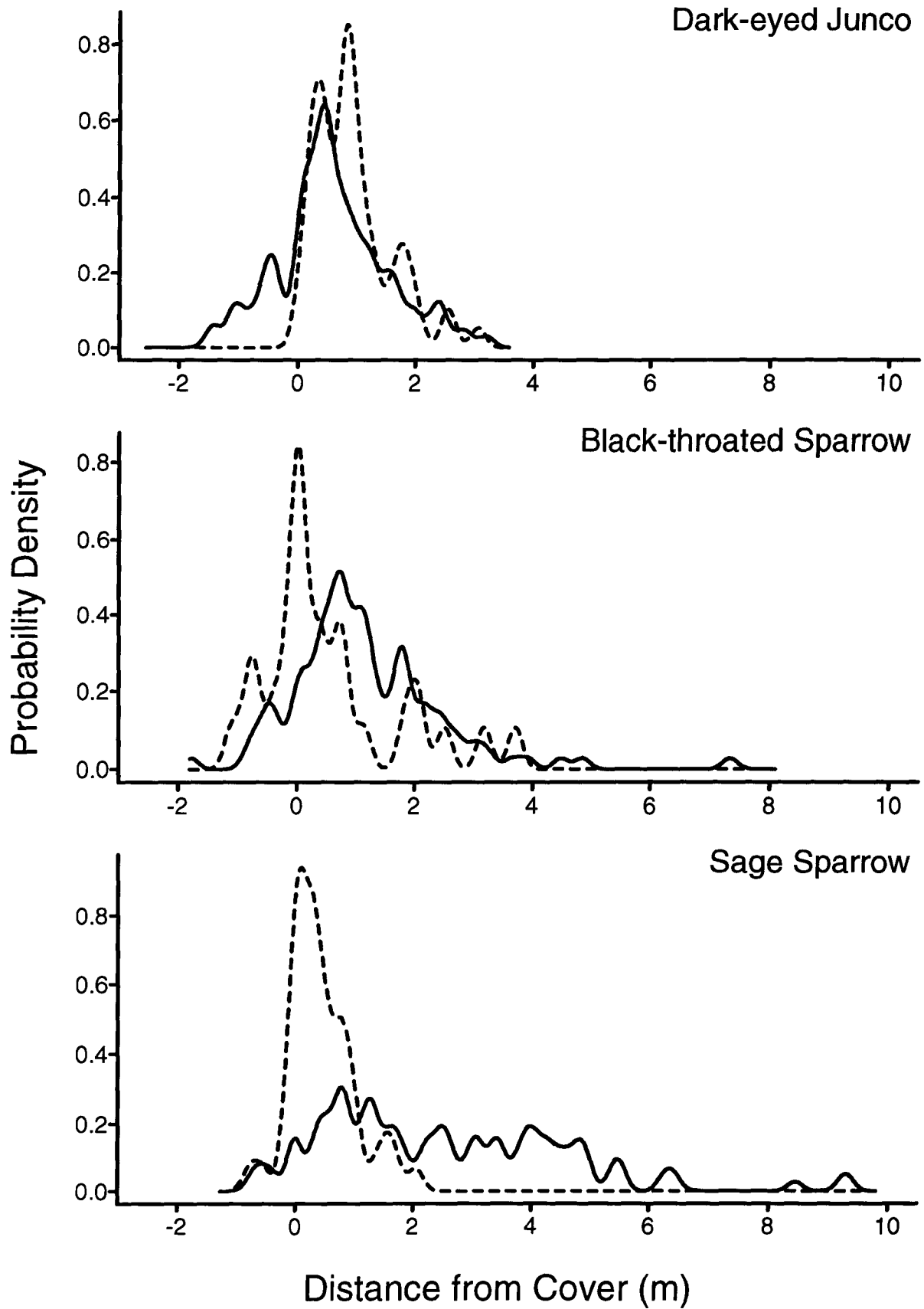


Figure 6. Food density as a function of distance to cover for: dark-eyed juncos in pinyon-juniper, black-throated sparrows on the alluvial fan, and sage sparrows on the valley floor. The curves in the figures were fit using the scatter plot smoothing algorithm lowess (Becker et al. 1988) at the default parameter settings.

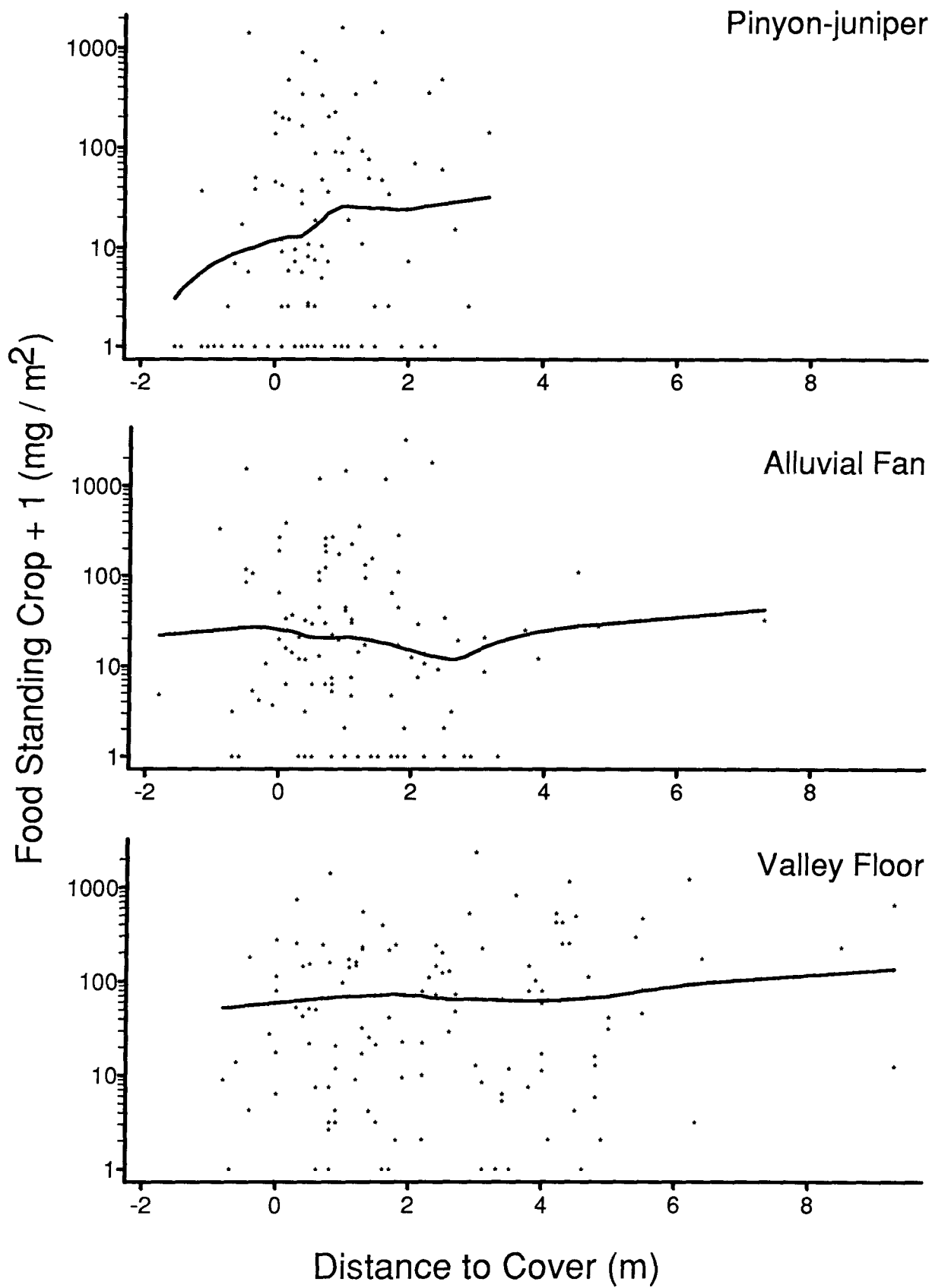
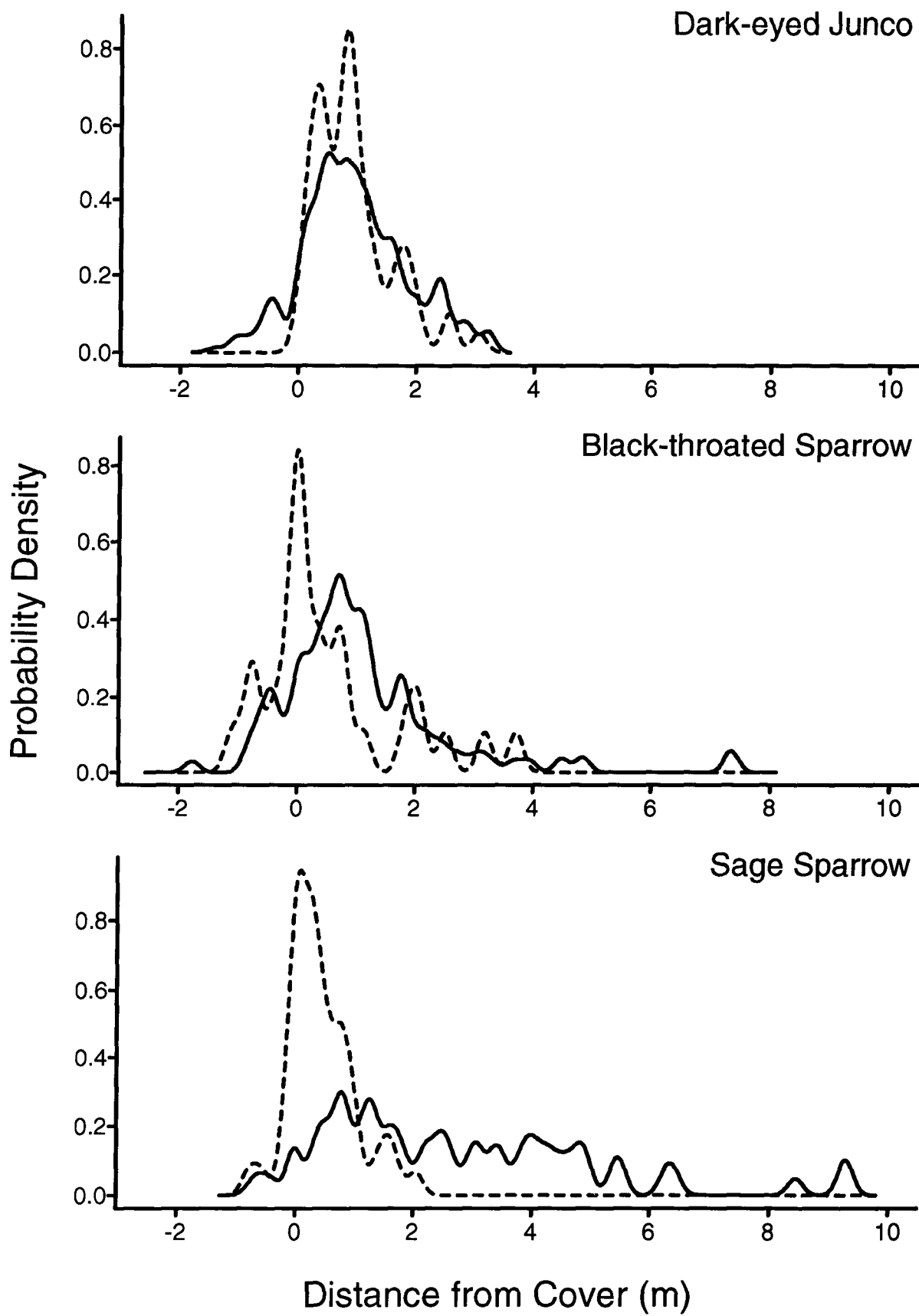


Figure 7. Distribution of distances from cover of foraging birds (- - - - -) and food availability (—————). Dark-eyed juncos in pinyon-juniper, black-throated sparrows on the alluvial fan, and sage sparrows on the valley floor. Distributions of foraging birds are from Figure 4. Food distributions were calculated by multiplying the probability density curves of the distance of random quadrats to cover (Figure 4) by mean food density (Figure 5) and standardizing so that the area under the curve is 1.



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 (Figure 8). Differences in adjusted standing crop between habitats were marginally significant (ANOVA – sage sparrow: $F = 9.91$, $df = 2, 3$, $P = 0.048$; black-throated sparrow 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.



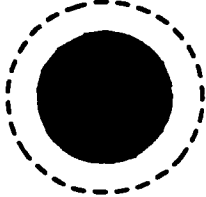


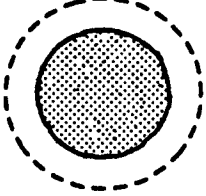


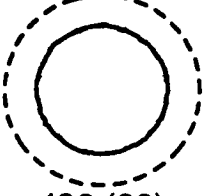
Habitat structure.— Structural features of habitat might be responsible for species distributions if they influence the foraging abilities of birds in ways that are not captured by the simple measures of food and predation that I used. To accommodate this possibility, I asked if the microhabitats used 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 (Figure 9). The only habitat variable that might 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 (Figure 9b, 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.

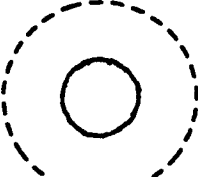
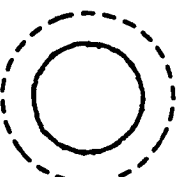
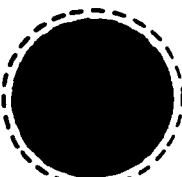
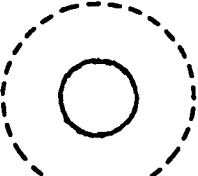

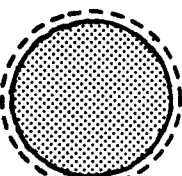
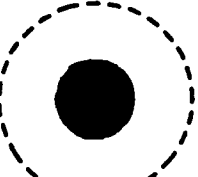
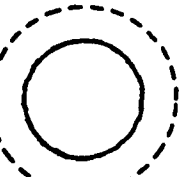
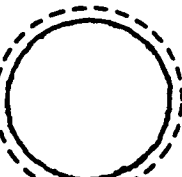
Competition.— The competition hypothesis is consistent with the nearly exclusive nature of species distributions. It is also consistent with disparities observed between species distributions and predictions from the food, predation and habitat structure hypotheses. I pursued the competition hypothesis further by testing for the existence of

Figure 8. Food standing crop discounted by risk of predation for three species of sparrow and sparrow population density in three habitats over 2 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 Figure 3. Circle coloration reflects population density as in Figure 3.

1985

Sage Sparrow	Junco			
		23 (10)	73 (29)	438 (88)
	Black-throated Sparrow			
		23 (10)	73 (29)	438 (88)
Sage Sparrow				
		23 (10)	74 (29)	438 (88)

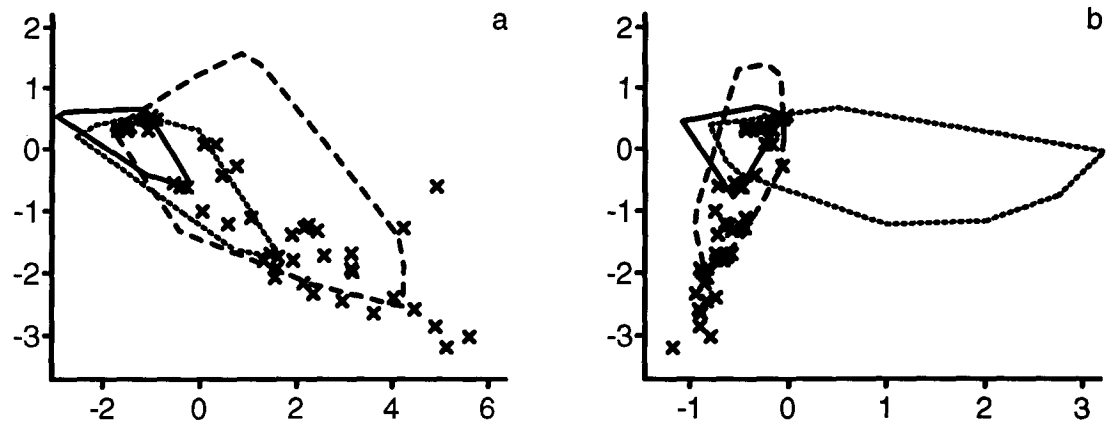
1986

Sage Sparrow	Junco			
		30 (5)	62 (6)	127 (111)
	Black-throated Sparrow			
		30 (5)	62 (6)	127 (111)
Sage Sparrow				
		30 (5)	72 (9)	133 (114)

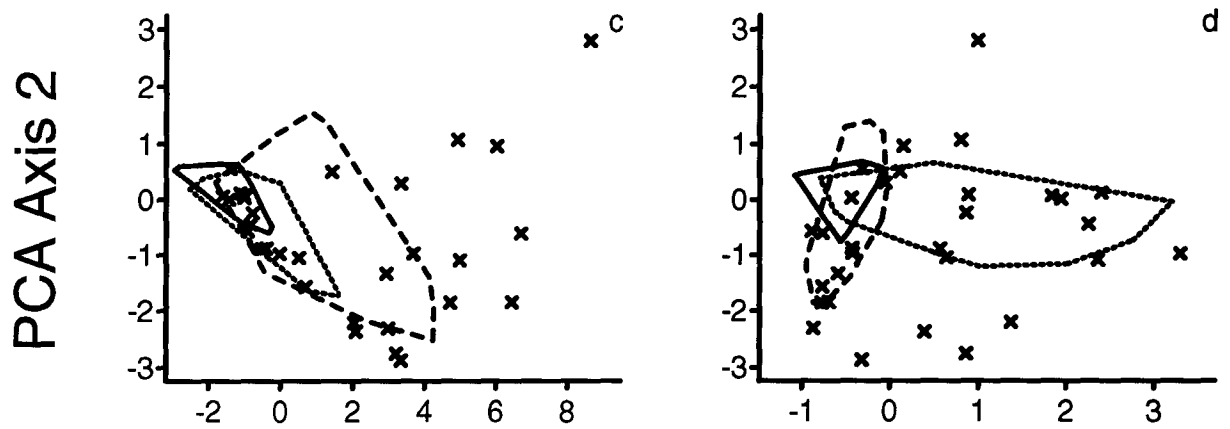
Valley Floor Alluvial Fan Pinyon-Juniper

Figure 9. 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 percent of each bivariate distribution (see text).

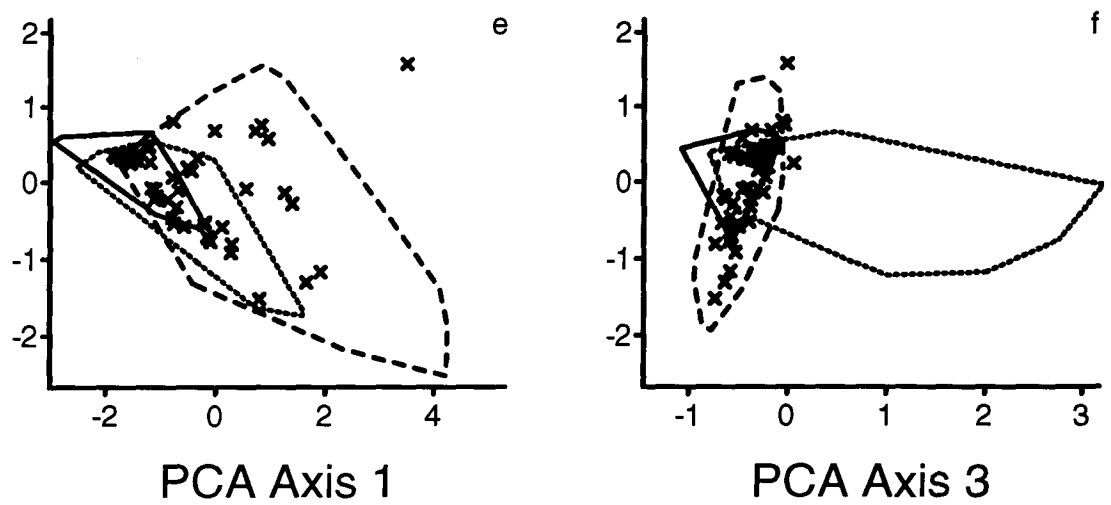
Sage Sparrow



Black-throated Sparrow



Dark-eyed Junco



two conditions that must exist if species are to compete: species must share resources, and the resources must be limiting.

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 (Figure 10). One of those exceptions (*Phacelia* spp.) was rare in the environment. Clearly, species share preferences for the same foods and are potential competitors.

The three species also overlap in their use of foraging microhabitats. There was significant overlap in the polygons depicting microhabitat use (Figure 11). 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 percent or 45 percent of that expected if overlap in microhabitat use was complete. Clearly, these species are potential competitors.

Are resources limiting? Bird abundance was positively related to food supply as expected if food is limiting (Figure 12), but the relationship was due largely to a single point. There was a large amount of food present in pinyon-juniper during the first year of study, and dark-eyed juncos were abundant there that year. If that point is eliminated, only a small range of food densities is included in the data set. (The relationship then appears to be negative, but again due largely to a single point.) Hence, my data are inconclusive regarding the hypothesis of food limitation. In the discussion I consider other evidence suggesting that food is indeed limiting.

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	Dark-eyed
	Sparrow	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	Dark-eyed
	Sparrow	Junco
Sage Sparrow	0.91 (0.0001)	0.90 (0.0002)
Black-throated Sparrow	—	0.84 (0.0010)

Figure 10. Profitability (seed mass / handling time) 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 barbiger*, 9) *Amaranthus albus*, 10) *Cryptantha* spp. bare seed, 11) *Phacelia* spp. either *P. crenulata* or *P. distans*.

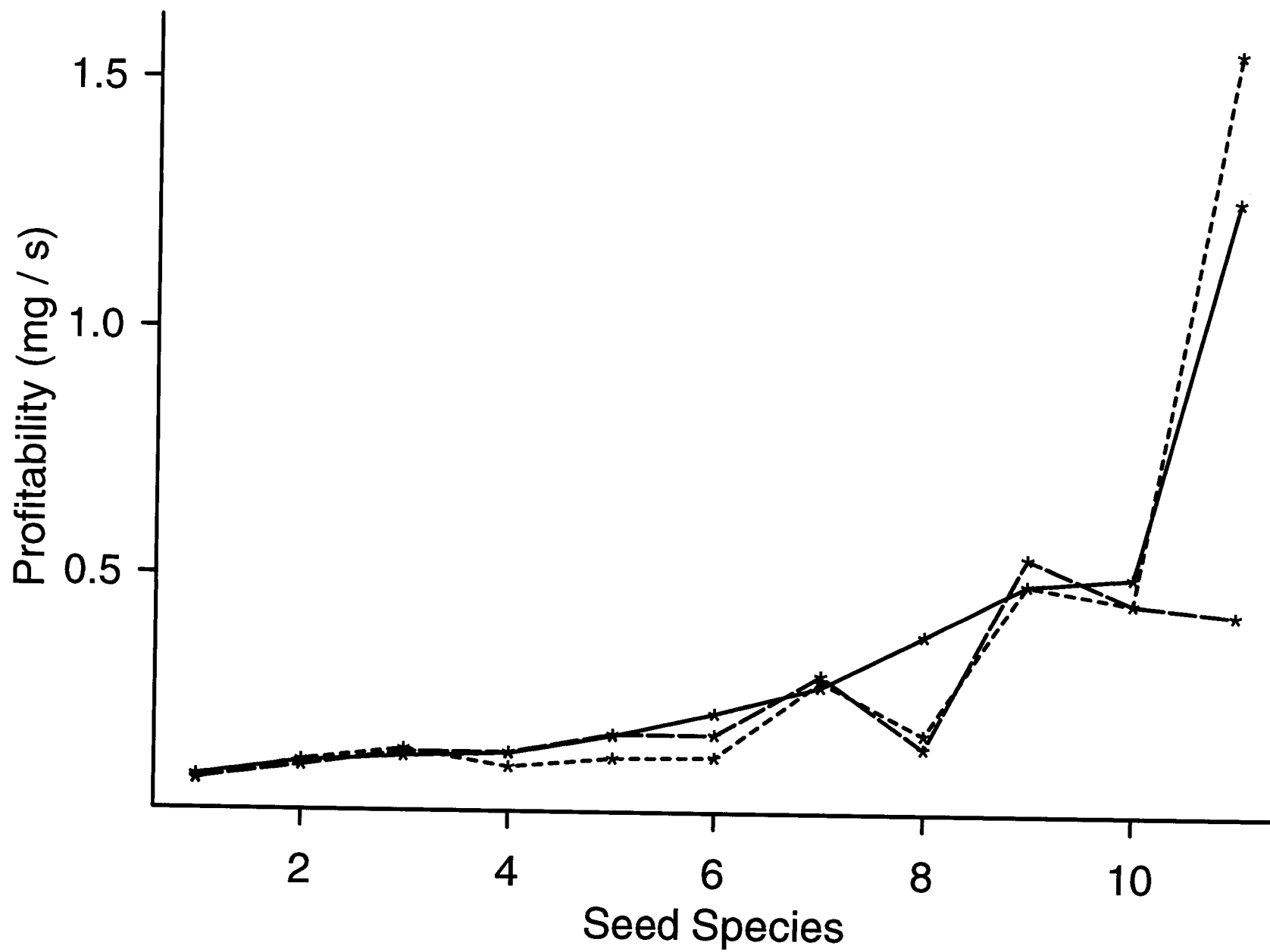


Figure 11. Overlap in the foraging microhabitats of sage sparrows (—————), black-throated sparrows (-----), and dark-eyed juncos (— — — — —). Axes represent principle components of habitat structure. Polygons enclose the central 75 percent of the bivariate distribution (see Methods – Hypothesis testing).

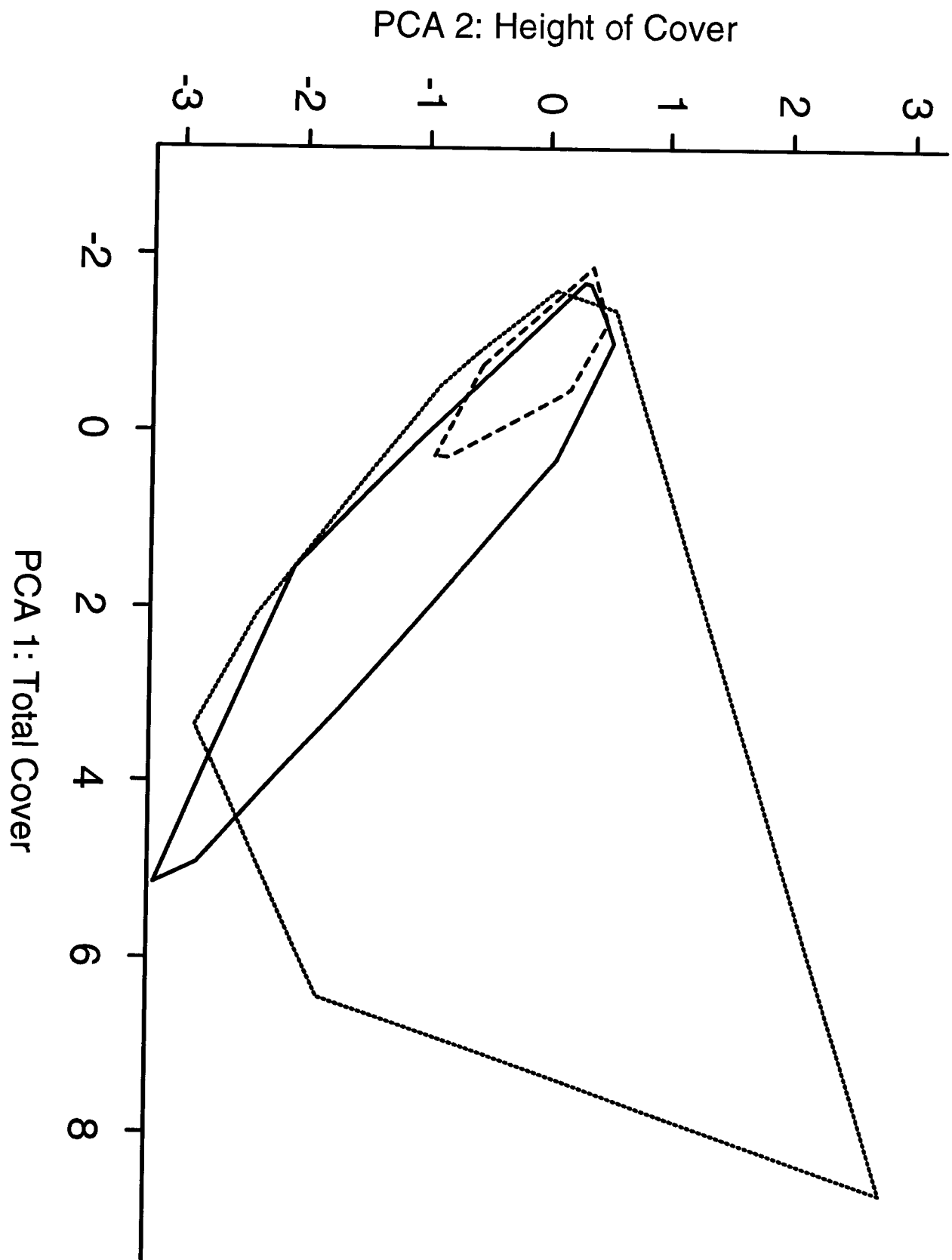
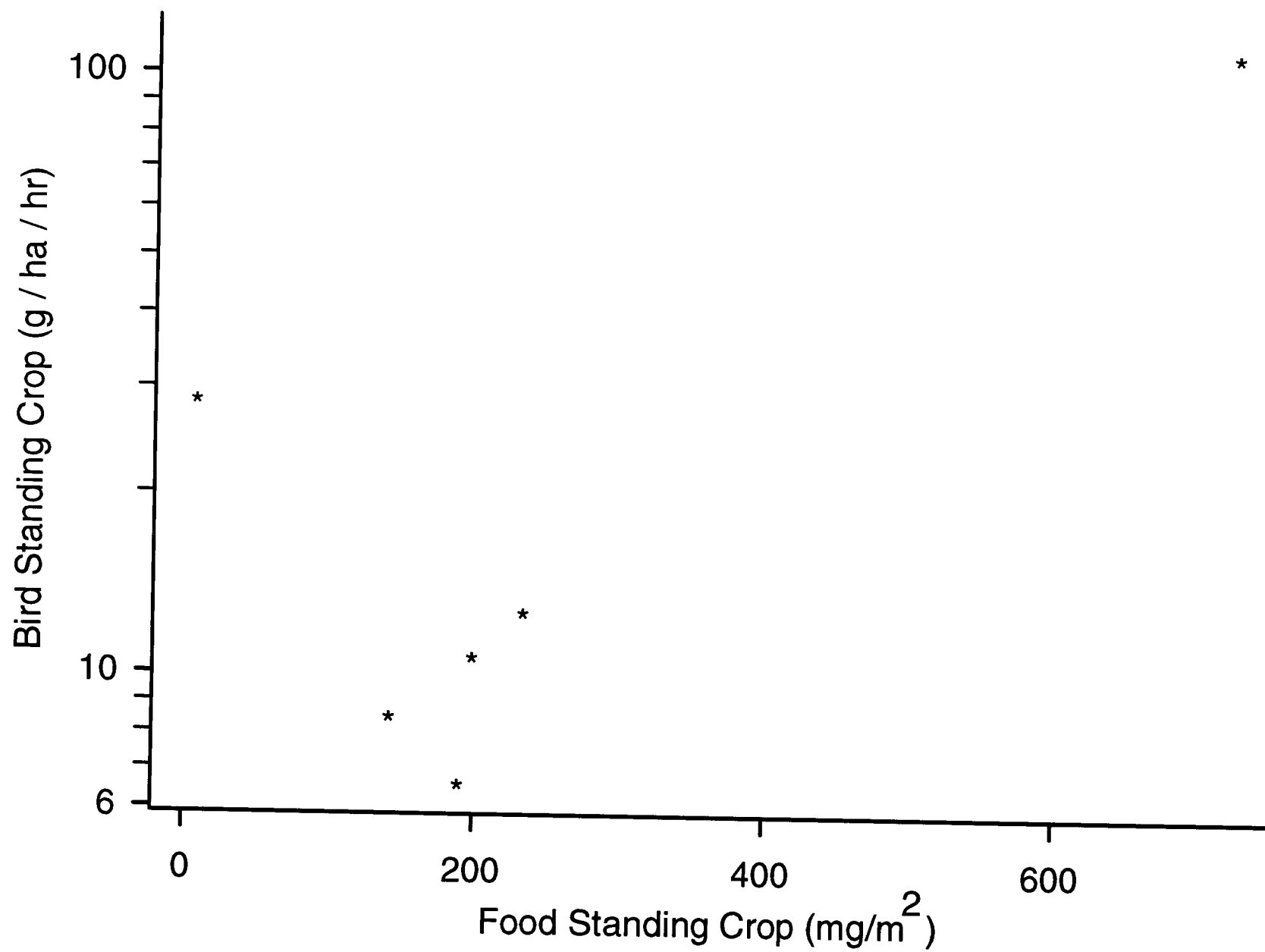


Table 5. Overlap in use of microhabitats quantified as the rate at which observations were misclassified by a discriminant function used to categorize foraging observations according to species on the basis of microhabitat characteristics. Zero error rates are expected if species do not overlap. Error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

Species	Misclassification Rate	
	Percent of observations	Percent 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

Figure 12. Total sparrow abundance and food abundance in three habitats in two years.
Each point represents a single habitat in a single year.



Discussion

Darwin (1859) argued that species replacements along environmental gradients result from interspecific competition. Although there are many examples of such replacements (e.g., Lack 1944, Terborgh 1971, MacArthur 1972), the hypothesis has rarely been tested. I tested several hypotheses that might account for abutting habitat distributions of sparrows, including food, predation, habitat structure and current competition. 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 habitat structure hypothesis was rejected: species used foraging microhabitats that were more widely distributed than the species themselves. I tested for two conditions that are necessary for competition. The fundamental niches of species overlap indicating that competition is indeed possible between them. However, my results regarding food limitation were inconclusive. Competition is the hypothesis most consistent with my results. Here, I discuss alternative hypotheses that might account for the distributions. I also discuss other evidence regarding competition and suggest that the competition hypothesis is worth pursuing by more direct tests.

Other possibilities

I 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 I considered or by abiotic factors which were not considered. Complex interactions among factors are outside the scope of this paper. Here I 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 my study area are in a desert.

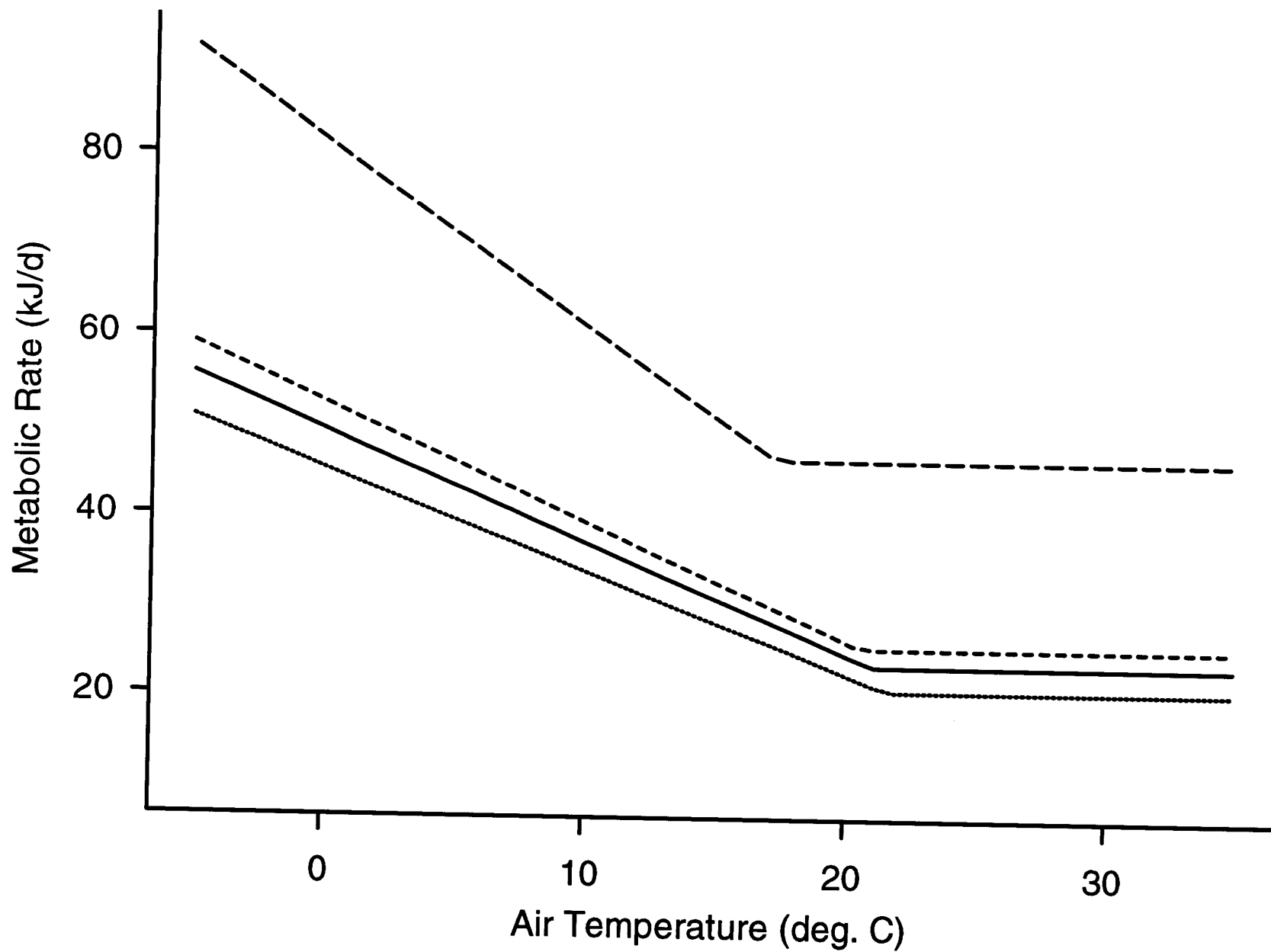
Neither the temperature hypothesis nor the water hypothesis yields the prediction that species are restricted to different habitats. Rather than forming absolute bounds to species distributions, temperature interacts with food and predation to limit distributions (Repasky 1991), modulating food requirements and hence the risks of starvation and predation (McNamara and 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 (Figure 13), 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 favorable 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.

Other evidence

My inferences are based on observation rather than experiment, and thus they are less convincing than experimental results might be. Here, I provide other evidence suggesting that food, predation and habitat structure are unlikely to shape the habitat distributions of sparrows and that the competition hypothesis is consistent with the data.

The results of an introduction experiment (Chapter 2) support my 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 species experienced smaller tradeoffs in feeding

Figure 13. 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 favorable to them. Estimates were based on allometric relationships in the literature: basal metabolic rate (the flat portion of each relationship) was calculated as $3.19M^{0.73}$ where M is body mass in grams (Aschoff and Pohl 1970); the threshold ambient temperature below which additional energy must be spent to maintain body temperature was $T_b - 11.5M^{0.19}$ where T_b is body temperature in degrees Celsius and M is body mass in grams (Weathers and van Riper 1982); the rate at which energy expenditure increases as ambient temperature declines below the threshold temperature is $0.28M^{0.54}$ in kilojoules per day per degree Celsius where M is body mass (Aschoff 1981).



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 my conclusion that species differences in predation risk are unlikely to be responsible for shaping the species' habitat distributions (Chapter 3). Sage sparrows and black-throated sparrows 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 habitat 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.

Do the species actually compete? My data clearly indicate that species share some foods. Although my observational data on food limitation were inconclusive, two other sources of evidence suggest that food is limiting. First, a short-term food addition experiment (Chapter 4) 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 and Dunning 1987).

Second, 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 and 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 and 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 and Repasky 1991). Although the worldwide study included data from the present study site, the pattern is clearly present without those data.

Future tests

On the basis of the evidence above, I suggest that the competition hypothesis is a plausible explanation of habitat partitioning by sparrows. Stronger tests are needed. Direct experimentation is one possibility. In the absence of direct tests, tests of hypotheses about the mechanism of competition would place the competition hypothesis at risk of falsification. Three possible mechanisms are: exploitation of food, behavioral interference and avoidance of habitats in which species suffer a competitive disadvantage.

The mechanism of competition among sparrows is more likely to be interference or avoidance than the exploitation of food. Species share food preferences (Figure 10), and they are expected to have similar distributions. Under these conditions, exploitative

competition would result in habitat partitioning if jointly preferred foods were depleted to the extent that distributions were governed by foods for which species do not share preferences. That is clearly not the case in the present study because species shared preferences for the foods that were present, and they were not distributed as predicted from food availability.

Chapter II

FORAGING SUCCESS

AND THE HABITAT DISTRIBUTIONS OF WINTERING SPARROWS:

A TRANSPLANT EXPERIMENT

Temperate birds are frequently habitat specialists, and adjacent habitats are often occupied by closely related species. Lack (1944) argued that this pattern of distributions results from interspecific competition. He reasoned that morphological differences between species have only minor consequences on fitness in different habitats and that species ought to be more widely distributed among habitats in the absence of congeners. Lack's argument is an attempt to refute the alternative hypothesis that habitat partitioning results from species differences in feeding ability. Although the competition hypothesis has frequently been tested (e.g., Terborgh 1971, Terborgh and Weske 1975, Pulliam 1975, Noon 1981, Garcia 1982, Schluter 1982), the feeding ability hypothesis has seldom been tested explicitly (Schluter 1982, Price 1991, Chapter 1).

Habitat specialization might result from food alone if species are adapted to feeding conditions in alternate habitats (e.g., Smiley 1978, Futuyma and Wasserman 1981, Schluter 1982). The tradeoff in feeding ability between habitats must be large enough to restrict species' distributions. Hence, there are two testable predictions from the foraging success hypothesis. First, a large tradeoff in foraging ability should exist between habitats. Second, each species should achieve its highest food intake rate in a different habitat, and each species should dwell where it is most successful at foraging.

I tested the foraging success hypothesis by comparing the feeding rates of sparrow species "transplanted" among habitats in the Sonoran Desert of southern California. Sage sparrows (*Amphispiza belli*), black-throated sparrows (*A. bilineata*) and dark-eyed juncos (*Junco hyemalis*) spend the winter in different habitats along an elevational gradient (Weathers 1983, Chapter 1). Sage sparrows dwell in a creosote bush-saltbush

(*Larrea tridentata*-*Atriplex* spp.) shrubland on the floor of the valley at the base of the elevational gradient. Black-throated sparrows occupy the creosote bush shrublands (other common species include brittlebush [*Encelia farinosa*], burrobrush [*Ambrosia dumosa*], sweetbush [*Bebbia juncea*], and cactus [*Opuntia* spp.]) located on rocky alluvial fans at the entrances of small valleys and on the rocky, lower slopes of the mountains. Dark-eyed juncos inhabit a woodland of pinyon pine (*Pinus monophylla*) and juniper (*Juniperus californicus*), located on a plateau above the other two habitats.

I carried out a “transplant” experiment because there were few natural opportunities to observe foraging success outside of species’ typical habitats. The advantage of such a manipulation is that observed food intake rates are the net effect of several factors affecting food availability, such as food abundance, vegetation and substrate structure and possibly predation risk (Chapter 1, Chapter 3). By measuring foraging success in the aviary, I tested the predictions from the foraging success hypothesis that large differences in foraging ability should exist between habitats and that species should occupy the habitats in which they forage most successfully. The results did not support the foraging success hypothesis: two species’ food intake rates were relatively similar in all three habitats and may actually be slightly higher outside of the habitats in which each typically occurs.

Methods

Experimental design

The experiment was carried out during the winter of 1988-89 in the vicinity of Deep Canyon Desert Research Center, Palm Desert, California (see Weathers 1983). Study sites in the different habitat types were located on ecological reserve lands along a transect on the north slope of the Santa Rosa Mountains.

Birds used in the study were captured from the wild shortly before the experiment began. They were housed individually and maintained on a mix of seeds commercially available for pet finches, meal worms, water and a vitamin supplement.

Sparrows generally search for seeds on the ground. Food intake rates were estimated by observing individual birds foraging on seeds naturally occurring on the ground inside of an aviary. The aviary measured 4 m x 4 m x 2 m (Figure 14). It was made to be portable by constructing it of wooden frames, each 1 m x 2 m, that could be bolted together. The roof and 14 of the 16 frames were covered with screening that could easily be seen through. The two remaining frames were covered with black fabric to serve as the front of a blind from which observations were made. An apron around the base of the aviary covered gaps between the base and the ground on uneven terrain. Birds entered the aviary from a holding cage attached to a port equipped with a door that could be remotely controlled. Rodent burrows were plugged with rocks to prevent birds from seeking asylum or escape.

Six individuals of each species were introduced singly into all three habitats. They were divided into two lots of three birds each, and lots were tested sequentially. Feeding trials were scheduled according to a design that experimentally controlled the order in which birds experienced habitats because performance might change as experience in the aviary increases. One individual in each lot of birds experienced each habitat as the first, second and third habitat in the aviary (Figure 15). Trials could not be carried out simultaneously in the three habitats, preventing experimental control of seasonal changes in foraging conditions beyond that afforded by dividing the birds into two lots. Hence, trials did not follow a standard cross-over design (see Mead 1988). Instead, habitat visits were scheduled to minimize the number of times that the aviary would be moved between habitats. For example (Figure 15), the aviary was located in habitat "a" where the first individual was tried. It was then moved to habitat "b" where the first and second individuals were tried. All three individuals were tried in habitat "c", and then the aviary was returned to habitats "a" and "b" to complete the trials of the second and third individuals. Habitats were randomly assigned to the visitation sequence. Individual birds were randomly designated as the first, second and third

Figure 14. Floor plan of aviary.

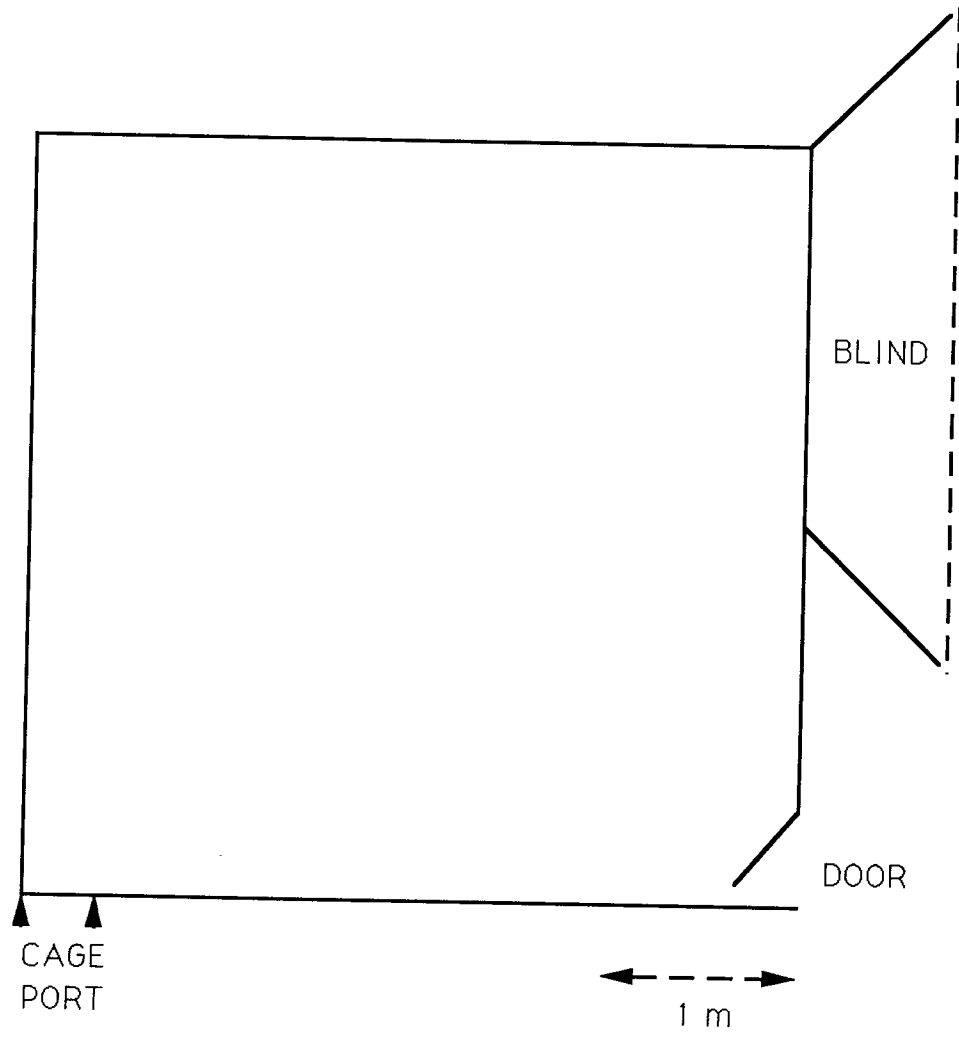
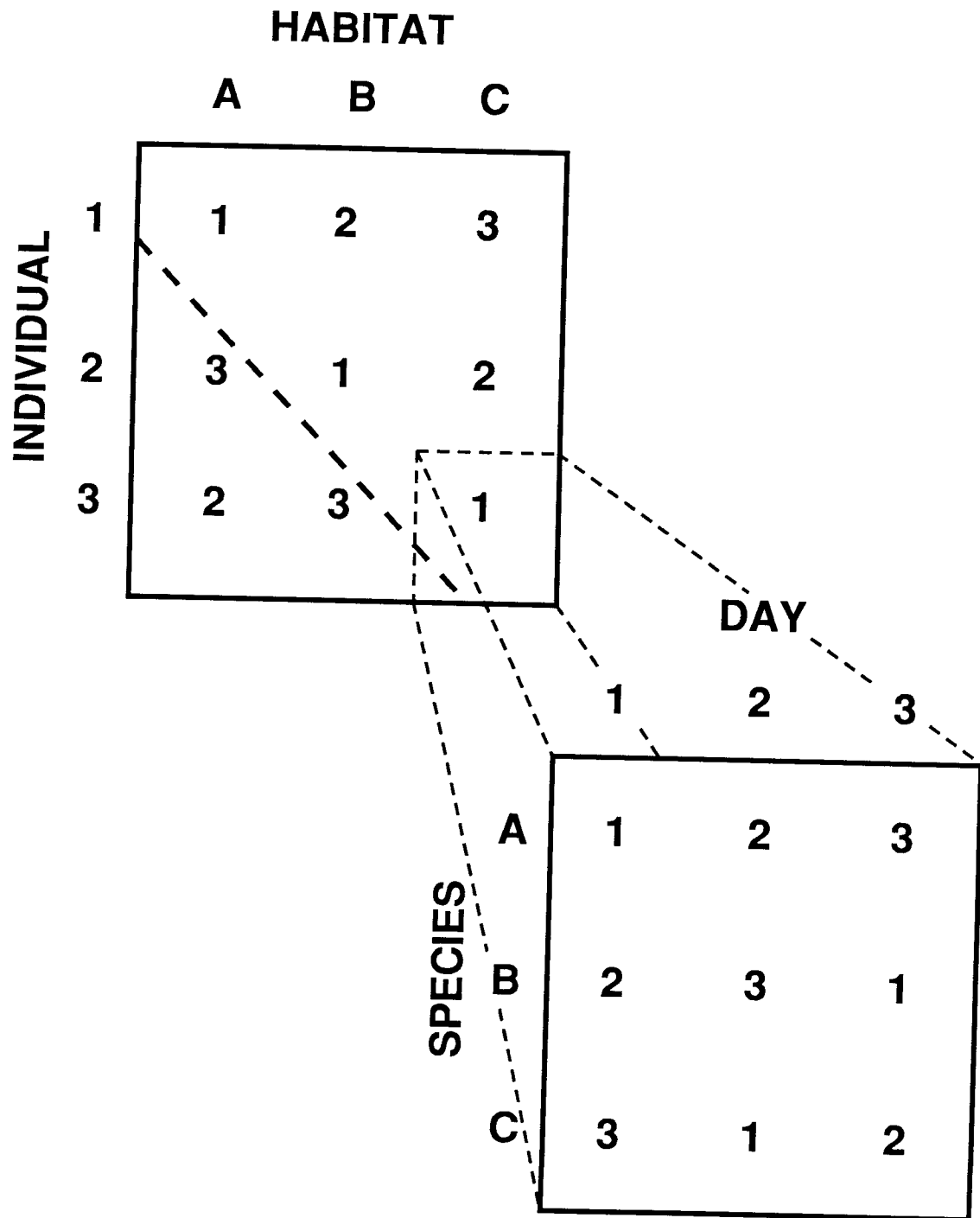


Figure 15. One block of the experimental design. Three individuals of each of three species were tried in three habitats. In the upper left box, numbers within rows represent the order in which individuals (regardless of species) were tried in habitats. The average amount of previous experience in the aviary is constant among habitats. Habitats were visited in the order “A”, “B”, “C”, “A”, “B”. The dashed diagonal line separates trials completed during the first visit to a habitat (above) from those completed during the second visit to a habitat (below). The lower right box is an example of how depletion was experimentally controlled during a visit to a habitat. Numbers within columns represent the order in which species were tried on any one day. Each species experienced equal amounts of depletion over a three day visit.



individuals of their species.

Each bird was introduced into the aviary for two 30-minute trials on each of three successive days during a visit to a habitat (Figure 15). Each day yielded an independent observation of an individual's foraging ability in a habitat because the aviary was moved to a new location each day. Birds were fasted for an hour before the first trial and for an hour between the two trials.

On any one day, one individual of each species was tested in the aviary (Figure 15). To experimentally control for possible depletion of food through the day, all birds were subjected to the same amount of it. This was accomplished by ensuring that an individual bird was the first bird in the aviary on one of the three successive days of trials, the second bird in the aviary on one day and the third bird on the remaining day (Figure 15). The particular sequence (first, second or third) was random. Comparisons of food intake rates between the first and second foraging trials of individual birds on the same day indicated that depletion throughout a day was undetectable.

Food intake rate

I was unable to estimate seed intake rates directly because I could not identify from a distance all of the seeds eaten, especially small ones. Instead, I obtained estimates of intake rates by recording the rate at which birds pecked at items on the ground or on plants, and multiplying this rate by the mean mass of seeds eaten. This calculation is an overestimate because it assumes that each peck yields a seed, whereas this assumption may not be true. For example, grass seeds are often enclosed in a set of bracts, but a set of bracts picked up from the ground or from a plant may not contain any seeds. Also, seeds may be spoiled or empty, and subsequently rejected. Hence, I also obtained a lower estimate of intake rate by assuming that birds are unable to determine beforehand whether items picked up are edible. From soil samples, I estimated the proportion of potential food items (seed cases, bracts, etc.) on the ground containing edible seeds. This proportion was multiplied by the upper estimate

of intake rate to obtain a lower bound on food intake rate that assumes birds did no better than chance at picking up good seeds. Results from the two estimates were nearly identical, and I present only the upper estimates here.

Variance in food intake rate was calculated by accumulating the variances of peck rate, probability of obtaining a seed, and mean seed size. The variance of the product of two variables was

$$VAR(A \cdot C) = VAR(A)VAR(C) + \bar{x}_A^2 VAR(C) + \bar{x}_C^2 VAR(A)$$

(Bickel and Doksum 1977), where, for example, A is peck rate and C is size of seeds eaten. Standard error was calculated as the square root of variance.

Peck rate.— An observer in the blind used a microcomputer programmed as an event recorder to register the time at which a bird began to forage, each peck at a potential food item made by the bird, and the time at which a bird ceased to forage. Peck rate was calculated as the total number of pecks divided by total time spent foraging during a half-hour trial. Peck rates from the two half-hour trials in a day were averaged.

Number of seeds per peck.— I estimated the proportion of pecks that might yield edible seeds. I collected seeds from quadrats placed in patches of high seed density. Seeds were collected from plants, and the surface soil was scraped to a maximum depth of 1 cm from an area of 0.125 m² (see Chapter 1). Seeds were assumed to be edible if they made an audible crack when crushed using a pair of forceps.

Size of seeds eaten.— Mean mass of seeds eaten by experimental birds was estimated by two methods. In the first, data on seeds consumed by birds foraging in the aviary were combined with prior expectations of seed size based on data from wild-caught birds. Estimates of mean seed size obtained by this method were potentially frail because of small sample sizes. The second method provided a way of judging the robustness of the first. A function describing seed size preference was calculated from

data on wild-caught birds and data on seed abundance, and it was used to predict diet composition in novel habitats. Mean seed size was calculated from these predicted diets.

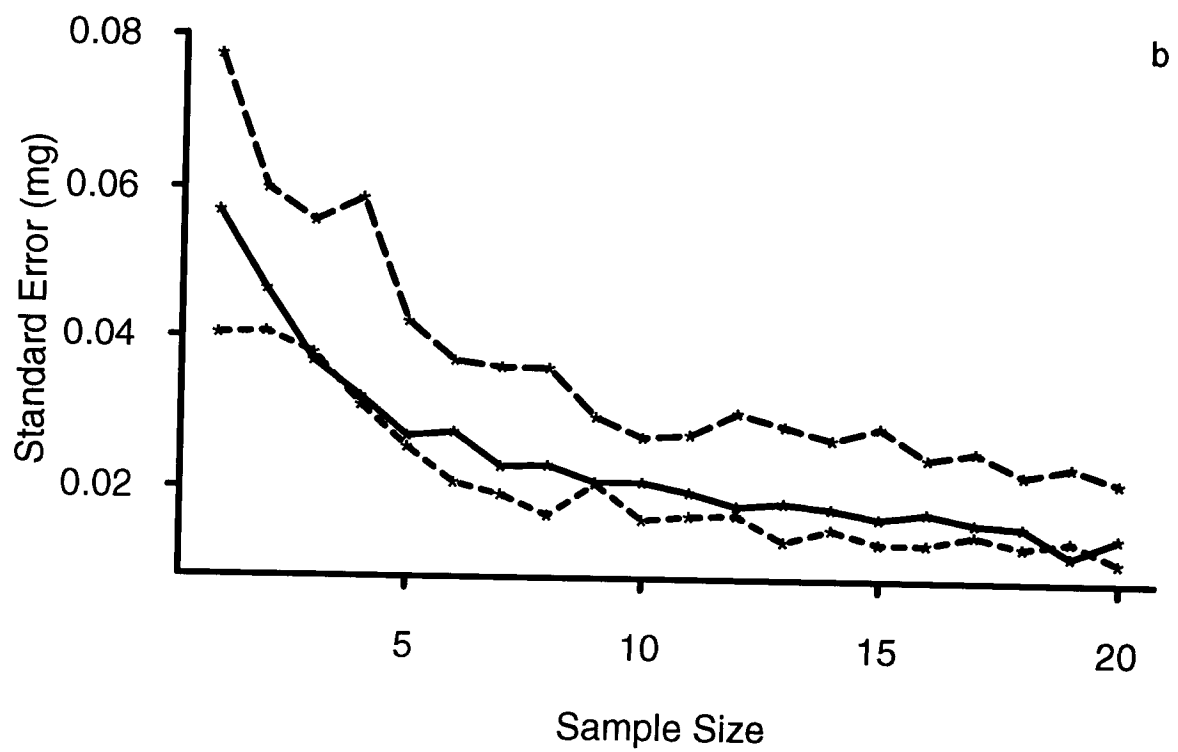
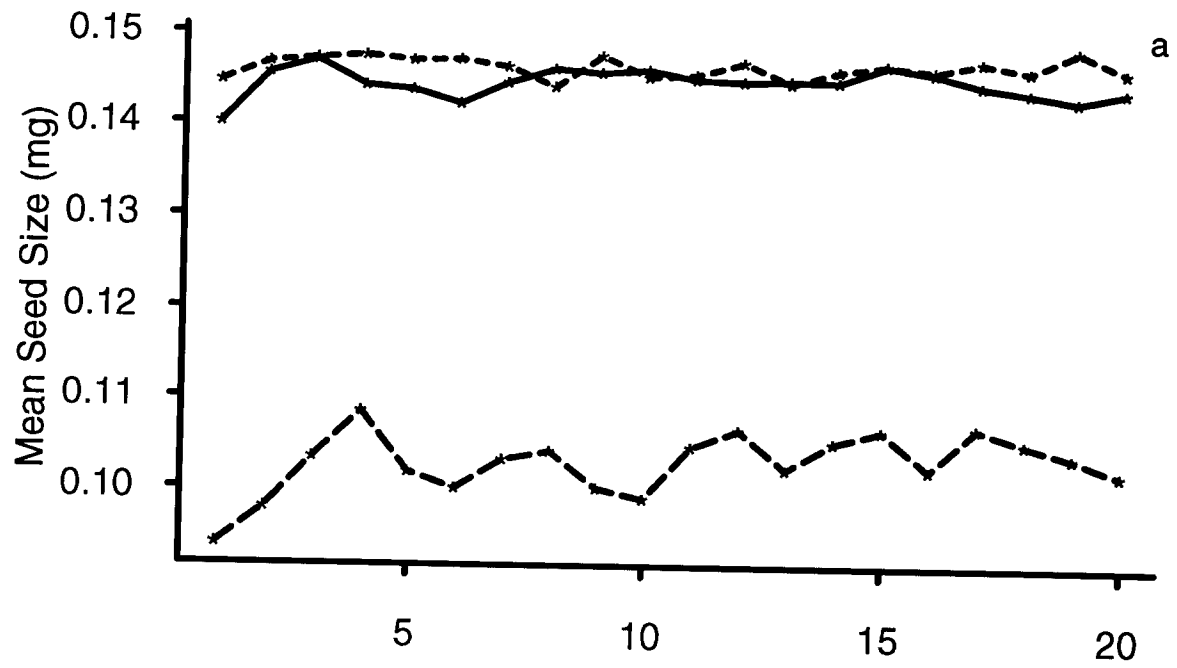
A sample of seeds eaten was obtained by administering the emetic apomorphine (see Schluter 1988b) to each bird after its final trial in the aviary. Vomit samples were obtained only after the final trial to avoid the possibility that birds might develop an aversion to foraging in the aviary. Hence, apomorphine was administered to two birds of each of the three species in each habitat type. Not all birds vomited with the result that $n = 12$ birds rather than $n = 18$. Despite these small sample sizes, mean seed size could still be estimated. Rarefaction analysis of mean seed size as a function of the number of wild birds sampled suggests that an unbiased estimate requires sample sizes of 3 to 5 birds (Figure 16).

I used a Bayesian estimate of mean seed size in which prior expectations of mean seed size obtained from field data were modified on the basis of samples obtained from birds foraging in the aviary. The posterior estimate of mean seed size was

$$\mu' = \frac{\frac{\mu}{s^2} + \frac{n\bar{x}}{\sigma^2}}{\frac{1}{s^2} + \frac{n}{\sigma^2}}$$

(see Stephens and Krebs 1986:77) where μ and σ^2 are the prior expectations of the mean and variance in seed size, \bar{x} and s^2 are the sample mean and variance, and n is sample size. μ and σ^2 were estimated from vomit specimens obtained from wild-caught birds during another portion of the project (Chapter 1). They provide only rough expectations of the mean and variance of seed size eaten in novel habitats because they are obtained from birds foraging only in their preferred habitat. \bar{x} and s^2 were calculated from the vomit specimens obtained from birds after they had foraged in the aviary. Theoretically, this method should yield an unbiased estimate of mean seed size. s^2 is based on the assumption that each seed eaten by an individual bird is an independent observation. This assumption was tested using an analysis of variance

Figure 16. Bootstrap estimates of mean (a) and standard error (b) of mean seed size in the diet as a function of sample size. Sage sparrow (— — — — —), black-throated sparrow (—————), and dark-eyed junco (— — — — —). Each point represents 200 repeated samples of vomit specimens from wild-caught birds.



of mean seed size eaten by wild-caught birds. Variance in seed size within a single vomit specimen of a given bird was at least as large as the variance between specimens suggesting that the assumption is valid.

Variance of seed size in the diet was estimated as

$$\sigma^{2'} = \frac{1}{\frac{1}{s^2} + \frac{n}{\sigma^2}}$$

(see Stephens and Krebs 1986:77) where σ^2 is the prior expectation of variance, s^2 is the sample variance, and n is sample size as for μ' .

The above method yielded an unreasonably large estimate of the size of seeds eaten by black-throated sparrows on the valley floor. Prior expectations of the mean (μ) and variance (σ^2) were large because black-throated sparrows eat a wide variety of seeds on the alluvial fan. Only small seeds were eaten on the valley floor, and as a result the sample mean and variance both were small. The sample variance was so small that a sample of at least 250 vomit specimens would have been necessary to bring the Bayesian estimate of the mean μ' to within 130 percent of the sample mean. Seeds of the size μ' were extremely rare on the valley floor, and they are large enough that I should have been able to observe birds eating them. Hence, I discarded μ' and used the sample mean.

Two other estimates of mean seed size in the diet could not be obtained by the method described above because both birds of a species failed to vomit. For sage sparrows foraging on the valley floor, I used the mean seed size in the diets of wild-caught birds because sage sparrows inhabit the valley floor. Observations of sage sparrows foraging in the aviary suggested that they ate mostly *Schismus barbatus* and *Cryptantha* spp., just as they do in the wild. Black-throated sparrows failed to vomit after foraging in pinyon-juniper habitat. Field notes made after each foraging trial suggested that black-throated sparrows foraged similarly to juncos, eating mostly *Bouteloua aristidoides*, although they occasionally picked up larger seeds, but less

frequently than sage sparrows did. Therefore, I used the mean size of seeds eaten by juncos (\bar{x}) to estimate μ' for black-throated sparrows. This estimate should be conservative because it probably underestimates seed size in the habitat in which intake rates were posited to be highest (see Chapter 1).

A second method of estimating the mean size of seeds in the diet was employed because of the small sample sizes associated with the Bayesian estimates. In the second method, preferences for seeds of a variety of sizes were calculated by dividing percentage seed abundance in the diet by percentage seed abundance in the environment. A small constant was added to seed availability to avoid division by zero. The effect of this was that seeds of sizes not available for consumption assumed preference value zero. Preferences were then multiplied by seed availability to predict diets in novel habitats. From the predicted diet, the mean size of seeds eaten in a habitat was the sum of seed mass weighted by numerical abundance in the diet.

Distributions of seed sizes in diets and of seed sizes available in habitats were described from data collected during winters prior to the present experiment (see Chapter 1). Briefly, seeds in randomly located quadrats on the ground and in vomit samples collected from mist-netted birds were identified to species and counted. Frequency distributions of seed mass were generated using a nonparametric probability density function (Becker et al. 1988). The description of a distribution consists of an array of coordinate data points in which x is seed size and y is an index of relative abundance. Abundance values were scaled to sum to 1. Calculations were made by performing arithmetic operations on abundance values at the same value of seed size.

Standard error of mean seed size was calculated by a bootstrap method (Efron 1982). Mean seed size was calculated in the manner described above 200 times, each time from a random sample of the vomit specimens and a random sample of seed quadrats. The standard deviation among the means was taken as the standard error of seed mass.

Comparisons

Comparisons of food intake rates among habitats were made by calculating 95-percent confidence intervals of the difference in mean food intake rate between habitats. This tack of analysis was taken because peck rate, the proportion of pecks yielding seeds, and mean seed size were collected from different sampling units. Peck rates of individual birds were observed in a manner appropriate for a repeated measures analysis of variance, whereas estimates of seed size and the proportion of pecks that yield seeds were unavailable for individual birds. Only one estimate of mean seed size eaten was available for each species in each habitat, and one estimate of the proportion of pecks yielding seeds was made for each habitat. Hence, there was only one independent observation of food intake rate and its variance for each species in each habitat. Habitats were compared by calculating 95-percent confidence intervals of the difference between the means. Differences were considered to deviate significantly from zero if zero fell outside of the confidence intervals. Confidence intervals were approximated as the mean food intake rate ± 2 SE.

*Results**Food intake rates*

Seed intake rates in habitats were determined primarily by the sizes of seeds eaten. Peck rate (Table 6) and the fraction of pecks that yield seeds (Table 7) were consistently highest on the valley floor, but seed intake rates there were never higher than in other habitats (Table 1). The proportion of pecks that yielded seeds had little influence on estimated intake rates or comparisons of food intake rates between habitats, and it is not included in the food intake rates presented here (Table 6, Figure 17). Estimates of seed size made by the two different methods (Table 6) were correlated ($r = 0.72$, $n = 9$, $P = 0.03$), and conclusions based on the results are the same regardless of which method is used. Results from both methods are presented in Table 1 and in Figure 17. Hereafter, I focus on results from data collected from birds

Table 6. Performance of captive sparrows foraging in an aviary for naturally occurring seeds. Entries are means (SE).

Method 1: seed mass estimated from vomit samples from birds foraging in the aviary. Method 2: seed mass estimated from preference data. Intake rate is the product of peck rate and seed mass. Entries in bold type are from the habitat that a species occupies. See Methods for details.

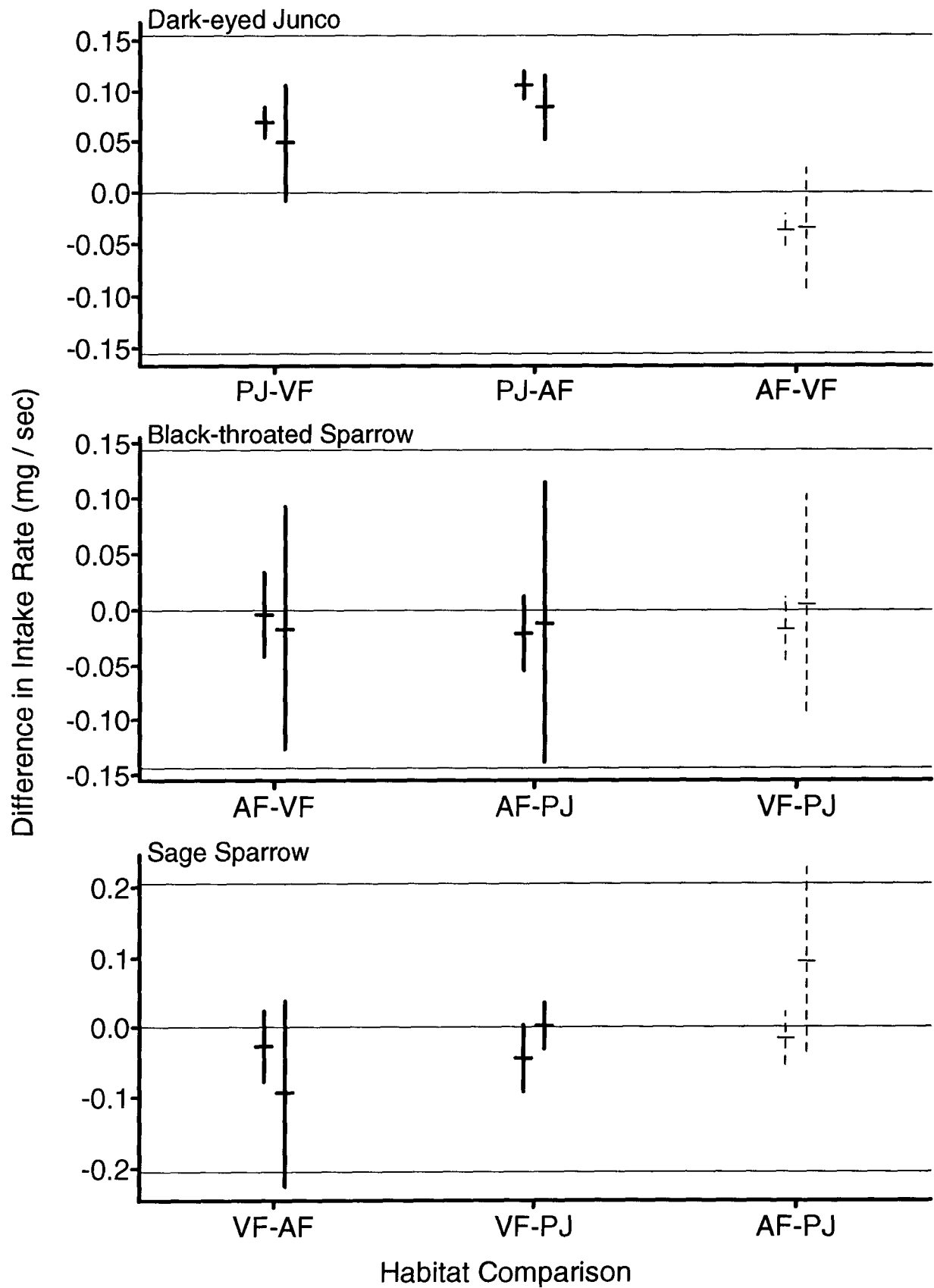
Species	Habitat	Peck Rate (pecks / s)	Seed Mass		Seed Intake Rate	
			Method 1 (mg)	Method 2 (mg)	Method 1 (mg/s)	Method 2 (mg/s)
Dark-eyed Junco	Pinyon-juniper	0.99 (0.03)	0.16 (<0.01)	0.16 (0.01)	0.16 (0.01)	0.15 (0.01)
	Alluvial Fan	0.52 (0.05)	0.09 (<0.01)	0.13 (0.02)	0.05 (0.01)	0.07 (0.01)
	Valley Floor	1.08 (0.07)	0.08 (<0.01)	0.10 (0.02)	0.09 (0.01)	0.10 (0.03)
Black-throated Sparrow	Pinyon-juniper	0.76 (0.04)	0.15 (0.01)	0.11 (0.01)	0.11 (0.01)	0.14 (0.04)
	Alluvial Fan	0.60 (0.04)	0.15 (0.02)	0.21 (0.08)	0.09 (0.02)	0.13 (0.05)
	Valley Floor	1.23 (0.07)	0.08 (0.01)	0.12 (0.02)	0.10 (0.01)	0.14 (0.03)
Sage Sparrow	Pinyon-juniper	0.67 (0.05)	0.22 (0.01)	0.16 (0.02)	0.14 (0.01)	0.11 (0.01)
	Alluvial Fan	0.70 (0.06)	0.18 (0.01)	0.29 (0.09)	0.13 (0.01)	0.20 (0.07)
	Valley Floor	1.18 (0.06)	0.09 (0.02)	0.09 (0.01)	0.10 (0.02)	0.11 (0.01)

Table 7. The fraction of potential food items that yields edible seeds, estimated by gathering seeds and squashing them.

Habitat	Edible Fraction of Seeds	
	p	Standard Error

Pinyon-juniper	0.69	0.02
Alluvial Fan	0.61	0.02
Valley Floor	0.80	0.01

Figure 17. Differences in foraging success between habitats ± 2 SE. Bold, solid symbols depict differences between habitats occupied by a given species and unoccupied habitats, calculated as (occupied habitat) – (unoccupied habitat). Light, dashed symbols depict differences between the two habitats not occupied by the given species. Habitat symbols: “PJ” pinyon pine-juniper woodland, “AF” alluvial fan, “VF” valley floor. Two estimates of each difference in foraging success are presented, based on the two methods of estimating mean seed size (Method 1 and Method 2, respectively).



foraging in the aviary (method 1) because they are less variable than results from seed preference data.

Habitat comparisons

Under the foraging success hypothesis, large differences in foraging success are predicted between habitats. Only dark-eyed juncos experienced a large and significant difference in foraging success between habitats (Figure 17). Juncos foraging on the alluvial fan ingested seeds at only 31 percent of the rate that they did in pinyon-juniper. On the valley floor they ingested seeds at 56 percent of the rate in pinyon-juniper. However, sage sparrows and black-throated sparrows showed similar differences in food intake rates between habitats. Sage sparrows on the valley floor consumed seeds at 71 percent of the rate in pinyon-juniper. On the alluvial fan, they consumed seeds at 93 percent of the rate in pinyon-juniper. Black-throated sparrows outside of pinyon-juniper consumed seeds at 82 to 91 percent of the rate that they did in pinyon-juniper.

A second prediction of the foraging success hypothesis is that species forage most successfully in different habitats and dwell in the habitats in which they are most successful. Only dark-eyed juncos achieved higher food intake rates in the habitat that they occupy than in other habitats (Table 6, Figure 17). It was unclear whether sage sparrows and black-throated sparrows are most successful at feeding in their usual habitats because both species exhibited small differences in seed intake rates between habitats relative to error (Figure 17). However, differences in mean seed intake rate between occupied and unoccupied habitats were zero or negative. This suggests that at best sage sparrows and black-throated sparrows gain only a slight feeding advantage by dwelling in the habitats that they occupy or, at worst, that they might suffer a disadvantage.

Discussion

I tested the hypothesis that nonoverlapping habitat distributions of sparrow species result from species' differences in foraging ability. This hypothesis can explain habitat

partitioning only if foraging ability can account for: why species prefer some habitats over others, why species distributions are restricted, and why each species occurs alone. Here, I summarize why the foraging success hypothesis fails on all three counts.

Under the foraging success hypothesis, habitat preferences should result from differences in feeding ability between habitats. Only one of the three species, dark-eyed junco, clearly experienced large significant differences in food intake rate between habitats. Sage sparrows and black-throated sparrows exhibited very similar foraging success in all three habitats. Are these differences in foraging success sufficient to restrict species habitat distributions? Juncos feeding outside of pinyon-juniper experienced food intake rates that were 30 percent to 60 percent of those inside pinyon-juniper. Such large disadvantages to foraging outside of pinyon-juniper are sufficient to explain why juncos are restricted to this habitat. Sage sparrows and black-throated sparrows clearly are not doomed to low foraging success outside of their usual habitats, but it is less certain whether such small differences in foraging ability between habitats may be sufficient to restrict their habitat distributions.

Insights from the theory of habitat selection and comparative data from other populations suggest that the sparrows that I studied would be more broadly distributed if food alone shaped their distributions. Theoretically, species could specialize on single habitats despite only slight tradeoffs in fitness between habitats. The difference in foraging success between two habitats at which a population switches from being a habitat specialist to a generalist depends upon population size and the rate at which feeding rate decays as population density increases (Fretwell and Lucas 1970, Fretwell 1972). A species might remain a specialist for either of two reasons: foraging rate is independent of population density or population density is low. However, neither of these conditions is likely to be true for sparrows. Feeding rates of sparrows decline as flock size increases (e.g., Caraco 1979) suggesting that foraging success is likely to decline as population density increases. Also, food appears to limit population density

during winter (Chapter 4) suggesting that intraspecific competition for food might be sufficient to force species into less than ideal habitats when habitats differ only slightly in foraging success.

Comparative data from other species also suggest that sparrows would be generally distributed if food shaped their distributions. Abundances of Galápagos ground finches (*Geospiza* spp.) in habitats are roughly proportional to food abundance along an elevational gradient (Schluter 1982). A habitat having half of the food of another has approximately half of the finch density of the other. In my study area, however, species' population densities are near zero outside of the habitats in which they are most abundant despite the presence of suitable foraging conditions in those habitats (see also Chapter 1). Hence, differences in foraging success between habitats are unlikely to be responsible for habitat specialization and habitat partitioning by sparrows.

Finally, different species must achieve their highest food intake rates in different habitats if foraging ability is to account for habitat partitioning. Because the species that I studied live in different habitats, each species should be most successful foraging in the habitat that it occupies. This prediction was not fulfilled. Although juncos clearly achieved higher feeding rates in the habitat that they occupied than in other habitats, sage sparrows and black-throated sparrows actually experienced slightly higher food intake rates in habitats other than those that they occupy. One of two conclusions follows from this result: either sage sparrows and black-throated sparrows are absent from the habitats in which foraging success is highest, or differences in foraging ability between habitats are minor, suggesting that species might be more widely distributed.

Conclusions from other studies of the role of food in shaping species distributions vary in the importance attributed to food. Food is not responsible for habitat partitioning by warblers (*Phylloscopus* spp.) breeding along an elevational gradient (Price 1991). Species specialize on forest habitat types (conifers vs. hardwoods) even though their foods are equally abundant in both habitat types. Also, individual birds

in transition areas between forest types readily forage in both types of trees. Among Galápagos ground finches, however, food explains species' distributions along an elevational gradient (Schluter 1982). Species' distributions corresponded closely with the distributions of their foods.

Obviously, food must play some role in shaping species distributions: species can live only where the food supply is sufficient for survival. The absence of species from areas in which food supply is adequate warrants explanation. What other factors might explain habitat partitioning by sparrows in the present study? In my work, I have addressed these: vegetation and substrate structure, predation, and interspecific competition (Chapter 1). Structural features of habitat might affect the ability of birds to search for food. Predation risk might affect food intake rates because of a tradeoff between feeding and scanning for predators (McNamara and Houston 1986, 1987, Chapter 3). However, foraging success should depend on both habitat structure and predation risk and hence both were incorporated in my test of the foraging success hypothesis. The aviary enclosed low vegetation, rocks and leaf litter that might influence foraging success. Also, sparrows in the aviary responded to birds of prey outside of the aviary, and predators occasionally attempted to attack sparrows inside the aviary. The failure of the foraging hypothesis suggests that the effects of habitat structure and predation risk on foraging success are too weak to account for habitat partitioning.

In a separate paper, I test more directly the hypothesis that predation risk itself could be responsible for habitat partitioning if species are safest in different habitats and risk is severe, but consistency in species' vigilance patterns between habitats suggests that this is unlikely (Chapter 3).

Finally, there is the competition hypothesis. My results support Lack's (1944) argument that species' differences in fitness between habitats are generally small and unlikely to be responsible for species distributions. The most conspicuous factor that

might restrict species' distributions is competition from ecologically similar species. Other indirect evidence suggests that current competition is possible among the species. The species share estimated preferences for the same foods, and they forage in similar microhabitats (Chapter 1). Finally, food appears to limit population density during winter, and the species are capable of depleting the amount of resources available to one another (Chapter 4). In view of this evidence, more direct tests of the competition hypothesis are desirable.

Chapter III

PREDATION, FOOD, VIGILANCE
AND THE HABITAT DISTRIBUTIONS OF WINTERING SPARROWS

Instances in which predation restricts the distributions of individual species are well known (e.g., Werner et al. 1983, Werner and Gilliam 1984, Aronson 1989). More interesting are situations in which predation affects the distributions of more than one prey species, shaping community structure. For example, prey species might segregate by habitat if they are safest in different habitats and the risk of predation is severe. A morphological characteristic that renders a species safe in one habitat may place it at risk in others, and species may occupy different habitats because they are safest in different habitats. This mechanism has received little attention in the literature, although it has been demonstrated among limpets (Mercurio et al. 1985). Limpet shells having undulate edges are well suited to irregular rock surfaces and poorly suited to flat rocks where the undulations can be used by predators to dislodge the limpet. Shells with smooth, flat edges are well suited to smooth flat substrates and poorly suited to irregular rock surfaces. This type of tradeoff in safety between habitats diminishes or eliminates competition between species that use similar resources. Alternatively, several prey species might all be safest in the same habitat (e.g., Mittelbach 1984, Longland and Price 1991), and predation could intensify competition if all prey species are forced into it to avoid predators (Mittelbach 1984).

Some data exist to suggest that predation might shape the habitat distributions of birds. Pulliam and Mills (1977) showed that granivorous bird species that use different methods of escaping predators dwell in different habitats. Species that forage close to vegetative cover and flee to it are safest there and at greater risk farther from cover (Watts 1990). Species that feed in open habitats, far from cover, and fly far away from danger approach vegetative cover reluctantly, suggesting that they may be at greater

risk close to cover than away from it (Lima 1990). Hence, species that escape predators by different methods may actually be safest in the habitats that they occupy.

Here, I test the hypothesis that tradeoffs in predation risk between habitats are responsible for habitat partitioning among three species of wintering sparrows along an elevational gradient in the Sonoran Desert of southern California. Although they live in different habitats, sage sparrows (*Amphispiza belli*), black-throated sparrows (*A. bilineata*), and dark-eyed juncos (*Junco hyemalis*) respond to predators similarly by fleeing into woody vegetative cover. All three species forage closer to cover than predicted by food availability (Chapter 1). I tested the hypothesis (1) that each species is safest in its preferred habitat against the alternative hypothesis (2) that all species are safest in the same habitat. I measured rates at which species scanned the environment, vigilance, and compared qualitative changes in vigilance levels of individual birds between habitats using an experimental enclosure. I predicted that if hypothesis (1) is true species should exhibit differences in vigilance between habitats. Furthermore, some species should increase vigilance when moved from one habitat to another whereas other species should decrease vigilance because predation risk increases for some species and declines for others. In contrast, hypothesis (2) predicts either similar levels of vigilance, or similar changes in vigilance when species are moved between habitats because they experience similar changes in risk between habitats. These predictions are derived in detail in the next section.

In the course of testing the above two hypotheses, I also tested a prediction stemming from the theory of vigilance that has not been tested previously in the wild. Vigilance for predators is assumed to occur at the expense of food intake, and the amount of vigilance that maximizes survival depends upon both the risk of being killed by predators and the risk of starving (McNamara and Houston 1986, 1987, Lima 1987b). Predictions of the theory of vigilance have been tested by measuring changes in vigilance in response to changes in factors that should affect predation risk (e.g., Lima

1987a, Lendrem 1983). Predictions of how vigilance should respond to changes in food abundance have not been tested.

My results support the prediction that food abundance affects vigilance. They also support the hypothesis that species perceive similar changes in predation risk between habitats, suggesting that tradeoffs in safety between habitats are not responsible for habitat partitioning among wintering sparrow species.

Predation, vigilance and starvation

To test the hypothesis that predation shapes species distributions, I test predictions of how predation risk and vigilance should change between habitats. Vigilance levels can be assessed by moving individual birds between habitats and recording the amount of time that they scan the environment. If species exhibit the same increase or decrease when moved from one habitat to another, I conclude that all species rank the two habitats similarly by the threat of predation. In this case, predation can not account for habitat preferences. If on the other hand, some species exhibit an increase in vigilance and others a decrease in vigilance when moved from one habitat to another, I conclude that species rank habitats differently and that predation could account for species distributions.

Here, I briefly describe the components of predation risk and how increased risk of different aspects of predation results in conflicting predictions of vigilance. I also describe how consistency in changes in vigilance between habitats can be used to infer that species perceive similar changes in the risk of predation between habitats.

Factors contributing to predation risk include: the probability of being attacked, the probability of discovering an attack, and the probability of escaping an attack given that it has been discovered. The effects of each of these factors on vigilance has been modelled by Lima (1987b). Probability of attack is represented by attack rate. Probability of discovering an attack is represented by the amount of time required for the predator to reach the prey once it has begun to attack: shorter attack times

result in lower probability of detecting an attack for any level of vigilance. Finally, the conditional probability of escaping an attack can be represented by the distance from cover: a bird that flees to cover is less likely to escape from a predator the farther it is from cover. If only one component of predation risk varies between habitats, effects on vigilance depend upon which component varies. Increased probability of attack should result in increased vigilance (Figure 3b in Lima 1987b). Decreased probability of detecting a predator should result in decreased vigilance (Figure 3a in Lima 1987b). Decreased probability of escaping an attack can result in either increased or decreased vigilance depending on the probability of being attacked: vigilance increases at high attack rates and declines at low attack rates (Figure 3b in Lima 1987b). All three of these factors probably vary between habitats, hampering the prediction of changes in vigilance. Hence, it is difficult to use observed changes in vigilance between habitats to make inferences about how predation risk varies between habitats. However, species can be expected to exhibit similar changes in vigilance rates between habitats if they are subjected to similar changes in predation risk. This is the prediction that I test.

Both food abundance and predation risk can theoretically affect vigilance levels. Hence, it is necessary to take into account differences in food abundance between habitats if meaningful comparisons of vigilance are to be used to test hypotheses about variation in predation risk between habitats. If vigilance and feeding are exclusive activities, the risk of being killed by predators is traded against the risk of starving to death (McNamara and Houston 1986, 1987, Lima 1987b). A bird that ignores the threat of predation risks being killed whereas a bird that is constantly vigilant risks starvation. Both risks can be described as functions of the amount of time spent vigilant, and the optimal level of vigilance is that at which the decrement in predation risk as vigilance increases is offset by an equal increment in the probability of starving (McNamara and Houston 1987).

How might changes in food abundance affect vigilance? A change in food abundance alters the probability of starving at any level of vigilance and is represented as a shift in the curve describing the risk of starvation as a function of vigilance (Figure 18). The resulting change in vigilance depends upon how the starvation curve is shifted. No change in vigilance is expected if the new starvation curve is parallel to the old one. A decrease in vigilance is expected if the slope of the starvation curve increases whereas an increase in vigilance is expected if the slope decreases (Figure 18).

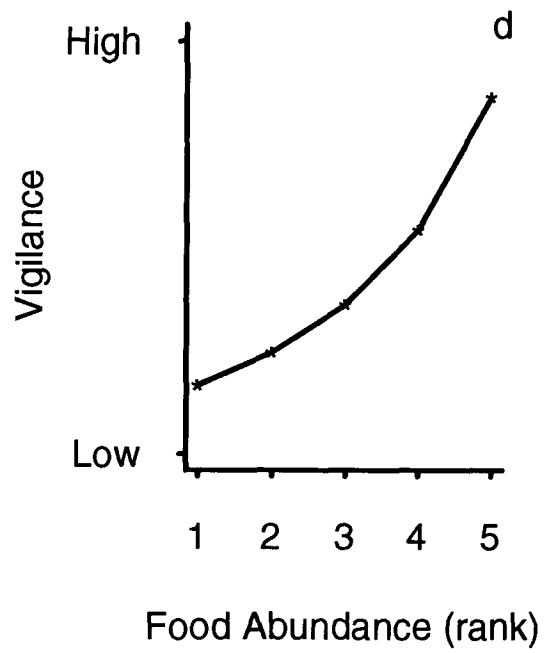
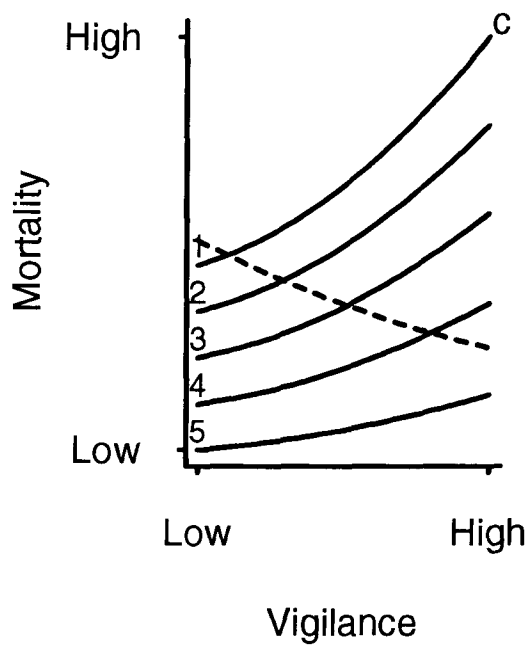
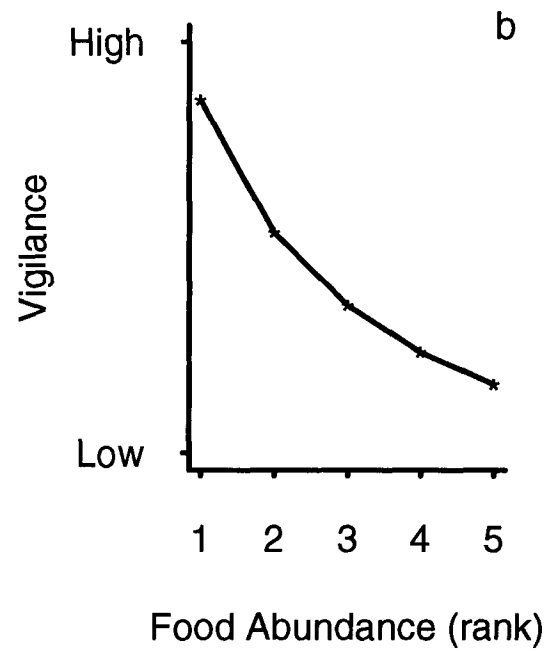
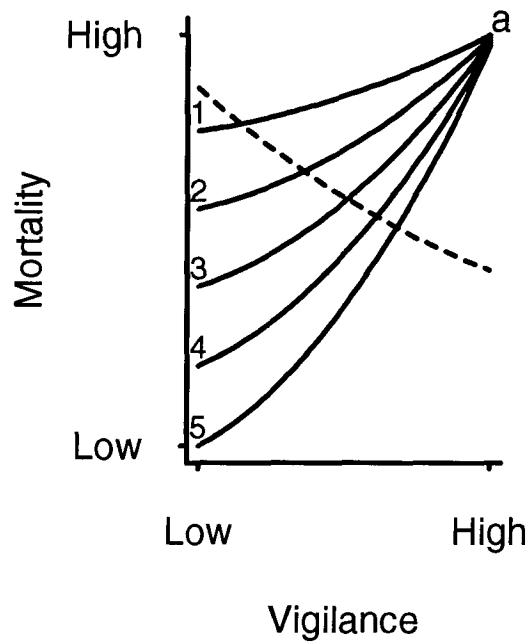
Because food abundance should affect vigilance, changes in food supply between habitats could produce changes in vigilance that are not attributable to differences in predation risk between habitats. Alternatively, changes in food supply could mask changes in vigilance resulting from differences in predation risk. One method of controlling for changes in food abundance between habitats is to describe the relationship between vigilance and food abundance within habitats and then ask whether differences in vigilance between habitats are greater or less than would be expected from the amount of food available. I accomplished this using analyses of covariance. The process of analytically controlling variation in food abundance is itself a test of the prediction from vigilance theory that food abundance affects vigilance level.

Methods

The experiment was carried out in a portable aviary placed over natural vegetation in habitats. The aviary measured 4 m x 4 m x 2 m and was constructed of wooden frames covered with screening that could easily be seen through (further details in Chapter 2). Video tape recordings of solitary birds foraging for naturally occurring seeds were made from a blind and used to estimate both vigilance and the foraging profitability of the patch of ground enclosed by the aviary.

The aviary was an appropriate venue for observing vigilance. Although the enclosure might provide foraging birds with a sense of security from attack, birds of

Figure 18. Hypothetical relationships between level of vigilance and the probability of starving and the resulting relationship between optimal vigilance level and food supply (after McNamara and Houston 1987). a, c) Family of solid upwardly-sloping curves represents the probability of starving in habitats differing in food supply. The number to the left of each curve indicates rank of food abundance (1 = low food abundance, 5 = high food abundance). Dashed downwardly-sloping curve is the probability of being killed by predators. b, d) Relationship between optimal level of vigilance and food supply resulting from the tradeoff depicted in the corresponding left panel. The sign of the slope depends upon whether starvation curves diverge or converge with increasing vigilance.



prey attempted to attack sparrows foraging in the aviary, and the sparrows appeared to exhibit normal levels of vigilance. Any effect of the aviary on vigilance should be constant among habitats. Finally, vigilance serves functions other than predator detection. It might also provide warning of attack by dominant members of a species (e.g., Waite 1987, Roberts 1988) or of attack by other, food-robbing species (e.g., Thompson and Lendrem 1985). Both of these factors were controlled by observing solitary individuals free from either threat.

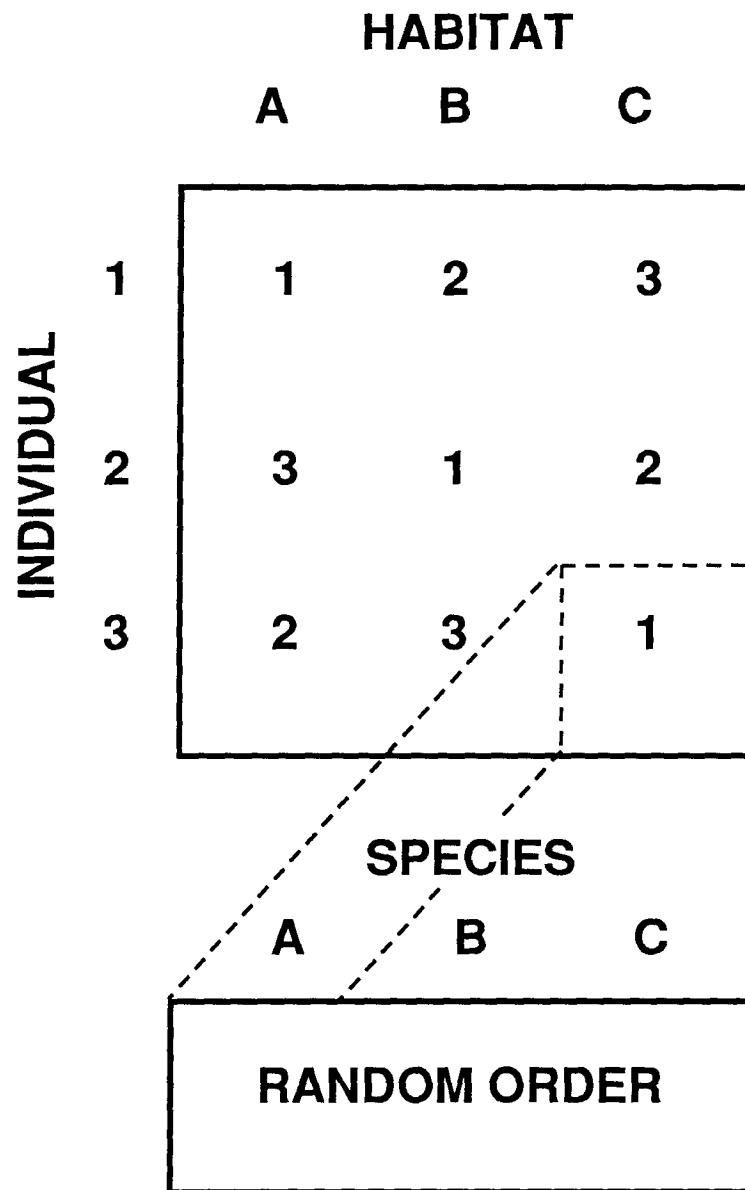
Experimental Design

The experiment was carried out according to a repeated-measures design (Figure 19). Six individuals of each species were caught from the wild 2 to 7 days before the study began. Birds were housed singly in outdoor cages and maintained on a commercially available mix of seeds for pet finches, meal worms, water, and a vitamin supplement. Each individual was videotaped during one 30-minute foraging trial in each habitat. This set of trials was a subset of trials conducted to test for differences in foraging ability between habitats (Chapter 2). Briefly, the experiment was carried out in two blocks, each containing three birds of each species. The first block was tested before the second. The design controlled any effect that previous experience might have on vigilance by ensuring that equal numbers of birds of equal experience were tested in each habitat (Figure 19). Each day, the aviary was moved to a new location, and three birds, one of each species, were tried in random order (Figure 19) beginning one hour after sunrise.

Variables and data collection

Vigilance was defined as any time that a foraging bird held its beak such that the long axis was horizontal to the ground or at an angle above the horizontal. Vigilance rate was calculated as the amount of time spent vigilant divided by net foraging time, defined as total time spent foraging less time spent vigilant. This measure based on net foraging time ensures that vigilance rate and peck rate (see below) estimated from

Figure 19. Schematic representation of one block in experimental design. One bird of each species was designated as the first, second and third individual of its species. upper) Each bird was introduced into the aviary in each habitat. Numbers within rows indicate the order in which individuals experienced habitats. Previous experience in the aviary was equalized among habitats. lower) Each day, three birds, one of each species, were tried in a random order. The experiment consisted of two experimental blocks.



the same foraging periods are independent measures and not related to one another simply because they are exclusive activities in a fixed time budget. I attempted to make one estimate of vigilance rate for each bird based on two minutes of foraging activity, although this was not always possible because of poor visibility or because the bird foraged for only a short period of time. Some estimates were made from several short periods of foraging which amounted to 2 minutes of cumulative foraging time. Estimates were made from the first segment(s) of video tape in which a bird could be seen well enough to determine what it was doing. Foraging time in a segment of video tape was measured using a microcomputer programmed as an event recorder. Then, vigilance time was determined by counting the number of frames in which the bird assumed a vigilant posture and dividing the count by the rate at which the camera recorded frames (30 frames / s).

I used the rate at which a bird pecked at either the ground or at plants to pick up seeds as a measure of the profitability of foraging in the patch of ground enclosed by the aviary. Total number of pecks was divided by net foraging time. Two difficulties arose with this method: time spent vigilant and time spent actively feeding are only partially independent because birds sometimes assume a vigilant posture while handling seeds, and it was often not possible to determine whether a seed was being handled while a bird was vigilant. Hence, patch profitability calculated in this manner assumes that no handling time is spent vigilant. I made a second calculation of peck rate that included the opposite assumption that all handling time was spent vigilant. Vigilance time was subtracted from total foraging time as in the first estimate, and handling time was added back in. Handling time was estimated as the total number of pecks times the mean handling time of the seed species being eaten. Mean handling times were estimated by observing birds consume seeds in the lab (Chapter 1). The results were unaffected by the method used to estimate patch profitability. For simplicity, I present the results calculated under the assumption that all handling time is spent vigilant

because that is probably the more realistic assumption in habitats in which birds eat seeds with long handling times.

Analysis

The goal of the analysis is to determine whether species exhibit consistent changes in vigilance between habitats. I used an analysis of covariance to estimate the difference in vigilance between habitats for each species. The model was

$$V = \tau_i + \beta X,$$

where V is vigilance rate, X is patch profitability, β is the slope of the relationship between patch profitability and vigilance, and τ_i is the intercept of habitat i . The difference between intercepts reflects the change in vigilance between two habitats. A statistical test for consistency among species was not possible because the analysis resulted in only one independent observation of change for each species: all of the observations of a species were used to estimate the difference between intercepts. Some degree of confidence in the interpretation of the results can be drawn from the statistical confidence surrounding individual ANCOVA's. Statistically significant differences between habitats strengthen confidence in the rankings.

A separate analysis was carried out for each pair of habitats. Each analysis was restricted to foraging periods in which seed types common to the two habitats were being eaten to ensure that whatever differences in vigilance were observed between habitats resulted from differences in predation risk between habitats rather than from differences in seed types. Seeds of different size could result in different rates of vigilance because they offer different opportunities to scan for predators without cost. Small seeds that require little handling time offer little opportunity for free vigilance whereas large seeds that require longer handling times offer more opportunity for vigilance. Sparrows usually consumed small seeds of the grass *Schismus barbatus* on the valley floor and larger seeds of *Bouteloua aristidoides* in pinyon-juniper habitat.

They consumed a mix of both of these grass species and a third large species *Aristida adscensionis* on the alluvial fan. Therefore, I analyzed data from the valley floor with data from the alluvial fan when birds there were feeding on *Schismus barbatus*, and I analyzed separately data from pinyon-juniper and data from the alluvial fan when birds were feeding on large seeds.

Analysis of the data was complicated by missing observations. Not all individuals could be observed eating both large and small seeds while foraging on the alluvial fan. One outlier was from a bird that was lethargic on one day, and it was removed. In a few other instances, good video tape footage was unavailable.

I used generalized least squares regression to analyze the results (see Rawlings 1988). The main advantage of generalized least squares was that it could incorporate repeat observations on individuals without estimating large numbers of parameters. Generalized least squares is a form of least squares regression in which the assumption of independent observations can be relaxed. This is accomplished by including a weight matrix in the least squares equation that describes the variance-covariance structure of the data. The matrix effectively adjusts the error mean square according to the degree of independence in the data set. I relaxed the assumption of independence to incorporate repeat observations on the same individual. This was reflected in a weight matrix in which 1's lay down the diagonal and off-diagonal elements representing paired observations on individual animals were set to the correlation coefficient between the residuals of repeat observations. The average correlation between paired residuals from separate analyses was -0.53 . It may result from changes in vigilance associated with previous experience in the aviary: a bird might be nervous when tried the first time, be calm for the second trial, and be frustrated with captivity by the third trial. Some individuals were reluctant to forage by their final trial. I used the mean correlation among analyses rather than using separate estimates for each analysis for two reasons. First, a single parameter estimate should be applicable to all of the analyses because

the same set of individuals is used in all analyses. Second, generalized least squares is sensitive to error in the estimation of weights, and a combined estimate of correlation should be more robust than individual estimates.

Results

Food supply affects vigilance

Plots of vigilance against food supply suggest that vigilance varies with food supply (Figure 20). Vigilance declined as foraging patch profitability increased in 4 of the 6 analyses, significantly so in three (Table 8). A positive relationship was observed in one analysis, although the pooled slope was not statistically significant (Table 8). In the sixth analysis (Figure 20a), no case could be made for a relationship between vigilance and food supply on the alluvial fan or valley floor where juncos do not usually occur.

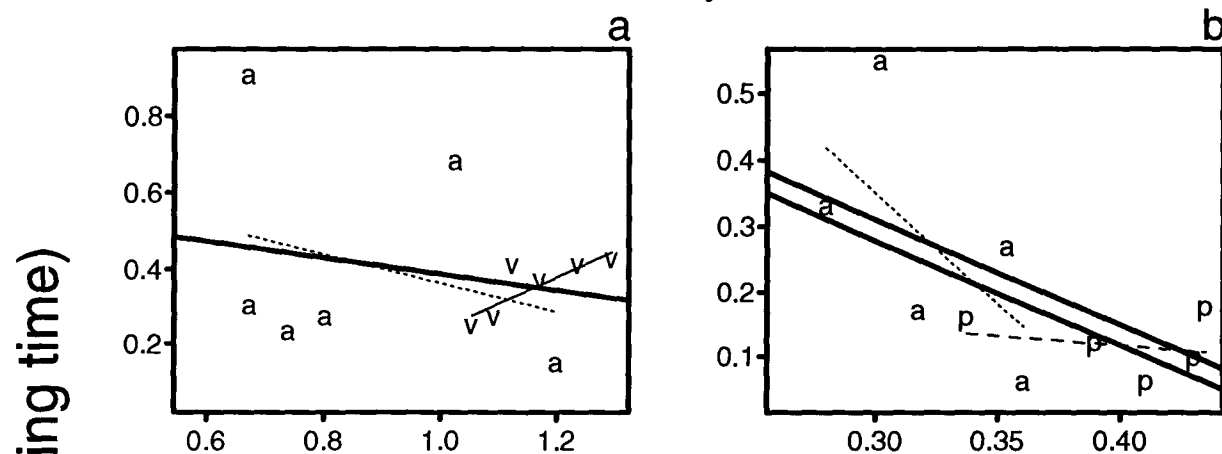
A decline in vigilance with increasing foraging patch profitability is counter to the intuitive reasoning that increased patch profitability lessens the threat of starvation and allows more time to be spent vigilant. A negative relationship between vigilance and patch profitability could be an artifact if both vigilance rate and peck rate are calculated from total time spent foraging because time is constrained and the number of pecks must decline as vigilance increases. This is an unsatisfactory explanation of the present results because I calculated vigilance rate and peck rate from net foraging time. The negative relationship is completely consistent with theory if the slope of the curve describing the risk of starvation increases with increased food abundance (Figure 18a).

Comparisons of vigilance rates between habitats

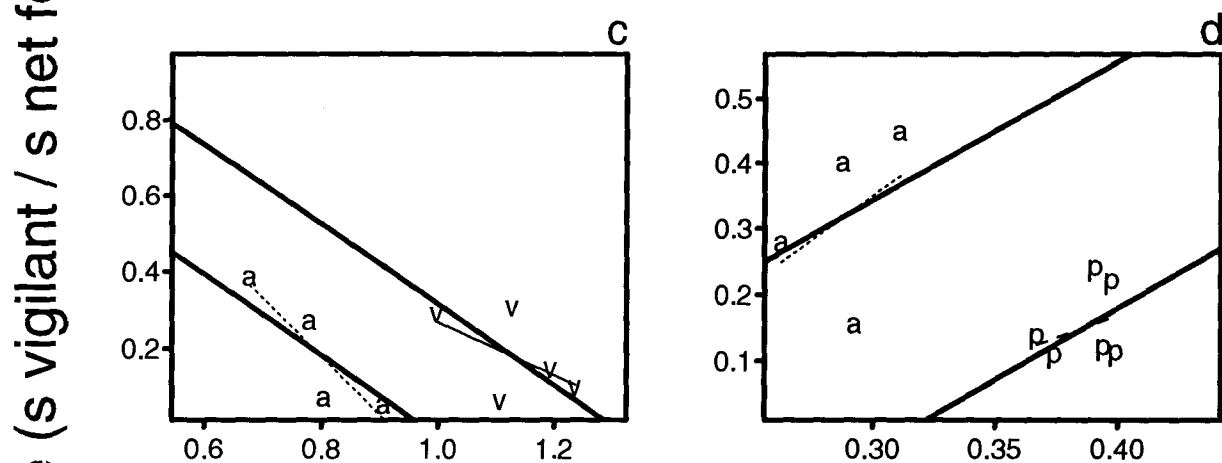
Evaluation of similarities in species' responses to changing habitats depends upon making habitat comparisons for each of the species. These comparisons were possible only between the valley floor and the alluvial fan. Comparisons were not feasible between alluvial fan habitat and pinyon-juniper habitat for several reasons. First, there were insufficient data on sage sparrows to make the comparison reliably. Second, the

Figure 20. Relationship between vigilance and food abundance for sparrows consuming similar seed types in pairs of habitats. Comparisons between valley floor habitat and alluvial fan habitat are in the left set of panels, and comparisons between alluvial fan habitat and pinyon-juniper habitat are in the right set of panels. Lines spanning only the range of data values are least-squares regression lines fit in a single habitat. Valley floor: “v”, (—————) ; alluvial fan “a”, (- - - - -) ; pinyon-juniper: “p”, (— — — — —) . Solid parallel lines spanning the entire range of the abscissa were fit by generalized least squares analysis of covariance (see Methods). Results of statistical inferences are in Table 8.

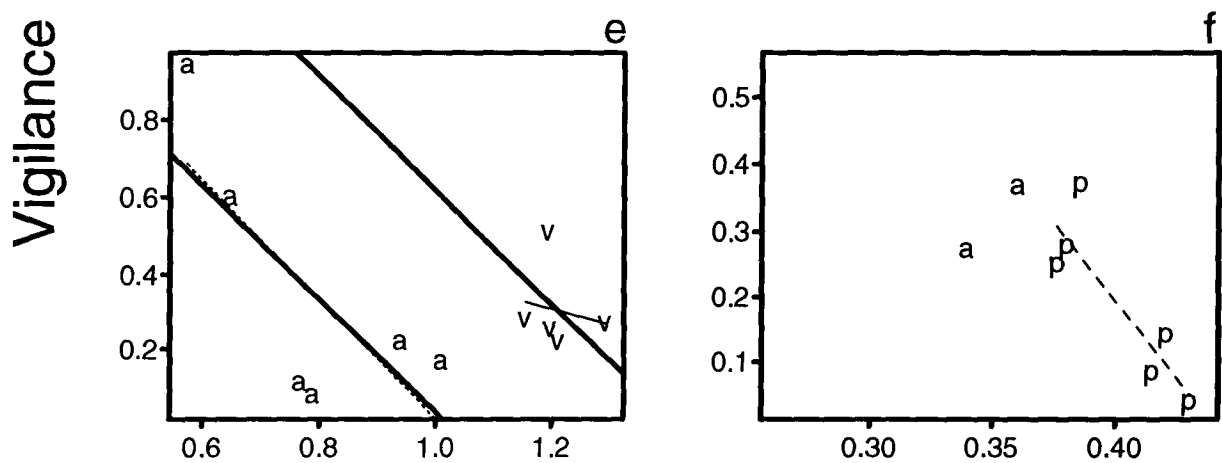
Dark-eyed Junco



Black-throated Sparrow



Sage Sparrow



Patch Profitability (pecks / s)

Table 8. Levels of statistical significance associated with tests of Analysis of Covariance models describing the relationship between vigilance and peck rate in pairs of habitats (Figure 20). The alternative hypotheses tested were: either slope differs from zero or mean vigilance rate differs between habitats (Overall ANCOVA), pooled slope differs from zero, the intercepts of the parallel lines are unequal, and the slopes of independent linear regression lines fit to each habitat are unequal.

Species	<i>P</i>			
	Overall ANCOVA	Pooled Slope	Unequal Intercepts	Unequal Slopes
Alluvial Fan – Pinyon-juniper comparison				
Dark-eyed Junco	0.03	0.03	0.81	0.68
Black-throated Sparrow	0.11	0.50	0.19	0.33
Sage Sparrow	–	0.17	–	–
Valley Floor – Alluvial Fan comparison				
Dark-eyed Junco	0.77	0.54	0.96	0.81
Black-throated Sparrow	0.02	0.01	0.03	0.40
Sage Sparrow	0.02	0.01	0.02	0.89

relationship between vigilance and food supply available to dark-eyed juncos was not amenable to simple comparisons between habitats because the lines did not appear to be parallel, suggesting that the difference in vigilance observed between habitats is dependent on the quantity of food available (Figure 19b).

Comparisons of vigilance rates between habitats were made to test the hypothesis that species exhibit similar changes in vigilance between habitats. Relative to food abundance, both sage sparrows and black-throated sparrows were more vigilant on the valley floor than on the alluvial fan. This result suggests that both species perceive similar changes in predation risk between habitats, and that they are both likely to be safest in the same habitat and at greater risk in the other. Hence, it is unlikely that species differences in the tradeoff in predation risk between habitats is responsible for habitat partitioning between these two species.

Discussion

Behavioral ecology has offered insight into how populations are affected by decisions made by individual animals. For example, the habitat distribution of a species reflects choices made by individuals weighing the tradeoff between the risk of predation and foraging profitabilities of habitats (e.g., Milinski and Heller 1978, Werner and Gilliam 1984, Gilliam and Fraser 1987, Todd and Cowie 1990). I used a defense behavior, vigilance, to detect perceived changes in predation risk between habitats and test two hypotheses of how predation might influence the distributions of wintering sparrow species. The first hypothesis was that sparrow species are distributed one-per-habitat because the species are safest from predators in different habitats. The alternative was that the species are all safest in the same habitat and that predation can not be responsible for habitat partitioning among them. The analysis was complicated because defense behavior itself is subject to a tradeoff between the predation and starvation. It was necessary to compare levels of defense between habitats after adjusting for variation in food abundance.

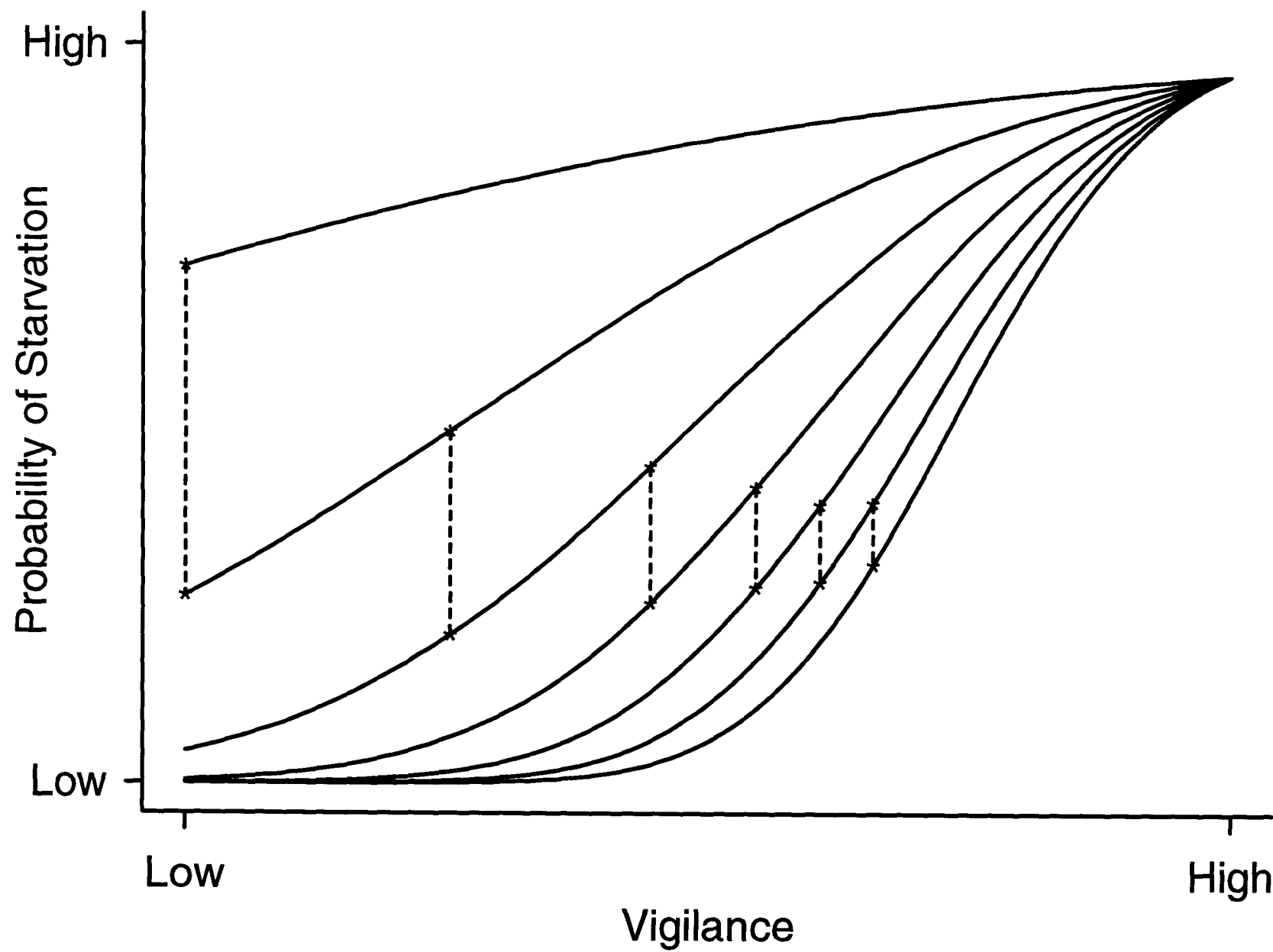
Vigilance and the tradeoff between food and predation

This study supports the previously untested prediction from vigilance theory that vigilance level is affected by food abundance (McNamara and Houston 1987, Lima 1987b, Figure 18). Vigilance declined in two species as food patch profitability increased, but the third species exhibited a positive although statistically insignificant relationship between vigilance and food supply (Figure 20).

A negative relationship between vigilance level and food patch profitability is consistent with theory (McNamara and Houston 1987, Figure 18), but it is inconsistent with the intuitive reasoning that increased food supply alleviates the threat of starvation, allowing more time for vigilance. The relationship begs the question: is a family of starvation curves that results in such a relationship (Figure 18a) likely to occur in nature? The answer is yes. McNamara and Houston's (1987) simple model of starvation results in a family of starvation curves that could yield either a positive or a negative relationship between vigilance and foraging patch profitability. In the model, food intake was assumed to be normally distributed with a mean and a variance, and the probability of starvation was the probability that food intake fell below some threshold. Increased vigilance reduced mean food intake and thereby increased the probability of starving. If habitats are assumed to differ in mean food intake, a family of starvation curves results that both diverges and converges (Figure 21), regardless of whether increasing vigilance reduces food intake linearly or curvilinearly, and regardless of whether variance in food intake is assumed to be constant or allowed to be proportional to net food intake. Solutions to the tradeoff between vigilance and starvation that lie in the area where curves diverge yield a positive relationship between vigilance and food abundance whereas those in the area where curves converge yield a negative relationship as in Figure 18.

An intuitive explanation of a negative relationship between vigilance level and food patch profitability follows from the family of curves in Figure 21. Starvation

Figure 21. A family of hypothetical starvation curves derived from the model of McNamara and Houston (1987). Food intake is assumed to be normally distributed, and the probability of starving is the probability of obtaining less than some threshold of food. Mean food intake in the absence of vigilance differs between the curves. Adjacent curves diverge with increasing vigilance to the left of the dashed vertical lines, and they converge to the right.



curves converge when the probability of starving is high. Under this condition, the benefit of increased food availability is so great that survival is maximized by sacrificing vigilance time to take advantage of it. This interpretation might be used to conclude that sparrows in nature are subject to high starvation risk, but that conclusion is unwarranted because birds used in this study were fasted prior to trials in the aviary and may have behaved as if the risk of starvation was inordinately high.

The family of starvation curves in Figure 21 also suggests a plausible explanation of why black-throated sparrows exhibited a switch from a negative relationship between vigilance and foraging patch profitability while feeding on small seeds to a positive relationship while feeding on large seeds. The sparrows may have been closer to starvation while feeding on small seeds than they were while feeding on large seeds. If so, they may have been subject to convergent starvation curves while feeding on small seeds and to divergent curves while feeding on large seeds. Why would this be true for black-throated sparrows but not for the other two species? Black-throated sparrows are smaller than the other two species (mean body mass 13 g vs. 17 g and 19 g for sage sparrows and dark-eyed juncos, respectively), and they should be less likely to starve at any food intake rate because they have smaller energy requirements.

Predation and the habitat distributions of species

Sage sparrows and black-throated sparrows exhibited similar changes in vigilance between habitats. This result suggests that species rank the danger of predation in habitats similarly and that predation is unlikely to shape their habitat distributions. If predation strongly affected species' distributions, species would have similar habitat distributions.

This conclusion is consistent with previous work on these three species in the study area. The species use similar methods to escape from avian predators, and they forage closer to woody vegetation than expected from the distribution of available food, suggesting that the species should be safest in the habitat with the greatest amount

of cover (Chapter 1). Interestingly, a similar conclusion was recently drawn regarding the risk of predation and microhabitat use by desert rodents (Longland and Price 1991). Heteromyid rodents tend to forage farther from cover than other species, and despite their remarkable adaptations for feeding far from cover (bipedal locomotion and large auditory bullae for hearing), these rodents are safest close to cover. Perhaps the predation hypothesis will explain the habitat distributions of a group of species differing markedly in their response to predators such as species that use different methods of escaping from predators like those observed by Pulliam and Mills (1977) or Lima (1990).

What might account for the habitat distributions of these sparrows if a tradeoff in predation risk between habitats is not responsible for them? There is another way in which predation might restrict species to different habitats. Species might segregate if they experience greater predation rates when they occur together than when they occur separately (Holt 1977, 1984, Schmitt 1987). This possibility remains to be tested. Food is an unlikely candidate. First, species are not distributed among habitats as predicted from food availability: some species are absent from habitats in which food is at least as abundant as those in which they occur (Chapter 1). Also, transplant experiments suggest that only small differences in foraging ability exist between habitats and that species might be predicted to have broader habitat distributions than they do if food governed distributions (Chapter 2). Habitat partitioning could result from interspecific competition (Lack 1944, Svärdson 1949, Noon 1981, Price 1991). Indirect evidence supports this hypothesis. Profitabilities of seeds in the different habitats rank similarly among species suggesting that species share preferences for the same resources, and indeed they consume some of the same seed species even though they occupy different habitats (Chapter 3). Food appears to limit population abundance, and sparrows are capable of depleting the amount of food available to one another (Chapter 4).

Hence, interspecific competition, rather than predation, is likely responsible for habitat distributions. More direct tests of the competition hypothesis remain to be done.

Chapter IV

INTERSPECIFIC COMPETITION

AND THE HABITAT DISTRIBUTIONS OF WINTERING SPARROWS:
EVIDENCE FROM A FOOD SUPPLEMENTATION EXPERIMENT

Direct experimental evidence of interspecific competition among birds is rare (see Schoener 1983, Wiens 1989b) because bird populations operate on a large spatial scale that defies experimentation (e.g., Wiens et al. 1986). Most evidence of competition between bird species is based on observational studies of patterns in morphology, distribution and abundance (see Wiens 1989a, 1989b). Patterns alone can be misleading, and it is desirable to challenge the competition hypothesis with further tests (e.g., Dayton 1973). An indirect test of the competition hypothesis can be achieved by measuring the requisite conditions: species should overlap in their use of limiting resources, and each species should deplete resources available to others. If either condition is absent, species do not compete for resources; hence verifying the conditions is a strong test of the competition hypothesis.

Here, I present the results of a food addition experiment carried out on granivorous birds wintering in the Sonoran Desert of California. The three common species of sparrows in the area are sage sparrows (*Amphispiza belli*), black-throated sparrows (*Amphispiza bilineata*) and dark-eyed juncos (*Junco hyemalis*). There is evidence that they partition habitats along an elevational gradient (Chapter 1). The species overlap extensively in the types of seeds they eat. Their distributions differ from what might be predicted from the availability of winter food alone: sage sparrows and black-throated sparrows are absent from the habitat in which their food, the seed of herbs, is most abundant. These distributions could result from interspecific competition, either interference competition occurring presently or evolutionary specialization on habitats resulting from competition in the past. I undertook the present experiment to test the

competition hypothesis. I sought evidence of food limitation and evidence that resource depletion could occur among sparrows if they were to occupy the same habitat. The experiment also afforded an opportunity to test a prediction that finches (Fringillidae and carduelinae: Emberizidae) use richer, more patchily distributed resources than sparrows (emberizinae: Emberizidae) (Benkman and Pulliam 1988). My results were consistent with the hypothesis that interspecific competition occurs among sparrows, and supported the prediction that sparrows and finches differ in the types of resources they use.

Possible inferences from a food addition

Food additions have been criticized recently (Wiens 1989b), so I shall first clarify what inferences about food limitation and depletion can and can not be drawn from their results.

Food is limiting when individual survival depends upon its availability. More food means higher food intake rates and thus lower chances of death from starvation or predation (McNamara and Houston 1987). One way that individual birds in these circumstances can enhance their food intake rates is to locate themselves in places where intake rate is high, provided that the cost of relocating is not exorbitant (Bernstein et al. 1991). Hence, the recruitment of individuals to a food addition plot would support the hypothesis that food is limiting to individuals. Note that this argument does not depend on the assumption that birds strictly maximize food intake rate in accordance with optimality theory; it assumes only that foraging birds are sensitive to spatial variation in food abundance and that they increase food intake rate over what it would be if spatial variation in food availability were ignored. Indeed, birds are sensitive to spatial variation in food abundance even if they do not strictly maximize food intake rates (Krebs et al. 1974, Smith and Sweetman 1974, Cowie 1977, Ydenberg 1984, Hanson and Green 1989, Kacelnik and Todd 1992). Behavioral evidence of food limitation is indirect, because a change in survival itself is not

demonstrated. Nevertheless, if resources are not limiting, then a response to a food addition is not expected (e.g., Pulliam and Dunning 1987). Therefore, a food addition experiment offers an opportunity to falsify the hypothesis that resources are limiting.

Depletion occurs when one species reduces the rate at which food may be gathered by another. To demonstrate depletion, resource availability in the presence of a potential competitor must be less than it would have been in the absence of that competitor. A food addition experiment provides an opportunity to examine the abilities of species to deplete resources. Supplying a single food profitable to several species mimics a pulse of food produced at the beginning, during or at the end of a growing season (e.g., Grant and Grant 1980, Schluter 1982, Repasky *personal observation*). As species deplete shared resources, diet overlap often declines (see also Schoener 1982). The dynamics of depletion can be observed easily after a food addition because resource production is zero. Depletion can be described as the percentage difference between the amount of food that was available to a species and the amount that would have been available in the absence of a potential competitor. Depletion can be calculated if food standing crop and removal rates are known.

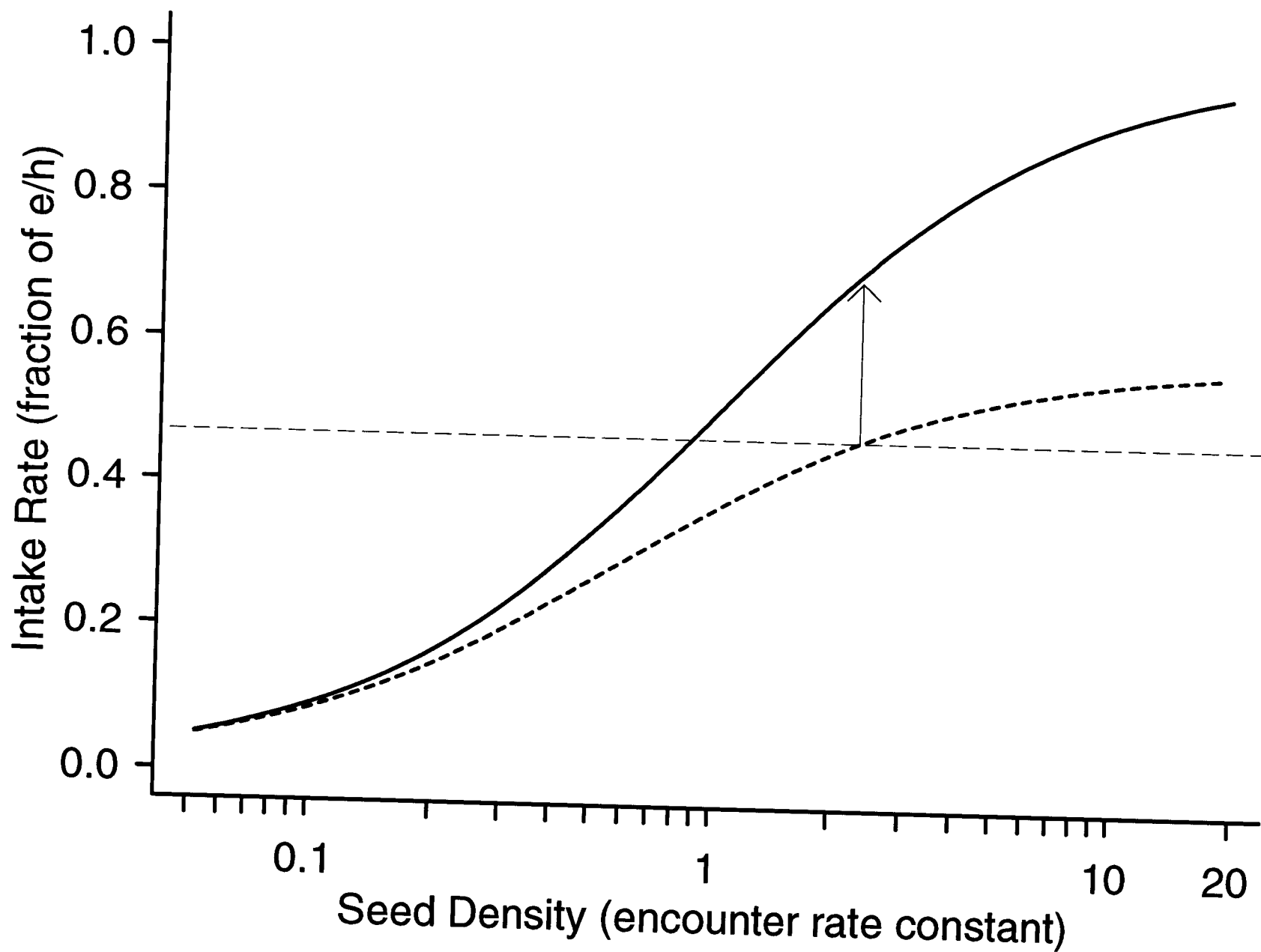
Food additions also illuminate overlap in the use of resources. Only species that can share a resource, that is species having overlapping “fundamental niches,” can respond to a food addition. Although these species are potential competitors, they can compete only in the presence of foods profitable to all. In the absence of common foods, they do not compete for food, and ecological differences between them should be manifested in the way they respond to the food addition. For example, sparrows and finches have been predicted to use different resources based on the rates at which they can handle seeds (Benkman and Pulliam 1988). In this view, a finch of a given size eats larger seeds than a sparrow of the same size because it can more profitably handle (seed mass ingested / handling time) large seeds than the sparrow. Finches, therefore, can obtain more of their daily energetic needs per seed, and they require fewer seeds

per day for the same metabolic expense. Because they need fewer seeds, finches can spend more time and energy searching out patches of particularly high seed abundance. Sparrows, on the other hand, must spend most of their time searching out and eating many small seeds, and they are less able to make use of very rich but scattered patches of food. Hence, finches should be more mobile and better able than sparrows to exploit rich, widely scattered patches of food.

How might differences in mobility between sparrows and finches be illuminated by a food addition? A food addition plot is effectively an extremely rich patch of food profitable to both finches and sparrows. Finches should recruit to a food addition plot faster than sparrows if indeed they are more mobile than sparrows, as predicted by Benkman and Pulliam (1988). Differences between species in the availability of natural food should be reflected by differences in the standing crop of seeds present when species depart a food addition. Birds are expected to remain in a patch of food (food addition plot) only while food intake rates there exceed the average in the environment (Krebs et al. 1974, Charnov 1976, Cowie 1977). If finches abandon a food addition plot earlier at a higher seed density than sparrows, it suggests that they experience higher intake rates in the environment than sparrows for the following reason. Finches foraging on a large seed such as millet can achieve a higher intake rate than similarly-sized sparrows at any food density because they handle seeds faster than sparrows (Figure 22). As seed abundance declines, finches should depart earlier than sparrows only if their foraging success off of the food addition plot is greater than that of sparrows (Figure 22).

Finally, competition can limit the number of species present in a guild. A food addition might relax food limitation and hence competition temporarily, allowing species number to increase. Hence, an increase in the number of species following a food addition would also support the competition hypothesis.

Figure 22. Food intake rate as a function of seed density for two species differing only in the time required to handle a single food type. The function is Holling's (1959) disc equation: $R = \frac{\lambda e}{1 + \lambda h}$ where R is intake rate, λ is the rate at which seeds are encountered, e is seed mass, and h is handling time. Food density is expressed as a constant which when divided by the shorter handling time gives encounter rate; intake rate is the proportion of the maximum intake rate attainable by the species having the faster handling time (————). The species having the lower intake rate (-----) handles seeds 70 percent slower than the species with the higher intake rate, corresponding to the rate black-throated sparrows handle millet seed relative to house finches (Repasky unpublished data). The horizontal dashed line is a hypothetical average food intake rate by the slow species and the intake rate at which it abandons a food addition plot. The fast species departs earlier than the slow species only if its average intake rate in the environment is greater than the intake rate that it would have when the slow species departs (arrow).



Methods

Study Area

I carried out the study in the Sonoran Desert of southern California, USA. Experimental and control plots were located in alluvial fan habitat in the Coachella Valley near Deep Canyon Desert Research Center. The rocky creosote-scrub vegetation has been described in detail by Zabriskie (1979). Briefly, an alluvial fan is a fan-shaped incline formed by the flow of rock and soil out of a narrow valley. The intermittent streams that feed an alluvial fan change course through time and dissipate as they descend. The resulting surface is a series of terraces and washes. Prominent plants on terraces are creosote bush (*Larrea tridentata*), brittlebush (*Encelia farinosa*), burrobrush (*Ambrosia dumosa*), sweetbush (*Bebbia juncea*) and the chollas (*Opuntia acanthocarpa*, *O. echinocarpa*) and the prominent plants of the washes are palo verde (*Cercidium floridum*), chuparosa (*Beloperone californica*), desert lavender (*Hyptis emoryi*), and cheesebush (*Hymenoclea salsola*).

Granivorous birds of the alluvial fan habitat include Gambel's quail (*Callipepla gambelii*), mourning dove (*Zenaida macroura*), house finch (*Carpodacus mexicanus*), black-throated sparrow and white-crowned sparrow (*Zonotrichia leucophrys*) (Weathers 1983). The white-crowned sparrow is a winter resident, whereas the other species are year-round residents (Weathers 1983). Sparrows consume the seeds of grasses (e.g., *Schismus barbatus*, *Aristida adscensionis*, *Bouteloua aristidoides*) and forbs (e.g., *Cryptantha* sp., *Perityle emoryi*, *Camissonia* sp.) whereas house finches tend to consume the seeds of shrubs such as creosote bush and desert lavender (Repasky unpublished data). Quail consume seeds of both shrubs and herbs (Goldstein and Nagy 1985). The natural diets of dove in the area are not known.

Experimental Manipulation

One control plot and one treatment plot were located on each of two alluvial fans. Deep Canyon alluvial fan and Devil Canyon alluvial fan (hereafter sites 1 and 2,

respectively) were approximately 11 km apart and separated by three mountains. Plots at each site were at least 1.6 km apart. At site 2, a coin toss was used to assign plots to treatment and control groups. Plot assignment at site 1 was dictated by ownership of the properties. The plot on the property of Deep Canyon Desert Research Center was designated as the control plot because seed additions were not permissible. Each plot was a 8.4-ha rectangle measuring 600 m by 140 m. Plots were marked with flagging tape.

I used white proso millet (6 mg/seed, Union Pacific Mills, San Bernardino, CA) in the experiment because it was preferred by captive black-throated sparrows over other seeds in a mix. Seeds were applied once at a density of 2.71 g/m². The dose was approximately 58 times the estimated standing crop of foods observed during the previous winter ($46.8 \pm \text{SE } 6.2 \text{ mg/m}^2$). Such a large dose was warranted because birds responded relatively slowly to the added seeds and recruited only after most of it had been removed by other granivores. The standing crop of native seeds, sampled during the experiment (see below), was relatively low ($17.4 \pm \text{SE } 2.9 \text{ mg/m}^2$) because of low rainfall during the previous growing season.

Seeds were spread by two researchers casting seeds as evenly as possible by hand while repeatedly walking the width of a plot. Although no placebo was spread on control plots, we paced about the plots to disturb them in a manner similar to that on treatment plots. The seed used in the study had been fumigated with methyl bromide to minimize germination.

Bird Censuses

Plots were censused six times over a six-day period prior to the seed addition and 10 times over a 31-day period afterward. Each plot was visited 4 or 5 times prior to the treatment and censused once or twice on each of those days. Post-treatment censusing began 12 days after the seed addition so that birds would have time to recruit undisturbed to the study plots. Each plot was then visited at 4-day intervals, and two

censuses, one in the morning and the other in the afternoon, were carried out each visit. Each census lasted 2 hours. Morning censuses began at sunrise, and afternoon censuses ended at sunset. Over the course of the experiment, equal numbers of censuses were conducted in each time period of the day and by each of two observers.

Censuses were carried out in a 2-ha strip (500 m x 40 m) centered within each 8.4-ha study plot. An observer walked the length of the strip down the center at a rate of 20 m every 5 min, recording the birds within the 20-m segment in front of him. Every effort was made to avoid double-counting individual birds that remained within the census strip, moving forward along with the observer, or that crossed the census strip turned and reentered it.

Depletion

Seed standing crop was estimated repeatedly after the seed addition to determine depletion rates. Fifty sampling points were randomly chosen in each census strip. At each point, a combined area of 0.125 m² was sampled from 8 square plots of equal size. Subplots were positioned at one-meter intervals along a straight line centered at the sampling point and oriented parallel to the width of the census strip. Seven or 8 samples were taken from each food addition plot on each of the five visits following the seed addition. Seed standing crop on control plots was sampled less systematically through time.

All seeds on plants were counted *in situ*. Surface soil was collected by scraping it into a bag using a toothbrush. The depth of the collection depended on surface hardness and was limited to 1 cm in soft soil in order to restrict the sample to seeds available to birds. Soil from all subplots at a sampling point was combined and was later spread over a large tray where seeds were counted visually.

Seed disappearance alone overestimates seed removal by birds because granivorous ants and rodents also took seeds. Therefore, I estimated seed removal by two methods.

First, I estimated the amount of seed removed by birds as the difference between total removal and an estimate of the seeds removed by other granivores (mainly ants and rodents). To accomplish this, I assumed that non-avian granivores removed seed at a constant rate, estimated as the rate at which seeds disappeared between the time the millet was spread and the time that birds began to recruit. Once birds began to recruit, the rate at which they removed seed was calculated as the difference between the removal rate observed then and the rate at which food was removed before they arrived. Removal rate was calculated as the instantaneous rate of seed disappearance $d = \frac{\ln p}{t}$ where p is the proportion of seed present at the beginning of a time interval that remained at the end of the time interval, and t is time elapsed (days). Removal was calculated for each period between visits to a plot and summed to give total removal by birds and other granivores. This method probably underestimated seed removal by ants and rodents and, hence, overestimated removal by birds because it assumed that ants and rodents began removing seeds at full speed immediately whereas their rate of removal undoubtedly accelerated as the numerical response of rodents was completed. (Functional responses probably were immediate, and a numerical response by ants from colonies adjacent to the site was probably limited because ants are central-place foragers that must commute from nest colonies to the study plot.)

Second, I estimated seed removal by birds more directly using census data along with estimates of metabolic requirements of birds taken from the literature. Seed removal on each census day was calculated as the product of bird density and individual consumption rate. Removal on days between census days was interpolated by calculating the change in daily removal between two census days and distributing it evenly among the intervening days.

Consumption rates were obtained from known allometric relationships between energy expenditure and body mass. The consumption rate of an individual free-living

bird was estimated as

$$R = \frac{E}{AC} \quad (1)$$

where R is the amount of seed removed by an individual bird (g/bird/d), E is total daily energy expenditure (kJ/bird/d) of free living birds, A is the assimilation efficiency and C is the energy content of seeds (kJ/g). E was calculated as $0.949W^{0.749}$ for passerines and $0.703W^{0.66}$ for non-passerines, where W is body mass in grams (Nagy 1987). Assimilation efficiency A was estimated to be 0.81, the mean of the values reported by Kendeigh et al. (1977:Table 5.7) for cardinals (*Cardinalis cardinalis*) and song sparrows (*Melospiza melodia*) feeding on seeds of hemp (*Cannabis sativa*) and foxtail (*Setaria faberii*). C , the energy content of seeds, was assumed to be 19.1 ± 0.8 (SD) kJ/g, which is the mean of the values presented by Kendeigh and West (1965) for grass seeds.

Seed removal calculated from census data underestimates true removal and so provides a lower bound of seed removal by birds. This is because both the number of birds removing seeds from the plots and the amount of seed removed by individual birds were probably larger than estimated for three reasons. First, peak densities of birds may have been missed. After a food addition, bird abundance increases and then declines. Censuses conducted at 4-day intervals are likely to miss the maximum abundance if the response is quick and short-lived as it was in this study. Second, on any day, more birds probably used a food addition plot than was assumed in the calculations. I assumed that the average number of birds observed during the four hours of census each day was the total number of birds using the plot and that those birds obtained all of their food from the plot on that day. Undoubtedly, more birds used the plot, and each bird obtained some fraction of its daily need from the plot. Under these circumstances, the amount of seed removed by the population would be

$$R_P = x \cdot R \cdot p_r / p_o \quad (2)$$

where R_P is seed removal by the population of birds (g/d), x is the number of birds observed on the census, R is the minimum daily food requirement of an individual bird (g/d) from eq. 1, p_r is the proportion of the daily requirements that a bird actually obtains from the study plot, and p_o is the proportion of birds using the plot that are actually observed on the census. If p_r is equal to p_o , eq. 2 reduces to the product of the number of birds observed and the daily requirements of individual birds, the estimate I used. Otherwise, my estimates should be biased according to the ratio p_r/p_o . That ratio was probably greater than one. Birds visiting the food addition plots may have obtained most of their daily food requirements there. The energy requirements of sparrows and finches, calculated as given above, could be met with fewer than 100 millet seeds per day. That amount of seed might theoretically be obtained in only 8 minutes by a house finch feeding non-stop from a dish of millet and in 13 minutes by a black-throated sparrow in the same circumstances (Repasky unpublished data). If either species took as long as 30 seconds to find a seed in the field, daily food requirements could be fulfilled in about an hour. Hence, birds visiting the plot probably obtained nearly all of their daily food requirements there. The proportion of birds actually observed on censuses, p_o , was certainly less than 1 because we counted only actively foraging birds and because I completely missed birds visiting the food addition plots outside the census periods. Finally, minimum daily energy requirements were probably greater than estimated from allometric relationships because energetic expenditure increases as ambient temperature declines. The relationships used describe energy expenditure during the breeding season whereas the study was carried out during the winter, when daily temperatures averaged 12°C. This bias may be ameliorated somewhat because thermoregulatory needs are partially compensated by energy spent in day-time activities (Webster and Weathers 1990).

Variances of seed removal rates based on energetics were calculated by compounding the variances of the component variables in eq. 1. Variance of the

estimate of daily energy expenditure, E , for an individual of a species was calculated using the equations given by Nagy (1987). Variances of assimilation efficiency, A , and energy content, C , were calculated from data in the original sources. Note that for each of these three variables I used the estimate of the population variance rather than the estimate of the variance of the population mean because I was interested in predicting values for individual species. To compound variances, the variance of the product of two estimates was calculated as

$$VAR(A \cdot C) = VAR(A)VAR(C) + \bar{x}_A^2 VAR(C) + \bar{x}_C^2 VAR(A)$$

(Bickel and Doksum 1977), where, for example, A is assimilation efficiency and C is seed energy content in the denominator of eq. 1. Variances of more complex functions of a variable such as the reciprocal or exponentiation were calculated using the delta method (Efron 1982). The variance of the sum of two estimates was calculated as the sum of the variances (Snedecor and Cochran 1967:190).

Number of Species

Measures of species richness tend to exhibit sample size biases (Hurlbert 1971, Simberloff 1972): on average, larger samples include more species. Therefore, I used rarefaction to standardize species richnesses by sample size before making comparisons. I used the flock as my resampling unit, defined as a group of birds encountered together at the same time and place during a census, because individual birds often forage in groups and are not independent observations.

Species richness on each plot was estimated for the entire period following the seed addition. Species richness was taken to be the actual number of species observed on the plot on which the fewest number of flocks (N_f) was observed. Species richness on each of the other plots was adjusted to the same number of flocks by resampling. Adjusted richness was calculated as the mean number of species in random samples of size N_f using the program NICHE (Schluter 1988b).

Statistical Tests

I treated plots on the same alluvial fan as paired samples because they might not provide independent observations of species abundances. Changes in bird abundances and species richness were, therefore, tested using one-tailed paired-sample *t*-tests (Snedecor and Cochran 1967) with $n = 2$ pairs. One-tailed tests were used because, *a priori*, abundance and diversity are expected to increase when food is added.

*Results**Density*

The density of granivorous birds increased 24 fold before it began to subside (Figure 23). Densities were higher on post-addition treatment plots than on control plots or on the treatment plots before food was added to them. The response was short lived. At site 2, densities began to increase as censuses resumed 13 days after the food addition, and they declined to pre-treatment/control levels by 31 days after the addition. The recruitment phase at site 1 began before censusing resumed, and only the decline phase of the response was observed.

Eight of nine species were more abundant on the treatment plots than on control plots (Table 9). The chance probability of an increase in that many species was approximately 0.018 by a one-tailed binomial test. Only the responses by house finches and white-crowned sparrows were statistically significant as judged by paired *t*-tests (Table 9).

Depletion

Millet disappeared quickly from the treatment plots (Figure 24). Ants began removing seed as we spread it, often within a few minutes of when it landed on the ground. They also altered the distribution of millet. By the end of the study, most of the millet on both study plots was in refuse piles of the desert harvester ant (*Messor pergandei*), and the remaining sparrows travelled between ant mounds and scratched through piles. The standing crop at site 1 declined 99.0 percent (2.71 g/m² to 0.03

Figure 23. Density of granivorous birds over the course of the food addition experiment on control plots (\times —————) and treatment plots (\diamond — — — — —). Vertical bars represent standard errors.

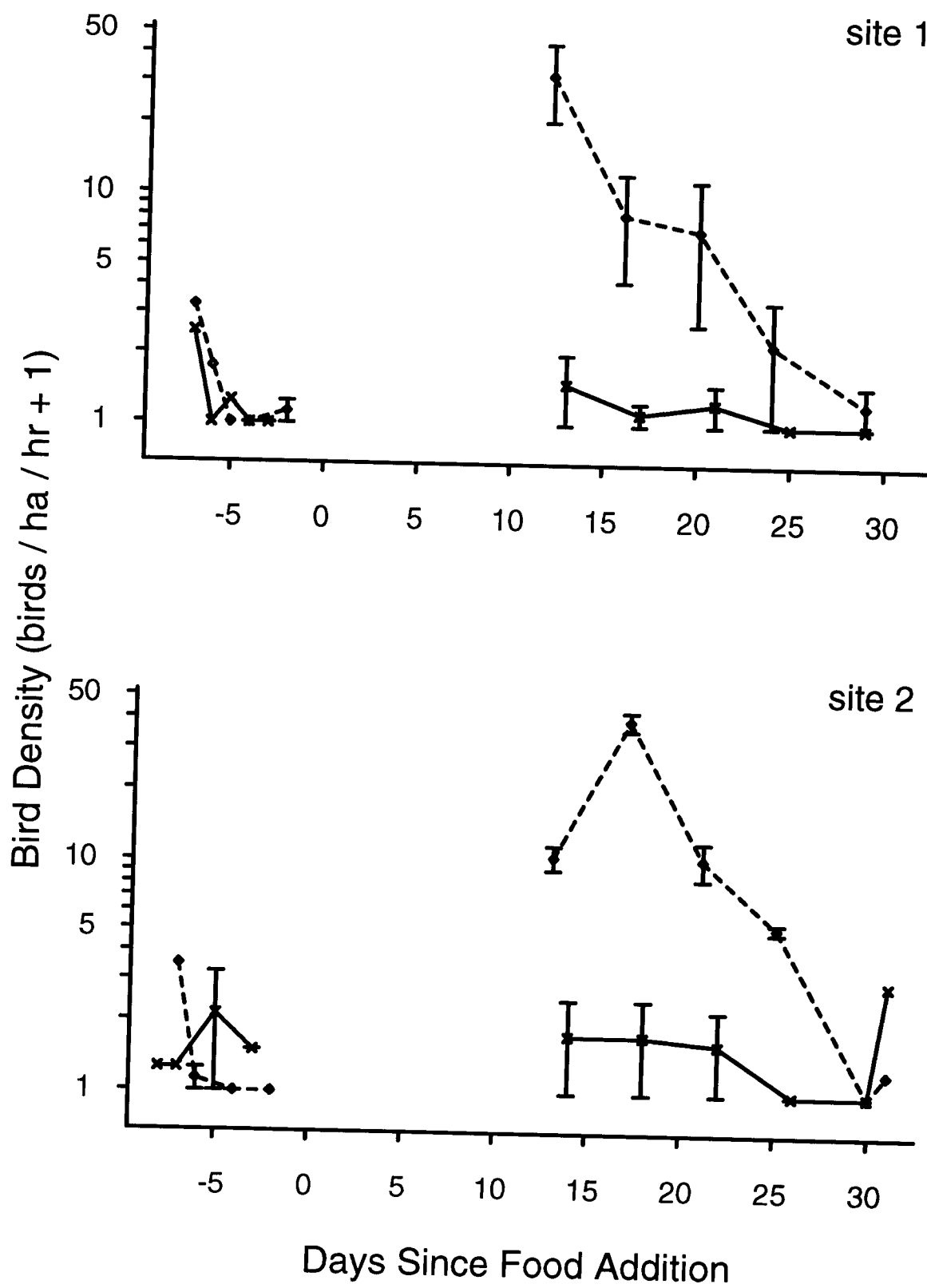


Table 9. Response of granivorous birds to a short-term food addition. Maximum density for each plot after the seed addition and the mean of the differences between the maxima of paired treatment and control plots (\bar{d}). Differences significantly greater than zero by a one-tailed one-sample t -test (one degree of freedom) are marked.

Species	bird density (birds/ha/hr)				\bar{d}
	site 1		site 2		
	Treatment	Control	Treatment	Control	
mourning dove	11.2	0.0	32.8	0.0	22.0
house finch	23.8	0.0	30.0	1.2	26.2*
white-crowned sparrow	9.5	0.0	8.8	1.2	8.5*
black-throated sparrow	1.0	0.5	3.0	0.2	1.6
Brewer's sparrow ¹	0.8	0.0	1.5	1.0	0.6
lark sparrow ²	0.5	0.0	0.5	0.0	0.5
Gambel's quail	1.2	1.0	0.0	0.0	0.1
dark-eyed junco ³	0.2	0.0	0.0	0.0	0.1
lesser goldfinch ⁴	0.0	0.0	0.0	0.5	-0.2
species combined	31.5	0.5	39.0	2.0	34.0*

* $P < 0.05$

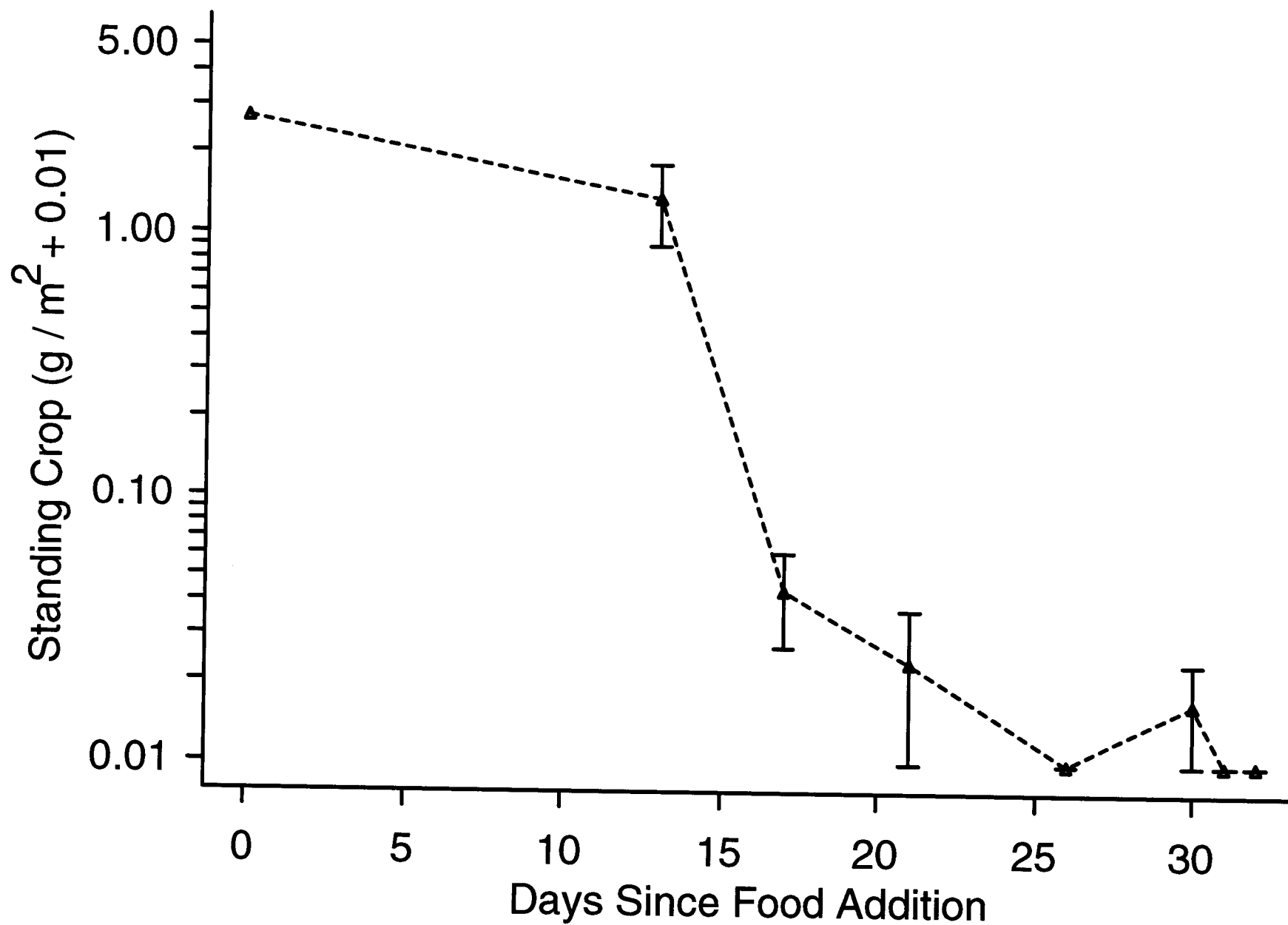
¹ *Spizella breweri*

² *Chondestes grammacus*

³ *Junco hyemalis*

⁴ *Carduelis psaltria*

Figure 24. Standing crop of millet over the course of the food addition experiment at Site 2. Standing crop was estimated by sampling seeds on the ground. Means and standard errors are connected by the dashed line. Data for Site 1 are not presented because millet standing crop had declined to levels lower than could be detected by the time sampling commenced.



g/m²) during the 12 days between the food addition and the resumption of censuses. It was too low to be detected (below 6.9 mg/m², 99.7 percent removal) by day 16. The decline in standing crop at site 2 occurred in three phases (Figure 24). First was a period of relatively slow decline during the first 13 days after food was added and before birds discovered the site. 50.5 percent of the millet disappeared during this period. Second was a period of rapid decline between days 13 and 17 when birds discovered the plot and 48.3 percent of the millet disappeared. Finally millet abundance declined slowly after day 17. It dropped below the minimum detectable standing crop by day 26.

Birds removed between an estimated 11 ± 0.3 (SE) percent and 46 ± 28 percent of the millet at site 2. Total removal by birds at site 1 was not estimated because most of the seed had been removed and bird abundance was declining by the time censuses resumed. The difference between the lower and upper estimates of seed removal at site 2 reflects differences in the assumptions that the methods make about the cause of the dramatic decline in millet abundance between days 13 and 17. Most of the decline is assumed to be by ants and rodents in the lower estimate whereas it is attributed to birds in the upper estimate. The lower estimate, based on bird abundance and food consumption, assumed that bird abundance between days 13 and 21 was never higher than it was on day 17. If bird abundance actually peaked at about day 17, it failed to increase enough to account for the dramatic decline in food abundance. The upper estimate, on the other hand, assumed that the dramatic decline was due largely to birds. Removal by ants and rodents was assumed to be constant at the average rate that had been established in the 13 days between the time food was added and censuses were resumed. Fluctuations in total removal around that rate, as happened between days 13 and 17, were attributed to birds. The actual amount of millet taken by birds should lie between these extreme values.

The pattern of recruitment by different species suggests that bird species depleted

the amount of food available to one another. Species recruited in sequence (Figure 25), and early arriving species reduced the amount of food available to later arriving species. At site 2, mourning doves and house finches peaked in abundance first followed by white-crowned sparrows and then black-throated sparrows. The pattern of species abundances was similar at site 1 where most of the seed was depleted before censusing began: mourning doves and house finches were at their peak abundances when censusing resumed whereas white-crowned sparrows peaked later and black-throated sparrows lacked a distinct peak in abundance. Indeed, species that peaked in abundance early recruited in greater numbers and removed more seed than those that peaked later (Table 10), and they depleted the amount of seed available to later arriving species.

The extent of depletion is the amount of seed that would have been available to species recruiting more slowly had species recruiting quickly failed to appear. To make the calculations it was necessary to assume that seed removal by birds did not affect the amount of seed removed by ants and rodents. The effects of removal on food availability were considerable (Table 10). At site 2, for example, the amount of food available to white-crowned sparrows would have been 3.2 times greater than actual values, had mourning doves and house finches not recruited. Food availability to black-throated sparrows would have been 23 times greater in the absence of all earlier species and 6.4 times greater in the absence of white-crowned sparrows. Hence, the more slowly recruiting species might have recruited in larger numbers than they did had the quickly recruiting species been absent.

Number of Species

Supplemental food did not increase the number of species present on plots significantly. Although more species were observed on the treatment plots than on control plots, all of the newly recruited species occur in alluvial fan habitat irregularly or in low numbers (Weathers 1983). The numbers of species were similar on control

Figure 25. Trajectory of millet seed removal rate at Site 2 over the course of the food addition experiment: all species including ants and rodents (————), all bird species (*————), mourning doves (◇-----), house finch (■-----), white-crowned sparrow (×-----), and black-throated sparrow (□-----). Total removal rate was estimated from a regression of standing crop against time, and removal rates for birds were estimated from energetic allometric relationships described in the text.

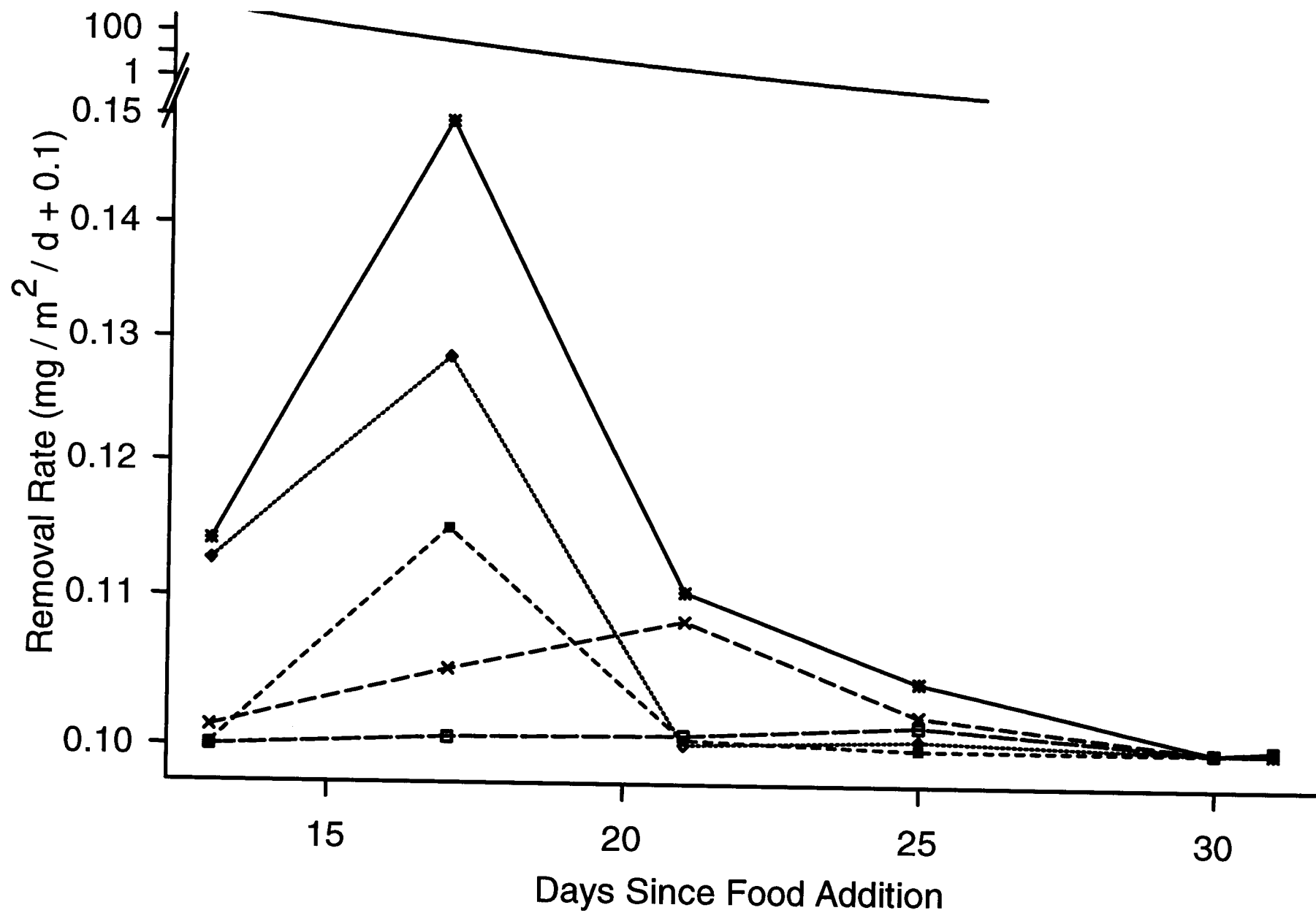


Table 10. Millet removal and extent of food depletion among predominant bird species. Each entry is the percentage increase in the amount of millet seed available to more slowly arriving species that would have occurred in the absence of the target species or of the target species and all species recruiting more quickly. Species are listed in descending order by recruitment rate.

Target species	Time of peak	Millet removed	Increase in food availability (percent) in the absence of a ...	
	abundance		Target	Target
	(days since	(percent of total	species	species and all
	food addition)	removed by birds)	only	faster species
<hr/>				
		<i>Site 1</i>		
Mourning dove ¹	12	24.4±0.2	34±0.4	34±0.4
House finch ¹	12	27.4±0.5	62±1.5	117±2.2
White-crowned sparrow	16	40.0±0.4	976±25.8	2239±56.0
Black-throated sparrow	- ²	4.1±0.1	—	—
		<i>Site 2</i>		
Mourning dove	17	50.5±2.7	105±10.5	105±10.5
House finch	17	21.1±1.9	79±14.3	268±43.2
White-crowned sparrow	21	22.5±0.7	536±54.8	2240±1251
Black-throated sparrow	25	4.2±2.3	—	—

continued ...

Table 10 continued.

¹ Depletion was underestimated because this species recruited to the food addition plots before censuses were resumed.

² No distinct peak occurred.

plots and treatment plots after being adjusted for sample size differences (Table 11), and the paired t -test was not significant ($\bar{d} = 0.442$, $t = 0.777$, $P > .05$). Although the power of the test was low ($P(\text{reject when } \mu_d = 3 \text{ species}) = 0.149$), the observed difference in species richness was small. Hence, richness itself was not increased; rather, rare species increased in local abundance and were more likely to be observed on the food addition plots. A true increase in species number is unlikely to occur in a such short-term experiment because species must be present in low numbers if they are to discover a food addition plot at all.

Discussion

I carried out an indirect test for interspecific competition by testing the conditions necessary for competition. In doing so, I put to a test the hypothesis that present-day competition is responsible for habitat partitioning among three species of sparrows. My results supported the competition hypothesis. Here, I clarify this interpretation and speculate on how the results bear on the interactions between other avian granivores.

Food limitation

Birds recruited to the food addition plots while food abundance remained elevated. This response is consistent with the hypothesis that food limits population abundance, although it is indirect support because a change in survival was not demonstrated. The strength of the support depends on whether bird abundance would be positively correlated with food abundance in the absence of food limitation. Here, I give two reasons why food is likely to be limiting when birds accumulate in areas of high food abundance. First, the only existing models that predict a positive correlation between consumer abundance and prey abundance are rate maximizing models describing systems in which the addition of food is likely to increase survival. Second, it is unlikely that consumers would exhibit behavior that enhances food intake rate if it were uncoupled from survival.

Food abundance probably affects survival of consumers that enhance food intake

Table 11. Species richness on control and treatment plots as observed and as adjusted for differences in sample sizes. The adjusted richness of each plot was calculated as the mean of a set of samples, each the size of the smallest sample, drawn from the original data. See text for details.

Plot	Species richness (No. species \pm S.E.)	
	unadjusted	adjusted
<i>Site 1</i>		
control	2	2.0
treatment	8	3.0
<i>Site 2</i>		
control	5	2.6
treatment	6	2.4

rate by choosing where to forage. The models of Bernstein et al. (1988, 1991) describe the distribution of consumers under circumstances similar to those of granivorous birds during winter, consumers searching for immobile prey during the non-breeding season. Consumers maximize intake rate by abandoning areas (patches) in search of better areas if the intake rate in them is less than the average intake rate that they experience in the environment. Increased food abundance should increase intake rate by decreasing both the number of poor patches and the amount of time consumers spend in them.

Would consumers enhance intake rate if it were independent of survival? Probably not, a consumer doing so would gain no benefit and might incur a cost. A likely cost is the risk of predation taken while needlessly searching out rich patches of food. Indeed, predation risk strongly influences the foraging behaviors of birds (e.g., Caraco et al. 1980, Valone and Lima 1987, Lima 1987, 1990). Hence, food is likely to be limiting in systems in which consumers actively distribute themselves according to prey abundance, as happens after a food addition.

Support for the food limitation hypothesis is consistent with a growing body of evidence that food limits the abundance of granivorous birds during the non-breeding season. First, finch abundance (broadly defined as the abundance of small, seed-eating passerines) is positively related to seed abundance across sites over four continents, suggesting that food abundance influences population abundance in a consistent manner in many places (Schluter and Repasky 1991). The present study sites in the Sonoran Desert were included in that analysis, and the additional evidence presented here of food limitation at the study sites further supports the hypothesis that the positive relationship between seed abundance and food abundance among continents results from food limitation.

Second, the present results are consistent with the conclusion of Pulliam and his colleagues that food limits sparrow abundance only during years of poor seed production. In their study site in southern Arizona, sparrow abundance is correlated

with food abundance during poor years but not in good years (Pulliam and Parker 1979). The species composition of the guild of sparrows is predictable from resource distributions in poor years but not in better years (Pulliam 1983). Third, grassland sparrows in southern Arizona failed to respond when food was supplemented in a year of moderate food abundance (Pulliam and Dunning 1987). In the present study, birds recruited to food addition plots in a year when rainfall, a surrogate measure for seed production, was relatively low (26th percentile of the long-term distribution). The positive response during a year of low productivity in the present experiment is consistent with the lack of response during a year of moderate productivity in Pulliam and Dunning's experiment.

Depletion

Birds are small players among desert granivores (Parmenter et al. 1984). I estimated that most of the seed removed during the experiment was taken by other granivores, probably ants and rodents. So much seed was taken by these other granivores that it might have been impossible to effect an increase in the amount of food available to birds without saturating ants and rodents with a large quantity of seed. The presence of abundant, competitively superior species that can drastically reduce food supplies could also make it difficult to detect interactions among less common species (e.g., Hairston 1980, 1981, Grubb 1986). That ants and rodents can severely deplete the availability of food to birds supports the hypothesis that competitors in non-avian taxa limit the morphological diversity of granivorous birds on continents (Schluter 1988a, 1988b).

Can sparrow species deplete the amount of food available to one another? Because birds removed less seed than ants and rodents removed, it might be argued that there is little potential for depletion. To the contrary, my results suggest that birds can significantly deplete the availability of resources to one another. For example, white-crowned sparrows and black-throated sparrows were the slowest species to respond

to the food addition and removed the least amount of seed. Yet, had white-crowned sparrows not recruited to plots, the amount of food available to black-throated sparrows would have been 6 to 11 times the actual amount (Table 10). Hence, species that occur together are capable of affecting one another's abundances through food depletion.

Competition among other granivorous birds

A number of species responded to the food addition, more than the three species hypothesized to partition habitats, suggesting that their fundamental niches overlap. In nature, these species might also overlap in diet at times when resources are available that are profitable to all. They would compete if resources were limiting and were being depleted at those times.

The extent to which species shared diets and may have been competing for natural foods at the time of the experiment should be reflected by similarities in the times that they arrived at the food addition plot and departed from it. Arrival time reflects mobility, and departure time the mean intake rate a species experiences outside of a food addition. Species that use the same resources and value them similarly should have similar intake rates and mobilities. More mobile species should recruit faster than less mobile species, and species with high intake rates are likely to depart sooner than those with low intake rates.

House finches differed markedly from sparrows in both arrival times and departure times, suggesting that house finches and sparrows were not competing for natural seeds during the experiment. House finches recruited quickly to the food addition and abandoned it early, while sparrows were still recruiting. High mobility and high intake rates of finches are consistent with the prediction that finches use profitable resources that are clumped into rich patches whereas sparrows use poorer, more evenly distributed resources (Benkman and Pulliam 1988). House finches are sufficiently mobile to specialize on clumped resources because they handle large seeds more efficiently than sparrows and require fewer seeds per day. Indeed, house finches eat

larger seeds than sparrows during mid winter (Repasky unpublished data).

Unlike the contrast between sparrows and finches, differences in arrival and departure times between other taxa lack easily identifiable causes. Here, I speculate on the causes and their implications for interspecific competition. Mourning doves responded much like house finches; they recruited early and departed early. They, too, probably use rich, spatially clumped resources similar to those used by house finches and are more likely to compete with house finches than with sparrows. Among the sparrows, white-crowned sparrows recruited more quickly than black-throated sparrows, and they began to leave the plot before black-throated sparrows. This difference in timing might be attributable to a difference between the diets of the two species. Although the species share many of the same seed species, white-crowned sparrows tend more toward herbivory than do black-throated sparrows (Repasky unpublished data). White-crowned sparrows eat mostly fresh vegetation, and they are abundant only during winters when sprouting plants are abundant (Repasky personal observation). If white-crowned sparrows are dependent upon fresh vegetation, competition between them and black-throated sparrows might be restricted to wetter winters in which there is a sufficient amount of fresh vegetation for white-crowned sparrows.

GENERAL DISCUSSION

My census data and earlier census data (Weathers 1983, Weathers unpublished data) suggest that species are distributed one species per habitat. Censuses were conducted in the interiors of habitats, away from habitat boundaries. Hence, sage sparrows, black-throated sparrows and dark-eyed juncos enjoy sole occupancy of the center portions of habitats, although it is unclear how much species distributions overlap at habitat boundaries and how closely distribution boundaries of species match habitat boundaries.

I tested alternative hypotheses that might explain why three sparrows are distributed one-species-per-habitat along an elevational gradient. The alternatives included: food, predation, structural features of habitat, and interspecific competition. Here, I summarize the evidence against the food, predation and vegetation structure hypotheses and show how the data are consistent with the competition hypothesis. I discuss alternative explanations of the results briefly and consider how the competition hypothesis might be pursued in the future.

Summary of results

Food is unlikely to shape species' habitat distributions. Several lines of evidence argue against the prediction from the food hypothesis that species specialize on alternate foods that occur in different habitat. First, species' foods are not restricted in distribution. Foods are at least as abundant outside the habitats that species occupy as they are inside. Second, species do not specialize on different types of food. Species in two different habitats eat seeds common to both habitats. Also, the foraging profitabilities (mass of seed ingested / handling time) of seed species rank similarly among the sparrow species. Finally, only dark-eyed juncos experienced significant tradeoffs in feeding ability between habitats when species were experimentally introduced into each habitat and allowed to forage. Differences between habitats in

the foraging abilities of sage sparrows and black-throated sparrows were small. Feeding rates outside of their typical habitats were at least as large as those inside, suggesting that these two species would be more broadly distributed than at present if food were responsible for their distributions.

Species differences in predation risk between habitats could account for use of different habitats by species if species are safest from predators in different habitats. This condition is unlikely to be true for the sparrows in my study area. Two results suggest that species perceive similar changes in predation risk between habitats rather than opposite changes in risk as predicted by the predation hypothesis. First, the three species rely on shrubby cover to escape from predation, and they forage closer to cover than predicted from the availability of food. This result suggests that the species are safest close to cover and that they are all safest in the habitat with the greatest amount of woody cover. Second, sage sparrows and black-throated sparrows both increased the amount of time they scanned the environment, relative to food abundance, when they were moved from the alluvial fan to the valley floor, suggesting that at least these two species perceive similar changes in predation risk between habitats. Hence, if predation were responsible for habitat distributions, the species should have similar distributions rather than specialize on different vegetation types.

Finally, species are unlikely to be adapted to structural features of their habitats that restrict their distributions. Foraging microhabitats used by individual species are more broadly distributed than the species themselves. The effects of habitat structure on foraging ability and predation risk appear to be minimal. Only small differences in foraging ability existed between habitats, whereas large changes would be predicted if habitat structure strongly influenced foraging ability. Also, changes in vigilance between habitats were consistent among species whereas disparate vigilance patterns would be predicted if species perceived the relative safety of habitats differently because of structural habitat characteristics.

Interspecific competition may be responsible for habitat specialization. The most conspicuous difference between habitats that might limit species' distributions is the presence of other species of sparrows. Species are capable of eating the same species of seeds, and they do so to the extent that seed species occur in more than one habitat. Data on seed profitability suggest that species would share preferences for the same seeds if they were to feed in the same habitats. Species also forage in similar micro habitats. Clearly, these species are potential competitors.

Competition is contingent upon resource limitation. Although observational data on sparrow abundance and food abundance were equivocal, the food addition experiment provided evidence that food limits population abundance. Sparrows recruited to short-term food addition plots indicating that individual birds are on the lookout for rich food sources as they ought to be if food is limiting. No such response is predicted in the absence of food limitation because individual birds would pay the cost of relocating without benefit. The experiment was carried out over the course of a month. Food limitation over such a short time period is sufficient to suggest that competition shapes species distributions along the elevational gradient because the pattern of distribution exists only during the winter. Sage sparrows migrate to breed in the Great Basin of the western United States, and dark-eyed juncos migrate uphill to breed in pine forest near the tops of the mountains (Weathers 1983).

Results of the food addition experiment also suggest that sparrows are capable of depleting the amount of food available to one another when they occur together. In the experiment, which was carried out in alluvial fan habitat, both white-crowned sparrows and black-throated sparrows recruited to the food addition. White-crowned sparrows recruited before black-throated sparrows and also departed before them. White-crowned sparrows reduced the amount of food available to black-throated sparrows.

Hence, competition is a plausible explanation for habitat partitioning among the species. If competition is indeed responsible for habitat partitioning, it is likely to occur

by one of two mechanisms. First, species might avoid habitats in which they would lose in competition. Second, species might segregate because of aggression among species. A third possible mechanism, exploitative competition, is unlikely to be responsible for sparrow distributions. Under exploitative competition species should be distributed as predicted from the availability of their foods. Species might occupy different habitats because food in preferred habitats has already been depleted to the extent that foraging is no longer profitable in them. These hypotheses are worth testing because they place the competition hypothesis at risk of falsification.

Alternative hypotheses

Hypotheses other than those considered here that might explain habitat partitioning by sparrows fall into two broad categories. The first is a set of hypotheses in which at least two factors account for all species' distribution boundaries. One factor might explain some boundaries, and other factors other boundaries. For example, competition might limit some species' distributions and predation others to produce the pattern one-species-per-habitat. The second set of alternatives consists of reformulations of the hypotheses that I have considered after some assumptions underlying the tests have been relaxed or refined. For example, I concluded that species should share preferences for seed species because the handling times of different seeds rank similarly among species. This conclusion rests on the assumption that seed types are equally digestible by different species, an assumption that may not be true. Many other simplifying assumptions have been made in this thesis. However, I believe that the present results are clear enough to suggest that the next logical step is to pursue the competition hypothesis by more direct tests. Should those tests fail, it will be worthwhile to sift through more complex hypotheses and the assumptions of the present analyses for avenues to pursue.

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