

## HABITAT DISTRIBUTIONS OF WINTERING SPARROWS: FORAGING SUCCESS IN A TRANSPLANT EXPERIMENT<sup>1</sup>

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**Abstract.** Why do birds partition habitats? Possible explanations include nonoverlapping food distributions, interspecific competition, and predation. If food limits distributions, species should forage most successfully in their preferred habitats and should experience poorer food intake rates elsewhere. These same predictions hold if species distributions are shaped by exploitative competition. We tested the foraging success hypothesis and exploitative competition hypothesis as explanations of the habitat distributions of Sage Sparrows (*Amphispiza belli*), Black-throated Sparrows (*A. bilineata*), and Dark-eyed Juncos (*Junco hyemalis*), which spend the winter in different habitats along an elevational gradient in the Sonoran Desert of southern California. Individuals of each species were transplanted between habitats in a portable aviary and observed while foraging on naturally occurring seeds. Predictions of the foraging success hypothesis and exploitative competition hypothesis were not confirmed. Only Dark-eyed Juncos achieved their highest foraging success in their preferred habitat. Black-throated Sparrows experienced nearly identical foraging success in all three habitats, yet are confined to only one of them naturally. Sage Sparrows foraged more successfully in habitats other than that in which they naturally occur. We conclude that immediate foraging gains do not explain habitat distributions of these birds, and that interference competition, predation, or other unknown factors are responsible. We contrast this finding with that seen in Galápagos finches in which bird distributions closely matched food supply.

**Key words:** *California; food; foraging success; habitat; habitat partitioning; Sonoran Desert; sparrow; transplant experiment.*

### INTRODUCTION

Temperate birds are frequently habitat specialists, and adjacent habitats are often occupied by closely related species. Lack (1944) argued that this pattern of distribution 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 rejected the alternative hypothesis that habitat distributions result from species differences in foraging success in different habitats. Although the competition hypothesis has frequently been tested (e.g., Terborgh 1971, Pulliam 1975, Terborgh and Weske 1975, Noon 1981, Schluter 1982, Garcia 1983), the foraging rate hypothesis has seldom been tested explicitly (Schluter 1982, Price 1991, Repasky and Schluter 1994).

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 trade-off in feeding ability between habitats must be large enough to restrict species' distributions. Hence, there are two testable pre-

dictions from the foraging success hypothesis. First, each species should achieve its highest food intake rate in the habitat in which it normally occurs. Second, the trade-off in foraging ability between habitats should be significant.

Similar predictions of foraging success result from a second hypothesis. Under exploitative competition, competitors shape the foraging success of one another as they deplete food supplies. Habitat partitioning results if species deplete food supplies in such a way that each habitat becomes suitable for only one species (Pimm and Rosenzweig 1981).

The foraging success and exploitative competition hypotheses can be tested by transplanting species among habitats and measuring foraging success. Both hypotheses are tested if foraging success is measured using natural levels of food supply that have been subjected to depletion by potential competitors. If species are distributed as one would predict from foraging success, the hypotheses are confounded and further experiments are necessary to distinguish between them. If not, both hypotheses can be rejected.

We tested the foraging success and exploitative competition 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

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the winter in different habitats along an elevational gradient (Weathers 1983, Repasky and Schluter 1994). 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 located on rocky alluvial fans at the entrances of small valleys and on the rocky, lower slopes of the mountains (other common species include brittlebush [*Encelia farinosa*], burrobush [*Ambrosia dumosa*], sweetbush [*Bebbia juncea*], and cactus [*Opuntia* spp.]). Dark-eyed Juncos inhabit a woodland of pinyon pine (*Pinus monophylla*) and juniper (*Juniperus californicus*), located on a plateau above the other two habitats. In an earlier study, we showed that the habitat distributions of these sparrows are unrelated to food availability (Repasky and Schluter 1994). Here, we experimentally address the foraging success and exploitative competition hypotheses to challenge that conclusion.

We 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 (Repasky and Schluter 1994, Repasky, *in press*). By measuring foraging success in the aviary, we tested the predictions from the foraging success and exploitative competition hypotheses that species should occupy the habitats in which they forage most successfully and that large differences in foraging ability should exist between habitats.

## METHODS

### *Experimental design*

The experiment was carried out during the winter of 1988–1989 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, mealworms, water, and a vitamin supplement.

Sparrows generally search for seeds on the ground. Food intake rates were estimated by observing solitary birds foraging on seeds naturally occurring on the ground inside of an aviary. We used solitary individuals to minimize the number of birds required in the experiment. Hence, our experiment rests on the assumption that birds feeding in a habitat that is well stocked with food will achieve higher food intake rates than birds feeding in a poorly stocked habitat so long as flock size is held constant between habitats. Although

food intake rate often increases with flock size (e.g., Caraco 1979), our assumption is reasonable in the absence of strong interactions between the effects of flock size on food intake rate and habitat. Indeed, the three species are likely to respond similarly to changes in flock size because they all travel in flocks, flee into woody vegetation to escape from avian predators, and feed near cover (Repasky and Schluter 1994).

The aviary measured  $4 \times 4 \times 2$  m. It was made to be portable by constructing wooden frames, each  $1 \times 2$  m, which 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 (Fig. 1). 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 crossover 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 (Fig. 1), 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 individuals of their species.

Each bird was introduced into the aviary for two 30-min trials on each of three successive days during a visit to a habitat (Fig. 1). 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. Locations were not strictly randomly chosen because some locations were simply too rugged for the aviary (e.g., terrace edges). Locations were chosen in such a way that over the course of the experiment the aviary was placed in different microhabitats in pro-

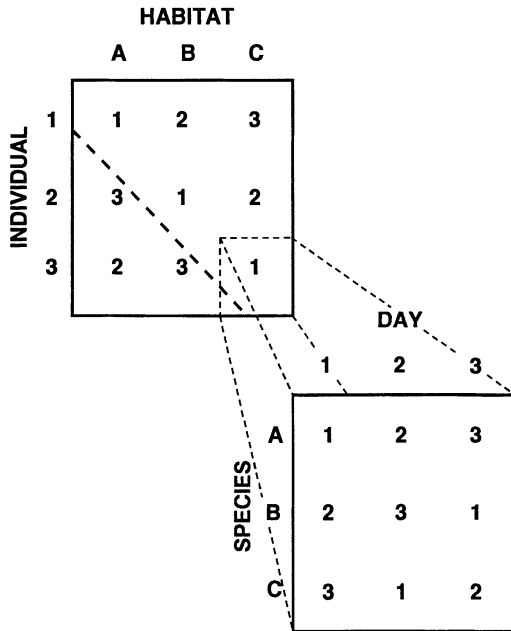


FIG. 1. One block of the experimental design. Three individuals of each of three species were tried in three habitats. The upper left box illustrates how the average amount of previous experience in the aviary was held constant among habitats. Numbers within rows represent the order in which individuals (regardless of species) were tried in habitats. Habitats were visited in the order A, B, C, A, B. The heavy 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 illustrates 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 3-d visit.

portion to their availability. Birds were fasted for 1 hr before the first trial and for 1 hr between the two trials.

On any one day, one individual of each species was tested in the aviary (Fig. 1). 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 (Fig. 1). 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

We were unable to estimate seed intake rates directly because we could not identify from a distance all of the seeds eaten, especially small ones. Instead, we 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 the actual number may be fewer. For example, grass seeds are often enclosed in a set of bracts, but a set of bracts picked up by a foraging bird may not contain any seeds. Also, seeds may be spoiled or empty and subsequently rejected. Hence, we also obtained a lower estimate of intake rate by assuming that birds are unable to determine beforehand whether items picked up are edible. We estimated the proportion of potential food (seed cases, bracts, and other items) on the ground containing edible seeds and multiplied this proportion by the upper estimate of intake.

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

$$s_{\bar{x} \cdot \bar{y}}^2 = s_x^2 s_y^2 + \bar{x}^2 s_y^2 + \bar{y}^2 s_x^2$$

(Bickel and Doksum 1977), where, for example,  $s^2$  is sample variance,  $x$  is peck rate, and  $y$  is seed size. Standard error was calculated as the square root of variance.

**Peck rate.**—An observer in the blind used a micro-computer 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.**—We estimated the proportion of pecks that might yield edible seeds. We 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 m<sup>2</sup> (see Repasky and Schluter 1994). Seeds were assumed to be edible if they made an audible crack when crushed using a pair of forceps.

Although the proportion of pecks that yielded seeds varied by as much as 20% between habitats (valley floor:  $0.80 \pm 0.01$ , alluvial fan:  $0.61 \pm 0.02$ , pinyon-juniper:  $0.69 \pm 0.02$ ), it 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 in the results.

**Size of seeds eaten.**—A sample of seeds eaten was obtained by administering the emetic apomorphine (see Schluter 1988, Esteban 1989) 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  $n = 18$  and that estimates of mean size of seeds eaten were unavailable for some species in some habitats. We calculated the mean and variance of seed size

in combined vomit samples, 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 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.

We estimated mean seed size by two other methods that allowed us to predict the mean size of seeds eaten in all habitats. In the first method, 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. 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 Re-pasky and Schluter 1994). 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 smoothing technique (Becker et al. 1988). 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.

Standard error ( $\sigma$ ) of mean seed size was calculated by a bootstrap method (Efron 1982). Mean seed mass was calculated 200 times in the manner described, 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.

Finally, we also estimated mean size of seeds eaten using a Bayesian method 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  $\mu$  is the prior expectation of the mean seed size,  $\sigma^2$  is the variance of seed size,  $\bar{x}$  and  $s^2$  are the sample mean and variance, and  $n$  is the number of birds sampled.  $\mu$  and  $\sigma^2$  were estimated from diet preferences and seed availability as described above.  $\bar{x}$  and  $s^2$  were calculated from the

vomit specimens obtained from birds after they had foraged in the aviary. The posterior estimate of the variance of mean seed size in the diet was

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

(see Stephens and Krebs 1986:77) where  $\sigma'^2$  is the variance,  $s^2$  is the sample variance, and  $n$  is the number of birds sampled as for  $\mu'$ .

Bayesian estimates of mean seed size were nearly identical to estimates made from preference functions alone. We used the Bayesian estimates to calculate food intake rates because their variances were less than variances calculated from preference functions.

Food intake rates attained by birds foraging in the aviary could underestimate food intakes of wild-foraging birds if the aviary confined their movements, excluding them from areas of high food abundance that they might prefer in the wild. Birds might be denied access to food-rich areas when the aviary happened to be placed on plots of ground that possessed only average or below-average food abundance. Hence, average performance of birds in the aviary might represent performance of hypothetical nonselective birds. Performance of wild-feeding birds might be better estimated by food intake rates achieved in the best places in which the aviary was placed. We repeated our analysis using the 80th percentile of food intake rate. We calculated 80th percentiles of food intake rates based on the 80th percentiles of peck rates in habitats and the 80th percentiles of seed mass consumed by birds in the aviary. Eightieth percentiles of peck rates were calculated using all 18 observations of each species foraging in each habitat. Standard errors were calculated by a bootstrap method in which replicate samples of six observations were drawn from each habitat. Our rationale for using different sample sizes to estimate percentiles and their standard errors is that only standard errors are biased by the lack of independence among repeat observations of individual birds foraging in a habitat.

### Comparisons

Comparisons of food intake rates among habitats were made by calculating 95% confidence intervals of the difference in mean food intake rate between habitats. One independent estimate of food intake rate and its variance was available for each species in each habitat. The standard error of the difference between habitat means was calculated as the square root of the sum of the variances of the two means. Confidence intervals were approximated as the mean food intake rate  $\pm 2$  SE. Differences were considered to deviate significantly from zero if zero fell outside of the confidence intervals.

TABLE 1. Performance of captive sparrows foraging in an aviary for naturally occurring seeds. Intake rate is the product of peck rate and seed mass. Seed masses are Bayesian estimates of mean seed mass based on food preferences of wild-caught birds and on seeds in vomit samples collected from birds foraging in the aviary. Entries in bold type are from habitats that species usually occupy. See *Methods* for details.

Species	Habitat	Mean $\pm$ 1 SE			80th percentile $\pm$ 1 SE		
		Peck rate (pecks/s)	Seed mass (mg)	Seed intake rate (mg/s)	Peck rate (pecks/s)	Seed mass (mg)	Seed intake rate (mg/s)
Dark-eyed Junco	<b>Pinyon-juniper</b>	<b>0.99 <math>\pm</math> 0.03</b>	<b>0.16 <math>\pm</math> 0.01</b>	<b>0.16 <math>\pm</math> 0.01</b>	<b>1.06 <math>\pm</math> 0.03</b>	<b>0.26 <math>\pm</math> 0.01</b>	<b>0.17 <math>\pm</math> 0.01</b>
	Alluvial fan	0.52 $\pm$ 0.05	0.10 $\pm$ 0.01	0.05 $\pm$ 0.01	0.72 $\pm$ 0.14	0.08 $\pm$ 0.01	0.06 $\pm$ 0.01
	Valley floor	1.08 $\pm$ 0.07	0.09 $\pm$ 0.01	0.09 $\pm$ 0.01	1.18 $\pm$ 0.15	0.08 $\pm$ 0.01	0.09 $\pm$ 0.01
Black-throated Sparrow	Pinyon-juniper	0.76 $\pm$ 0.04	0.18 $\pm$ 0.05	0.14 $\pm$ 0.04	0.93 $\pm$ 0.12	0.18 $\pm$ 0.05	0.17 $\pm$ 0.06
	<b>Alluvial fan</b>	<b>0.60 <math>\pm</math> 0.04</b>	<b>0.18 <math>\pm</math> 0.02</b>	<b>0.11 <math>\pm</math> 0.02</b>	<b>0.71 <math>\pm</math> 0.08</b>	0.09 $\pm$ 0.02	<b>0.06 <math>\pm</math> 0.02</b>
	Valley floor	1.23 $\pm$ 0.07	0.10 $\pm$ 0.01	0.12 $\pm$ 0.01	1.46 $\pm$ 0.15	0.08 $\pm$ 0.01	0.11 $\pm$ 0.01
Sage Sparrow	Pinyon-juniper	0.67 $\pm$ 0.05	0.23 $\pm$ 0.01	0.16 $\pm$ 0.01	0.76 $\pm$ 0.10	0.16 $\pm$ 0.01	0.12 $\pm$ 0.02
	Alluvial fan	0.70 $\pm$ 0.06	0.23 $\pm$ 0.02	0.16 $\pm$ 0.02	0.98 $\pm$ 0.17	0.39 $\pm$ 0.02	0.39 $\pm$ 0.07
	<b>Valley floor</b>	<b>1.18 <math>\pm</math> 0.06</b>	<b>0.09 <math>\pm</math> 0.01</b>	<b>0.11 <math>\pm</math> 0.01</b>	<b>1.37 <math>\pm</math> 0.15</b>	<b>0.09 <math>\pm</math> 0.01</b>	<b>0.13 <math>\pm</math> 0.02</b>

## RESULTS

### Food intake rates

Variation in foraging success among habitats was more closely related to variation in the size of seeds

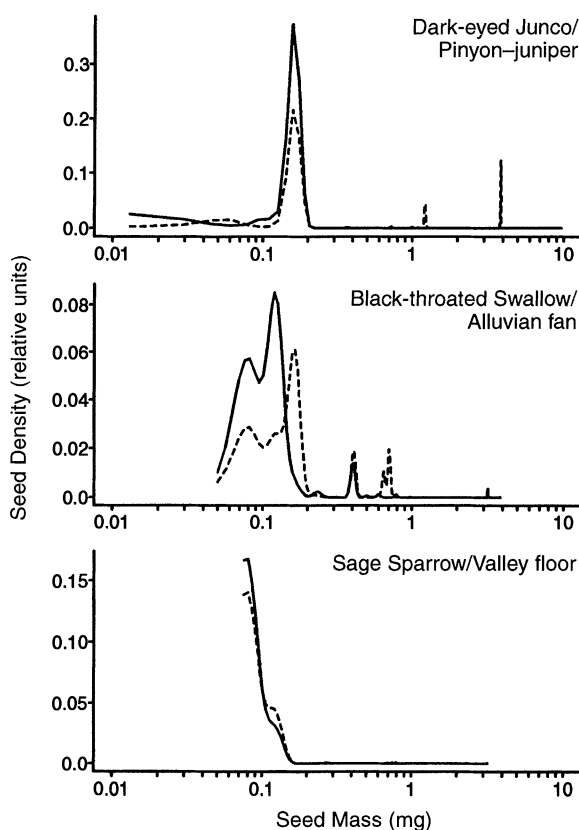


FIG. 2. Size distributions of seeds in the diets of wild-foraging birds (—) and in their preferred habitats (---). Data were collected during two winters prior to the present study (for details see Repasky and Schluter 1994). Distributions were smoothed using a nonparametric density function (Becker et al. 1988).

eaten than it was to peck rate or to the rate at which pecks yielded seeds. Peck rate was consistently highest on the valley floor, but food intake rates there were lower than in other habitats for two of the three species studied (Table 1), chiefly because only very small seeds (mostly *Schismus barbatus*) are present in that habitat.

Because food intake rates were closely related to seed size and because our estimates of the mean seed mass were made indirectly, we examined estimates of seed mass made by different methods to determine whether our results were contingent upon the methods used. Sparrows foraging in the wild eat seeds between 0.06 and 0.20 mg (Fig. 2). Preference functions calculated from the diets of wild-foraging birds and data on food availability performed well at predicting the diets of sparrows foraging in the aviary. Predictions of mean size of seeds eaten by sparrows were positively correlated with the mean size of seeds consumed by birds in the aviary (Fig. 3,  $r = 0.76$ ,  $n = 7$ ,  $P < 0.05$ ). Also, differences between observed and predicted

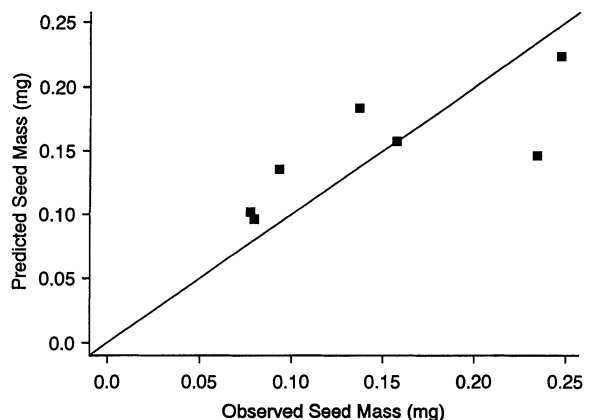


FIG. 3. Mean size of seeds eaten by birds foraging in an aviary and means predicted from diet preferences of wild-foraging birds and food abundances. The reference line depicts a 1:1 relationship.

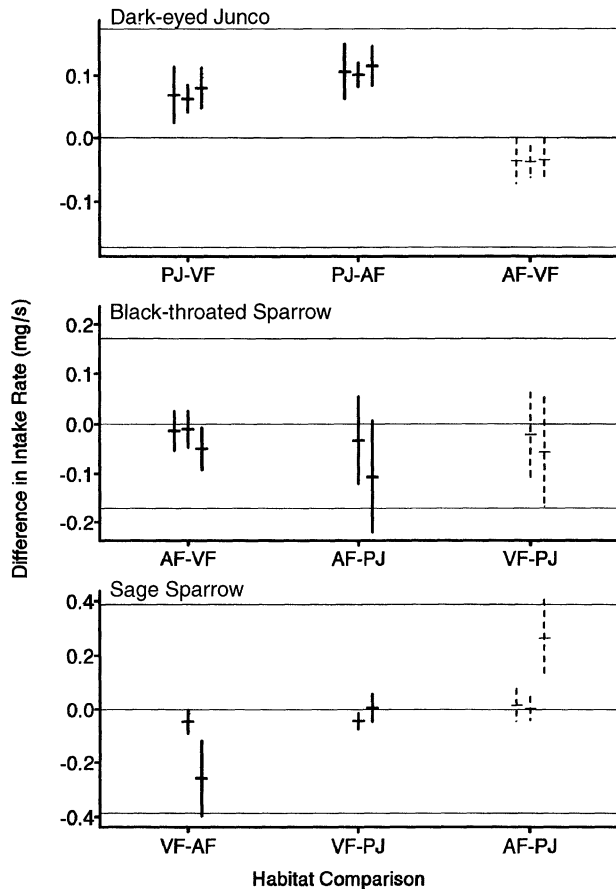


FIG. 4. Differences in foraging success (intake rate) between habitats. Error bars indicate  $\pm 2$  SE. Bold, solid symbols depict differences between habitats occupied by a given species and unoccupied habitats, calculated as (occupied habitat) - (unoccupied habitat). Comparisons displaced to the left of the corresponding tick marks on the x axis are based on mean mass of seeds in vomit specimens collected after feeding trials in the aviary. Comparisons directly above the corresponding tick marks are based on a Bayesian estimate of mean seed mass in the diet (see *Methods*). Comparisons displaced to the right of the corresponding tick marks are based on the 80th percentiles of peck rate and mass of seeds in vomit specimens (see *Methods*). Light, dashed symbols depict differences between pairs of habitats not occupied by species. Habitat symbols: PJ = pinyon pine-juniper woodland, AF = alluvial fan, VF = valley floor.

mean size of seeds in the diet did not differ significantly from zero ( $\bar{x}_d = 0.003$  mg,  $s_{x_d} = 0.018$ ,  $df = 6$ ,  $P = 0.89$ ). These data suggest that food preferences in one habitat can be used to predict diets in other habitats. We present comparisons based on observed diets of birds foraging in the aviary and on Bayesian estimates of diets to allow the reader to compare results.

To test whether our conclusions about foraging performance in habitats are contingent upon whether we compared mean food intake rates or food intake rates achieved in food-rich areas, we calculated adjusted food intake rates from the 80th percentiles of peck rate and mass of seeds consumed by birds in the aviary. Adjusted food intake rates averaged 14.5% higher than mean food intake rates (Table 1). Several adjusted food intake rates were actually less than the corresponding mean food intake rates, owing to differences between the 80th percentile and mean mass of seeds consumed. The 80th percentile of seed mass was in some cases less than mean seed mass because of a few very large seeds in diet samples, which strongly influenced means. Nevertheless, changes were independent of habitat, and our comparisons of food intake rates between habitats were unaffected. We discuss only comparisons of mean food intake rates, although we also present adjusted food intake rates.

*Habitat comparisons*

Under the foraging success hypothesis, species dwell in the habitats in which they forage most successfully. Only Dark-eyed Juncos achieved higher food intake rates in the habitat that they occupy than in other habitats (Table 1, Fig. 4). It was unclear whether Black-throated Sparrows are most successful at feeding in their usual habitats because they exhibited small differences in seed intake rates between habitats relative to error (Fig. 4). Sage Sparrows actually achieved their lowest food intake rates in their usual habitat (Table 1), and they achieved their highest food intake rates in the habitat (alluvial fan) occupied by Black-throated Sparrows. These results suggest that Sage Sparrows suffer a disadvantage in the habitat that they occupy and that Black-throated Sparrows gain at best only a slight feeding advantage by dwelling in the habitat that they occupy. Clearly, neither the foraging success hypothesis nor the exploitative competition hypothesis can explain the habitat distributions of these species.

A second prediction of the foraging success and exploitative competition hypotheses is that foraging success in one habitat is gained at the expense of success in other habitats. Dark-eyed Juncos and Sage Sparrows experienced large and significant trade-offs in foraging

success between habitats (Fig. 4, Table 1). Juncos foraging on the alluvial fan ingested seeds at only 40% of the rate that they did in pinyon–juniper. On the valley floor they ingested seeds at 67% of the rate in pinyon–juniper. Sage Sparrows on the valley floor consumed seeds at 55% of the rate on the alluvial fan. In pinyon–juniper, they consumed seeds at 75% of the rate on the alluvial fan. Black-throated Sparrows experienced only small trade-offs in food intake rate between habitats and achieved nearly equal food intake rates on the valley floor and in pinyon–juniper. They consumed seeds on the alluvial fan at 86% of the rate that they did on the valley floor and in pinyon–juniper.

#### DISCUSSION

Hypotheses to explain habitat partitioning by the three sparrows must account for three of its features: why each species prefers one habitat over others, why each species is restricted to a single habitat, and why each species occurs alone. We tested the hypotheses that nonoverlapping habitat distributions of sparrow species result from species' differences in foraging ability and from exploitative competition. Here, we summarize our results showing that the foraging success hypothesis and the exploitative competition hypothesis fail on all three counts.

Under the foraging success hypothesis, habitat preferences should result from differences in feeding ability between habitats. Under exploitative competition, habitat preferences result from food remaining after depletion by competitors. Observed differences in foraging success can explain the habitat distribution of only one of the three species. Dark-eyed Juncos clearly were most successful at foraging in the habitat that they occupy, and they experienced large, significant differences in food intake rate between habitats. Sage Sparrows also experienced significant differences in foraging success between habitats, but they were least successful at foraging in the habitat that they usually occupy. Black-throated Sparrows achieved very similar foraging success in all three habitats.

Are differences in foraging success sufficient to restrict species' habitat distributions? Juncos feeding outside of pinyon–juniper experienced food intake rates that were 40–67% of those inside pinyon–juniper. Such large disadvantages to foraging outside of pinyon–juniper might be sufficient to explain why juncos are restricted to this habitat. Black-throated Sparrows experienced very small differences in foraging success between habitats.

Insights from the theory of habitat selection and comparative data from other populations also suggest that the sparrows we studied would be more broadly distributed if food alone shaped the distribution of each species independently of the others. Theoretically, species could specialize on single habitats despite only slight trade-offs 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. Interference among feeding sparrows and finches generally increases as flock size increases (e.g., Caraco 1979, Barnard 1980) and limits flock size (Barnard 1980), suggesting that foraging success is likely to decline as population density increases. Also, food appears to limit population density during winter (R. R. Repasky, *unpublished manuscript*) 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 more widely 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 our 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. Indeed, earlier work indicates that species are absent from habitats in which food is at least as abundant as in those habitats that they occupy (Repasky and Schluter 1994). 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. This prediction was not fulfilled. All three species experienced favorable food intake rates in pinyon–juniper. Juncos clearly achieved higher feeding rates in pinyon–juniper than in other habitats. Black-throated Sparrows achieved slightly higher, although not significantly higher, food intake rates in pinyon–juniper than in other habitats. Sage Sparrows achieved similar feeding rates in pinyon–juniper and the alluvial fan, and those rates were higher than food intake rates that Sage Sparrows achieved on the valley floor.

Conclusions from other studies of the role of food in shaping species' distributions vary in the importance attributed to food. Among Galápagos ground finches food explains species' distributions along an elevational gradient (Schluter 1982). Species' distributions corresponded closely with the distributions of their foods. However, 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.

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 or even superior warrants explanation. What other factors might explain habitat partitioning by sparrows in the present study? In our work, we have addressed these: vegetation and substrate structure, predation, and interspecific competition (Repasky and Schluter 1994). Structural features of habitat might affect the ability of birds to search for food. Predation risk might affect food intake rates because of a trade-off between feeding and scanning for predators (McNamara and Houston 1986, 1987, Repasky, *in press*). However, both habitat structure and predation risk were incorporated in our 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, we 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 (Repasky, *in press*).

Finally, there is the interference competition hypothesis. Our results support Lack's (1944) argument that species' differences in feeding ability 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. Competition, if it occurs, is unlikely to be through depletion of food resources because food remaining after exploitation by competitors would shape species' distributions, a prediction that is inconsistent with our results. Species could compete through interference, and the presence of one species in a habitat could be sufficient to exclude others from that habitat (e.g. Pimm and Rosenzweig 1981, Rosenzweig and Abramsky 1986). 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 (Repasky and Schluter 1994). Finally, food appears to limit population density during winter, and sparrows are capable of depleting the amount of resources available to one another (R. R. Repasky, *unpublished manuscript*). In view of this evidence, more direct tests of the competition hypothesis are desirable.

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