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Foraging Behavior and Switching by the Grasshopper Sparrow *Ammodramus savannarum* Searching for Multiple Prey in a Heterogeneous Environment

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ABSTRACT: Switching among four alternative grasshopper species by the grasshopper sparrow (*Ammodramus savannarum*) through frequency-dependent predation was examined. Grasshoppers were presented against a heterogeneous natural background in an outdoor aviary where total density was held constant but relative density of each grasshopper species varied. Switching among prey, primarily between two of the four species, and inter-bird variability in switching was observed. Species-specific preferences and interactions among the alternative grasshopper species affected the final diet choice as one grasshopper species was always preferentially selected and another disregarded independent of changes in relative density. Attributes of avian foraging behavior, including: (a) proportion of total time spent handling prey, searching for prey or engaging in nonforaging activity; (b) capture success; (c) time required to catch prey (relative to either total or search time), and (d) attack distance did not vary according to the relative abundance treatments. Results of this study are related to quantitative estimates of predation and relative densities of grasshopper species in a natural grassland setting.

INTRODUCTION

Generalist predators have been shown to switch among alternative prey as the relative densities vary (Hassell, 1978; Murdoch, 1969; Murdoch and Oaten, 1975). Switching involves a frequency-dependent functional response where predators change from selecting the predominant prey type to another as its relative density increases.

The dynamics of switching are contained in the functional response of the individual predator. Functional responses relate the predator attack rate to prey density (Hassell, 1978). Mechanisms proposed to explain switching behavior include: foraging for alternative prey in different patches, the formation of search images by the predator, decreases in handling time with experience, or increases in searching efficiency within patches (reviewed in Murdoch and Oaten, 1975). The first two mechanisms have been studied in most detail. When predators forage for alternative prey living in different patches and transit time among the patches is not negligible, increased foraging activity in the patch with higher prey availability will lead to the sigmoidal switching response described by Oaten and Murdoch (1975). Predators may form search images where the psychological processes involved with locating and recognizing prey against the background are altered depending on the relative abundances of the various prey types (Dawkins, 1971; Gendron and Staddon, 1983; Pietrewicz and Kamil, 1979, 1981). It is likely that all of these mechanisms operate in natural foraging situations.

Switching by predators has important implications for many other ecological and evolutionary processes. Frequency-dependent predation within a population is affected by the degree of morphological (or behavioral) polymorphism among individuals in a population and is expected when foraging on alternative prey species as well (Clarke, 1962). Visually orienting predators may select for morphological divergence of coexist-

ing prey and thus determine which species can coexist (Clarke, 1962) and may explain some patterns of prey assemblies (Jeffries and Lawton, 1985; Joern and Lawlor, 1981; Rand, 1967; Ricklefs and O'Rourke, 1975; Levin and Segal, 1982). In this manner, the number and taxonomic composition of coexisting prey species may be determined through switching among prey by a visually orienting predator. Other plausible predator-mediated mechanisms involving switching may also affect organization of prey assemblages (*e.g.*, apparent competition, Holt, 1984; compensatory mortality, Connell, 1978).

Most studies which have documented switching have employed two alternate prey species presented to predators in relatively simple environments (Murdoch and Oaten, 1975). The results of these studies must readily extrapolate to more complex and realistic situations if these mechanisms are to be invoked to interpret multiple-species assemblies. Whether such extrapolation is justified is seldom examined. In the present study, I presented visually orienting grasshopper sparrows (*Ammodramus savannarum*) with a choice of four grasshopper species (*Amphitornus coloradus*, *Ageneotettix deorum*, *Cordillacris occipitalis* and *Melanoplus sanguinipes*) and varied the density of each prey species. The background was heterogeneous and consisted of naturally growing vegetation. By adding both multiple prey and a heterogeneous background to the experiment, important insights concerning the role of switching in structuring assemblies of insect prey may be gained.

I asked the following questions: (1) Do components of foraging behavior such as proportion of time spent searching (or in nonforaging activity), search time per prey, probability of capturing observed prey and time spent handling prey, change in response to changes in relative densities of alternate prey? (2) Do grasshopper sparrows switch among multiple prey in a frequency-dependent manner when foraging in a heterogeneous environment? (3) If switching is observed, do preferences by the predator exist or are there other synergistic interactions among available prey which influence the final pattern of diet choice by the predator?

METHODS

Experimental subjects.—Experimental subjects were chosen to be representative of naturally occurring assemblages observed at a Nebraska sandhills study site (Arapaho Prairie, Arthur Co.). A detailed description of this site is found elsewhere (Barnes, 1980; Joern, 1982). Although additional grasshopper and bird species are found at these sites, the number of species used in the experiments was chosen as a compromise between natural complexity and the need for a manageable number of species for experimentation.

Four grasshopper species (and mean body lengths) were used in the experiment: *Ageneotettix deorum* (Scudder) (19.6 mm), *Amphitornus coloradus* (Thomas) (24.1 mm), *Cordillacris occipitalis* (Thomas) (23 mm), and *Melanoplus sanguinipes* (Fabr.) (24.7 mm). These species were chosen because of the availability of sufficient individuals of these species to stock experiments and the general similarity in size. None of these species exhibited extensive intraspecific polymorphism. Only females were used for the first three species and mostly females were used for *M. sanguinipes*. Morphological comparisons between the sexes of *M. sanguinipes* indicated no statistically significant differences so both sexes were used when there was a shortage of females. Microhabitat use varied somewhat among these species. *Ageneotettix deorum* and *C. occipitalis* tended to be found in more open areas while *A. coloradus* was more likely to use denser vegetation in addition to open areas; *M. sanguinipes* was less restrictive in microhabitat use than the other species.

Morphologically, *Amphitornus coloradus* and *Cordillacris occipitalis* are superficially more similar, compared with any other species pair, and *Ageneotettix deorum* is slightly smaller than the other species. All species are typically common in Nebraska sandhills and nearby shortgrass prairie assemblages (Joern, 1982). Phenologically, all species overlap

extensively although populations of *C. occipitalis* tend to disappear before the other species.

Grasshopper sparrows (*Ammodramus savannarum*) are small (ca. 16 g), widespread grassland passerines (Smith, 1963; Robbins *et al.*, 1966). Their diet consists largely of insects; grasshoppers (Acrididae) and other Orthoptera comprise the great majority of prey in the diet of grasshopper sparrows at Arapaho Prairie. Grasshopper sparrows are numerically dominant among the avian insectivores at Arapaho Prairie (M.E. Kaspari, pers. comm.) and greatly contribute to the depression of grasshopper densities under natural conditions (Joern, 1986). Feeding trials in the laboratory have demonstrated that these birds readily eat each of the above grasshopper species (Kaspari, 1985). It is likely that grasshopper sparrows readily distinguish among grasshopper species based both on observations of grasshopper sparrows under controlled and natural conditions (pers. observ.) and on laboratory studies with bobwhite quail (Morris, 1982).

Experiments. — Foraging experiments were performed sequentially in a single 4 m x 4 m x 2 m outdoor aviary constructed of wire screening on the top and three sides. The fourth side was completely covered with plywood to prevent the birds from easily spotting the observer. Vegetation on the aviary floor was natural (mostly grasses) but modified by adding open sandy patches. Sandy patches tended more toward a uniform distribution than either random or clumped and were partially covered with small amounts of litter. Experiments were performed at the Cedar Point Biological Station (near Ogallala, Nebraska) in late July and August, 1983 (four birds) and 1984 (one bird). Observations were made through a slit approximately 2 cm wide which ran along the length of the plywood side of the aviary.

Grasshopper sparrows were collected using mist nets and placed in the aviary for at least 24 hr (usually 48 hr or longer) before experiments were begun; some birds had been previously used in another study. Birds used in the experiments rapidly settled down and generally foraged readily; two additional birds which did not readily forage and which were very wary were released without further experimentation.

At the beginning of each experiment, grasshoppers were introduced into the center of the aviary within an area of approximately 3-4 m². A bird was already present. Typically, grasshoppers quickly dispersed throughout the aviary. Birds often began foraging within several minutes after the observer had left the aviary and always within 15 min. Based on continuous observations, birds encountered prey sequentially.

Six treatments (Table 1), each consisting of different relative densities of the grasshoppers, were presented to each bird in random order. Overall density was maintained at four individuals/m² (64/ treatment). This is within the range of overall grasshopper densities observed at Arapaho Prairie over a 7-year period (Joern, 1982). *Amphitornus coloradus* was varied over the greatest range of relative densities (0.09-0.56) and the other three species *Ageneotettix deorum*, *Cordillacris occipitalis* and *Melanoplus sanguinipes* were presented at equal relative densities within trials in order to maintain constant initial density of all grasshoppers among trials. Since it was not possible to exactly balance the number of individuals of these alternative species and maintain a constant density, one

TABLE 1. — Frequencies of available grasshoppers in each experimental treatment. Overall density was maintained at four individuals/m²

Grasshopper species	Treatment					
	1	2	3	4	5	6
<i>Amphitornus coloradus</i>	0.09	0.19	0.28	0.37	0.47	0.56
<i>Ageneotettix deorum</i>	0.30	0.27	0.24	0.21	0.18	0.15
<i>Cordillacris occipitalis</i>	0.30	0.27	0.24	0.21	0.18	0.15
<i>Melanoplus sanguinipes</i>	0.30	0.27	0.24	0.21	0.18	0.15

species (usually a different species) was represented by one additional individual in each treatment. This slight difference in specific prey availability was incorporated when electivities were calculated.

Specific foraging trials were run until 10 prey individuals were taken or 2.5 hr had elapsed. Prey were not replaced after capture; overall prey depletion was 15.6% when 10 individuals were taken. Two trials per bird were run per day if weather permitted. The first run was begun between 0700-0800 and the second begun between 1530-1600. Sequence of the treatments for each bird was randomly assigned and each treatment was run once per bird. At the completion of a treatment, remaining grasshoppers were left as food for the bird. Most if not all of these prey were taken in the intervening period as I was unable to collect any when I checked the aviary before new trials were begun. Birds began each trial at approximately the same hunger level based on the initial rates of foraging. All birds were maintained on the same schedule of food availability and the time between treatments was constant.

Analyses.—When data were not normally distributed and sample sizes small, I analyzed attributes of foraging behavior using nonparametric tests (*e.g.*, Friedman Two-Way Analysis of Variance). Regression analysis for detecting quadratic relationships was performed using Proc GLM of the SAS statistical package (SAS Institute, 1982). A sample of five birds was obtained for each treatment.

Electivity measures the preference for particular food items relative to the other food items present. If switching occurred, the electivity for a given prey type should increase as the relative density of that prey type increased (Chesson, 1983; Murdoch, 1969). Electivity was measured by the normalized $\hat{\alpha}$ as derived by Chesson (1978, 1983; from Manly *et al.*, 1972; Manley, 1974) based on a simple stochastic model which incorporated the probability of prey encounter and the probability of capture given encounter. An advantage of this index is that it measures instantaneous preferences and does not change with food density unless consumer or prey behavior changes; this permits the detection of ecologically significant processes such as switching (Chesson, 1983). Prey depletion during trials was accounted for by using the approximate maximum likelihood estimate of:

$$\hat{\alpha} = \frac{\ln ((n_{j0} - r_i)/n_{j0})}{\sum_{j=1}^m \ln ((n_{j0} - r_j) / n_{j0})}, \quad i = 1, \dots, m$$

where n_{j0} is the number of items of prey type j present at the beginning of a foraging bout, r_i is the number of items of food type i taken in the consumer's diet, and m is the number of prey taxa involved (Chesson, 1983). When foraging is nonselective, (*i.e.*, prey taxa are taken in the same proportion as they are available), $\hat{\alpha} = 1/m$ or 0.25 in these particular experiments. Greenwood and Elton (1979) have criticized Manly's β model and by extension the closely related $\hat{\alpha}$. The main objection is that $\hat{\alpha}$ may be modified because of changes in the predator behavior. This is exactly what I wish to examine in these experiments so $\hat{\alpha}$ will be an appropriate index (*also see* Willis *et al.*, 1980).

RESULTS

Foraging behavior.—Approximately 10% of the time is actually spent handling prey, 53% searching and 38% in nonforaging activity (Table 2). Pursuit time was negligible in relation to these activities and was not accurately measured; estimates of pursuit time range from 5-15 sec per attack. No significant treatment effect was observed for the proportion of total time spent handling prey, searching or in nonforaging activity (Friedman 2-Way ANOVA, $P > 0.10$). Average elapsed time per prey capture, based on either search time or total time (including nonforaging activity), does not differ among treatments (Friedman 2-Way ANOVA, $P > 0.10$), although the time per capture drops in

TABLE 2. — Foraging performance for the experimental treatments described in Table 1. Means of five birds and 1 sd are presented. No significant treatment differences are observed for any foraging category (Friedman 2 Way Analysis, $P > 0.10$). Capture success is the proportion of prey caught relative to all attempts

	Treatment					
	1	2	3	4	5	6
Proportion of total time						
Handling time	.10 (.03)	.09 (.03)	.11 (.05)	.10 (.02)	.12 (.03)	.18 (.08)
Search time	.47 (.23)	.63 (.26)	.53 (.10)	.56 (.17)	.62 (.13)	.38 (.14)
Nonforaging time	.43 (.22)	.28 (.25)	.35 (.14)	.34 (.18)	.25 (.16)	.43 (.10)
Search time per capture (Sec)	302.9 (179.1)	392.0 (152.3)	312.1 (65.5)	352.7 (114.7)	334.6 (144.7)	228.6 (122.3)
Total time per capture (Sec)	600.6 (110.6)	627.7 (71.8)	601.3 (171.0)	635.1 (111.6)	540.4 (271.0)	398.9 (267.7)
Capture success (%)	78.5 (13.2)	83.8 (9.3)	80.3 (11.5)	91.9 (5.2)	88.7 (13.4)	88.7 (8.9)

treatment 6 using either measure. Capture success averaged 85.3% overall and showed a slight but statistically nonsignificant increase going from treatment 1 to treatment 6 (Friedman 2-Way ANOVA, $P > 0.10$).

Mean attack distances in cm (and 95% confidence intervals) for instances when a bird attempted, or succeeded, to capture a grasshopper for each species are: *Ageneotettix deorum*—46.0 (14.6), *Amphitornus coloradus*—28.5 (4.2), *Cordillacris occipitalis*—31.6 (5.2), and *Melanoplus sanguinipes*—47.1 (11.1). It was not possible to estimate detection distance except when an attack was involved. No differences in attack distances were evident among treatments or individual birds.

Switching among alternative prey.—In the composite picture, the proportion of *Amphitornus coloradus* in the diet as a function of relative availability increases at a faster rate than would be expected based on random foraging when preferences are constant and equal ($C = 1$) (Fig. 1). A significant quadratic relationship (SAS, GLM Procedure, $P < 0.05$) is obtained which supports this observation. If there are constant but unequal preferences for *A. coloradus*, the expected diet changes; two additional possibilities are shown in Figure 1. The same general conclusion holds and is again supported by the results of the regression analysis. Expected curves in the general range of those presented are probably reasonable.

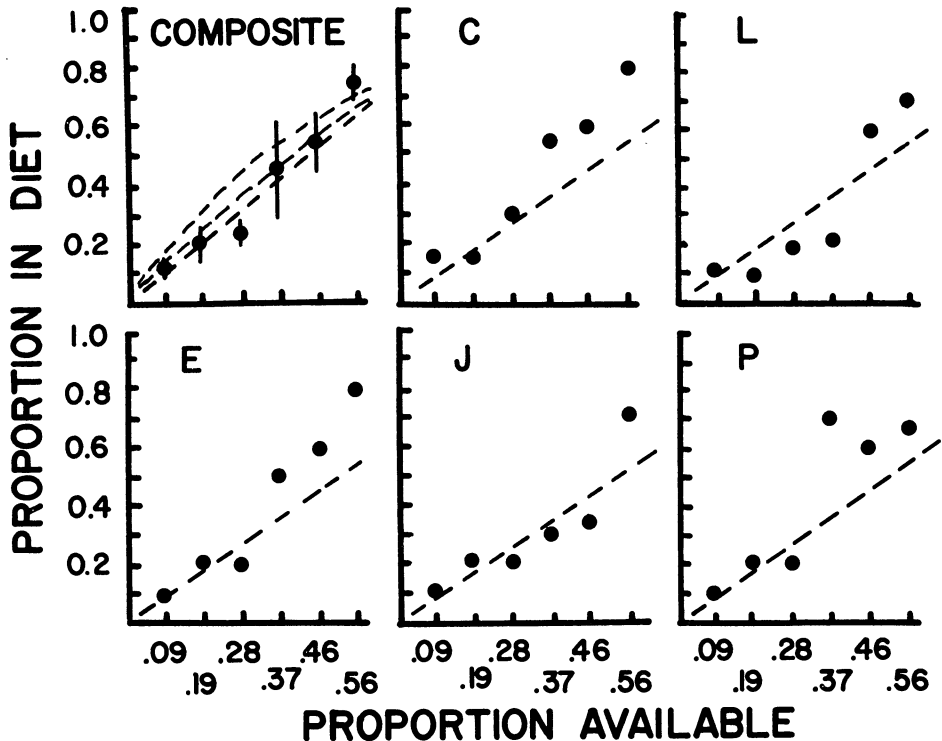


Fig. 1.—Proportion of *Amphitornus coloradus* in the diet in relation to the proportion of *A. coloradus* in the available prey pool for individual grasshopper sparrows and a composite average. Error bars in the composite represent 2 se about the mean. The dashed lines in each panel (from top to bottom) represent the proportion which should be included in the diet if the birds are randomly selecting prey with constant and either equal ($C = 1$) or unequal ($C = 1.5$ or 2) preferences for *A. coloradus* relative to the other species. These expectations are calculated using the formula given in Murdoch and Oaten (1975). Letters (C,E,J,L,P) represent individual grasshopper sparrows

Behavior varied among individual birds (Fig. 1). Some individuals showed dramatic changes in the proportion of *Amphitornus coloradus* included in the diet as its relative density increased while others changed gradually. No obvious differences in the order of treatment presentation or other external factors affecting the birds were detected to explain these interindividual differences.

Cordillacris occipitalis was clearly a preferred prey species as it had uniformly high electivity values even when uncommon (Fig. 2). Typically, electivity of *C. occipitalis* was either greater than or not significantly different from *Amphitornus coloradus*. When all species were nearly equally abundant (treatment 3), the ranking of the prey species was: *Cordillacris occipitalis*, *Melanoplus sanguinipes*, *A. coloradus* (not significantly different from *M. sanguinipes*) and *Ageneotettix deorum*. As the relative density of *A. coloradus* increased, electivity also increased which indicated that the birds were switching to this prey item. However, species-specific differences in electivity among the alternative prey were observed as the relative density of *A. coloradus* increased. The electivities of *M. sanguinipes* and to a lesser degree *A. deorum* dropped, while the mean electivity of the birds for *C. occipitalis* did not change qualitatively. Electivity for *C. occipitalis* did not change significantly among the treatments (Friedman 2 Way ANOVA, $P > 0.05$) while significant changes in electivities among the treatments were observed for the other species (Friedman 2 Way ANOVA, $P < 0.05$).

DISCUSSION

Switching and prey selection.—Switching affected the composition of the diet of grasshopper sparrows. As the relative density of *Amphitornus coloradus* increased, proportionally more individuals of this species were taken and the electivity of the birds for this species increased. Conversely, the electivities and relative densities in the diet of *Melanoplus sanguinipes* and *Ageneotettix deorum* simultaneously decreased as the relative densities of these species decreased. Wild passerines (Allen, 1976), captive quail (Manly *et al.*, 1972; Cook and Miller, 1977) and domestic chicks (Fullick and Greenwood, 1979; but see Willis *et al.*, 1980) have previously been shown to take disproportionately more of the common type in two prey experiments. This experiment shows that the response is also observed in multiprey situations.

Standard descriptions of switching invoke a sigmoidal functional response where a prey type should be underrepresented in the diet when rare. Although only a portion of the functional response curve for *Amphitornus coloradus* was actually investigated (Fig. 1), it is very likely that the shape is sigmoidal. Since the functional response increased in quadratric fashion to the highest level tested, the rate of inclusion of *A. coloradus* into the diet must slow as it becomes relatively more abundant since it must approach 1.0. Equally interesting is the result that *A. coloradus* was not necessarily underrepresented in the diet at lower relative densities when assuming constant preferences, a result inconsistent with switching. Electivities at the lowest densities of *A. coloradus* approximated those expected if the birds were foraging randomly and if constant and equal preferences exist. If *A. coloradus* is preferred to the other species on average, it may be underrepresented in the diet as expected if switching is taking place (indicated by curvilinear expected relationships in Fig. 1). Although the experiments did not directly address this problem, preferences for specific prey taxa do exist (Fig. 2, Treatment 3), according to those expected from optimal foraging theory (Krebs *et al.*, 1983) or as yet unspecified rules.

Birds did not always spot seemingly conspicuous prey within the reactive distance of the actively searching bird. Yet, the bird bypassed these individuals without seeming to recognize their presence and either pursued another grasshopper (of the same or another species) farther away or continued searching. Such results are consistent with the hypothesis that crypsis and associated microhabitat selection by prey are important in regulating encounter, detection and recognition rates by predators (Gendron and Staddon, 1983; Hughes, 1979). However, I typically could not locate the positions of prey from my observation post independent of bird foraging behavior so I was unable to de-

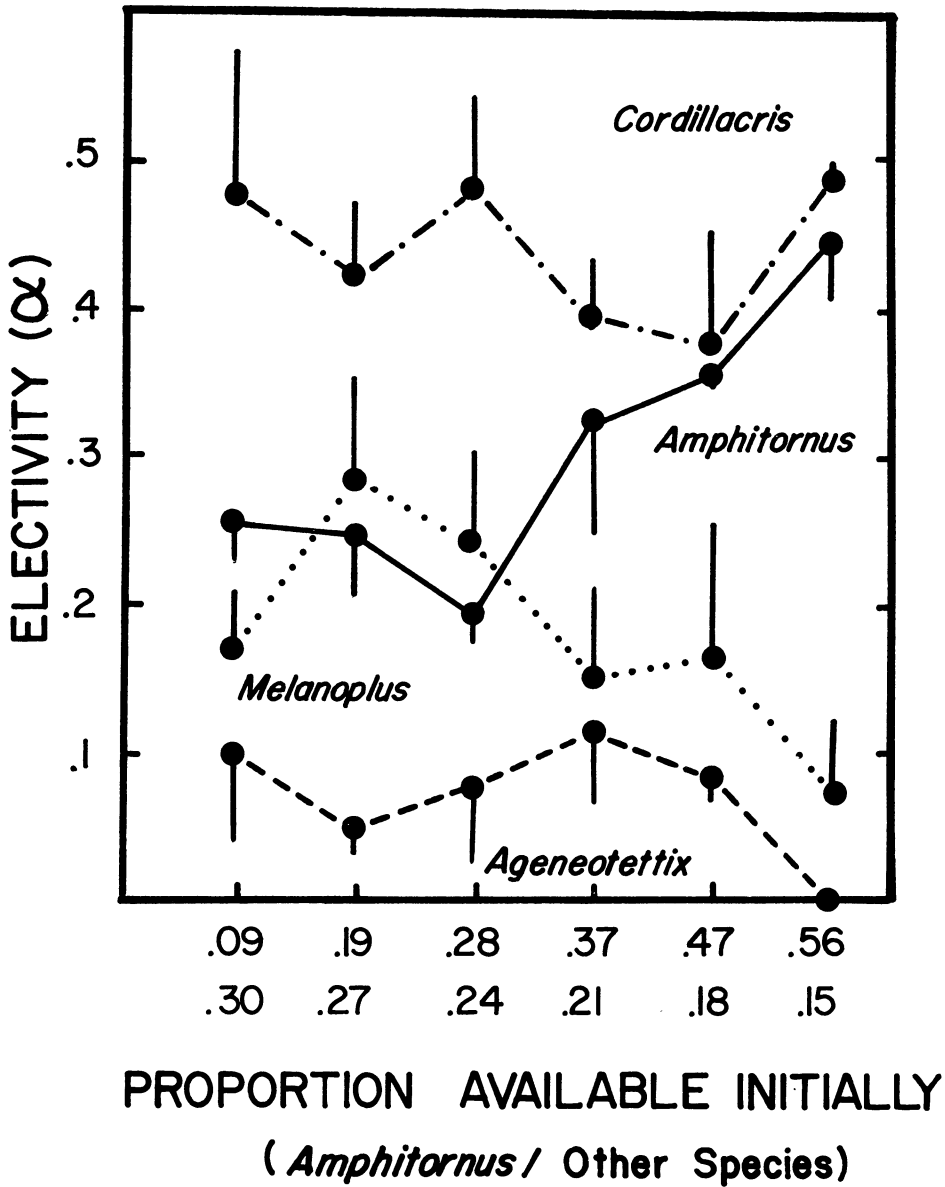


Fig. 2.—Electivity by grasshopper sparrows for each grasshopper species when presented concurrently for the six treatment combinations outlined in Table 1. Means and 1 se (shown on only one side of the mean) are indicated. Grasshopper species are represented as: *Ageneotettix deorum* (---); *Amphitornus coloradus* (—); *Cordillacris occipitalis* (— · —); and *Melanoplus sanguinipes* (·····). Electivity is calculated according to Chesson (1983)

termine how often birds failed to detect prey. These data are required to rigorously test optimal foraging models incorporating such functions.

Relative density alone does not explain species-specific prey choice by grasshopper sparrows, as interesting species-specific effects were also evident. In these experiments, *Cordillacris occipitalis* was the preferred prey based on electivity measures (e.g., Treatment 3). As the relative abundances of *C. occipitalis* varied, the electivity of the birds for this grasshopper did not vary markedly. Similarly, electivities did not vary greatly for the least preferred prey, *Ageneotettix deorum*, which was typically underrepresented in the diet. In Treatment 6, *A. deorum* dropped out of the diet of all birds when it was at its lowest relative density (which accounted for the statistically significant change in electivity).

Switching behavior observed in this series of experiments appears to be largely keyed on the effect of the interaction between *Amphitornus coloradus* and *Melanoplus sanguinipes* on foraging by the grasshopper sparrow. These species are equally preferred when equally abundant. More detailed investigations are required to determine the importance of such clear-cut differences in the effect of specific species in multispecies switching experiments.

Relationship of results to natural setting.—On average, the relative density of the most common species at Arapaho Prairie, independent of actual taxonomic identity, is ca. 0.25-0.3, with the second most common species about 0.2 (Joern, 1982). Thus, the experiment bracketed naturally occurring relative and total densities for grasshopper assemblies. The effect of switching may be significant for explaining field observations of relative densities of coexisting grasshoppers. Electivities for *Amphitornus coloradus* in the aviary experiments increased when the relative density reached ca. 0.3-0.35 compared to the normally observed maximum relative density of 0.3 for the naturally occurring dominant species at Arapaho Prairie. A working hypothesis would be that differential predation by birds reduces the numbers of this species whenever its relative density reaches 0.3. This correspondence may also be merely fortuitous. Significant impact of avian predation is most likely in patches approximated by the immediate searching area used by a foraging bird. Field tests which critically examine whether frequency-dependent predation is responsible for the observed relative densities of coexisting species have not yet been performed.

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