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Central place foraging in grasshopper sparrows: opportunism or optimal foraging in a variable environment?

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Optimal foraging models provide a logical alternative hypothesis to that of dietary opportunism (sensu Wiens and Rotenberry). Central Place Foraging models (Orians and Pearson) predict that, with increasing distance from the nest, parents should select larger prey (Single Prey Loading model) and/or more prey (Multiple Prey Loading model). The thirteen grasshopper sparrows (*Ammodramus savanarrum*) sampled do both, but show a stronger tendency – with less inter-individual variability – to multiply-load small (< 10 mm) abundant grasshoppers. Fledgling success and food delivery rate to the nest were also correlated across a sample of 23 nests. Thus a population of grassland birds from a temporally variable environment did not forage opportunistically but selected prey in a manner consistent with a model of energy maximization.

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Community ecologists have often concluded that populations of breeding grassland birds are opportunistic foragers (Cody 1968, 1974, Fretwell 1972, Wiens and Rotenberry 1979, 1980, Rotenberry 1980). Although difficult to define precisely, Wiens and Rotenberry (1979) equate opportunistic foragers with those that are "*eating by and large whatever they encounter*" (italics mine). Opportunism, they argue, arises from the lack of food limitation. Subsequently, individuals which do not maximize food intake are not penalized relative to birds which do (Wiens 1977). Evidence for dietary opportunism, however, has been sketchy and inferential, based on large dietary overlaps between coexisting species (Wiens and Rotenberry 1979) and a strong temporal component to the diet (Rotenberry 1980).

Optimal foraging theory provides an ideal alternative model to the null hypothesis of opportunism. Optimal foraging models are based on a hierarchical set of assumptions. At the heart of these models – their "hard core" (Mitchell and Valone 1990) – is the assumption that foragers that maximize intake rates accumulate in the population via differential survival and reproduction. Thus these models assume food limitation (i.e., reproductive and/or survival benefits to increasing intake rate) and subsequently predict rules by which foragers may maximize intake subject to specified constraints.

Central Place Foraging Models

One set of optimal foraging models appropriate to assemblages of breeding birds are the Central Place Foraging models of Orians and Pearson (1979). These models assume that foragers make trips to and from a central place (i.e., the nest), that prey are encountered randomly and singly, searched for simultaneously, and that predation risk is homogenous throughout the process.

Orians and Pearson (1979) consider how prey size and number should vary as birds forage progressively

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farther from the central place. They model these questions separately. Single Prey Loader (SPL) models assume that foragers select a single prey, varying its size with distance from the nest. SPL's assume that prey densities do not vary with distance from the nest. SPL's predict that larger prey should be returned as the forager travels farther from the central place (Orians and Pearson 1979, Stephens and Krebs 1986).

The Multiple Prey Loader (MPL) model assumes that foragers vary the number of prey returned based on distance from the nest. The MPL assumes that a forager's ability to capture prey decreases as additional prey are acquired (i.e., the loading curve is negatively accelerated, Orians and Pearson 1979). It predicts that a forager should return with larger loads as it travels farther from the nest. An explicit derivation of these and other predictions of Central Place Foraging theory is available in Orians and Pearson (1979) and Stephens and Krebs (1986). Although treated as separate problems, there has been little exploration of the possibility that a forager may choose to increase both prey size and number as it travels farther from the nest.

When should a forager switch to a MPL tactic? Orians and Pearson (1979) present two hypotheses. The first, the Escape Syndrome Hypothesis, suggests that SPL's should predominate if prey are active and escape-prone. They reason that carrying such a prey item would especially decrease capture efficiency relative to inactive prey which could simply be picked up. The second, the Prey Size Hypothesis, suggests that SPL's should predominate when the typical prey size is too large, relative to the bird's bill, to allow multiple loads. I am aware of no studies that have tested these hypotheses.

Herein I report on a four-year study of a breeding population of the grasshopper sparrow (*Ammodramus savannarum*), an emberizine bird of the Sand Hills grasslands of western Nebraska. The primary goal of this paper is to evaluate in detail Orians and Pearson's (1979) model of Central Place Foraging. I evaluate three critical assumptions, predictions of both the SPL and MPL models, and predictions regarding the types of prey that are multiply versus singly-loaded. I use data from 13–17 individuals and 23 nests. I relate these findings to the hypothesis that birds breeding in temporally variable grasslands are dietary opportunists.

Materials and methods

This study was conducted from 1981 through 1984 on Arapaho Prairie, two sections of mixed-grass prairie in the Sand Hills of western Nebraska (Keeler et al. 1980).

Grasshopper sparrows are migratory, arriving at Arapaho Prairie from late April to early May. The sparrows are not philopatric between years (Kaspari and O'Leary 1988). Thus lacking long-term survival data, I measured seasonal reproductive success as a component of fitness. Grasshopper sparrows build cryptic nests on the ground, which I located by walking the prairie and flushing brooding sparrows.

Evaluating fledging success and intake rate

I evaluated the assumption that nests with a higher prey delivery rate produced more offspring. Fledging success was evaluated by checking nest contents every 1–2 (rarely 3) d. Empty nests found when nestlings were six days-old or older were assumed to have fledged, given the ability of nestlings to abandon the nest at this age, although they may stay in the nest up to eight days (Kaspari, unpubl. data).

I observed 23 nests with a spotting scope from a blind 5 m from the nest. I placed surveying flags 5 m from the nest (in 4 directions) and 10, 20, and 40 m from the nest (in 8 directions) and estimated distances flown by parent birds to and from foraging sites. When a parent returned, I noted its sex based on individual plumage differences and the territorial song of the male (Kaspari and O'Leary 1988).

Grasshopper sparrows perch next to the nest for up to a minute before delivering prey, allowing for thorough scrutiny of bill contents. I identified the prey type(s) delivered, at least down to sub-family, often down to species for most of the grasshoppers and tettigoniids. Prey were categorized by size (< 0.5 cm, 0.5–1.0 cm, 1.0–2.0 cm, 2.0–3.0 cm, > 3.0 cm) based on comparisons with the bill size. Independent estimates of prey size and type by A. Joern (pers. comm.) – also familiar with the local insect assemblage – closely matched my own. I typically observed a nest for two three-hour periods daily. Nests were observed from 0530 to 2030 hours with 69% (147 h) of the observations between 0930 and 1530.

I calculated prey delivery rates by 1) converting prey length into prey mass using equations specific for each prey group (Kaspari and Joern, unpubl. data); 2) calculating grams of prey delivered in 30 min blocks (e.g., 0530–600 hours); and, 3) calculating the average delivery rate for each day (=nestling age) that a nest was studied.

Since provisioning rates increases with nestling age (Willson 1966, Royama 1966), I evaluated the relationship between food delivery rate and fledging success using nestling age as a covariate and fledgling number as a main affect in an Analysis of Covariance. Since nest predation and the unpredictable nature of nest discovery influenced the age distributions of nestlings sampled, I analyzed relationships using SAS (1983) General Linear Models, which allows for empty cells in the data.

Table 1. Analysis of fledging success as it varies with prey delivery rate with nesting age as a covariate, 23 nests are sampled. Age and Fledgling are one-way comparisons. Prey delivery rate is in units of grams freeze-dried weight of prey * 30 minutes^{-1}.

Source	df	Type III SS	p	$r^2=0.2202$
Age	1	0.06890	0.0500	
No. Fledged	3	0.16710	0.0460	
Age*Fledged	3	0.08301	0.3459	
Error	45	1.12414		

Testing the central place foraging models

Because Arapaho Prairie consists of rolling hills, only 11 of 23 grasshopper sparrow nests (1 in 1982, 4 in 1983, 6 in 1984) had suitable locations allowing me to follow parent birds to and from foraging sites. From these nests, 13–17 birds provided sufficient sample sizes (see below) for statistical analyses.

The SPL model assumes equal prey availability with distance from the nest. I evaluated this assumption at five nests (4 in 1983, 1 in 1984). I placed aluminum rings with an area of 0.1 m^2 next to the surveying flags at distances 5, 10, 20, and 40 m from the nest. Daily, and sometimes twice daily, I counted grasshoppers (divided into three size categories: < 1 cm, 1–2 cm, > 2 cm) within each ring (see Onsager and Henri 1977).

The SPL model predicts increasing prey size with distance from the nest. I used a two-way ANOVA, comparing distance foraged from the nest across individual birds and prey size (lumping the five observed size categories into the three corresponding to the grasshopper census). I must have recorded a minimum of ten provisioning trips with distance and prey-size data for an individual to be entered into the analysis (mean sample size per bird: 40 prey; range 12–97).

The MPL models predict increasing number of prey with distance foraged from the nest. I compared the mean distance foraged for single versus multiple-prey loads using a two-way ANOVA, with individual birds as the second main affect. Thirteen birds, with at least 5 samples in each category (mean sample size$_{SPL}$ / bird=32, range 6–97, mean sample size$_{MPL}$ / bird=14, range 5–32), were used in the analysis.

I evaluated the Escape Syndrome hypothesis with two common prey types. Grasshoppers (Orthoptera) escape imminent capture by leaping; caterpillars (Lepidoptera) escape through crypsis or aposematism (pers. obs.). I tested the prediction that the quiescent caterpillars would be singly-loaded more relative to actively escaping grasshoppers.

To test the Prey Size hypothesis I compared prey sizes of multiple and single prey loads for individual birds with at least 5 samples in each class using separate Mann-Whitney U-tests. However, splitting the analysis among the 17 birds meeting this criterion decreases the power of the test compared to a two-way ANOVA. I thus evaluated the prediction at the population level by using a binomial test to evaluate the probability that the observed number of birds exhibits the predicted trend of smaller prey in multiple loads. In all statistical analyses, significance values were set at p = 0.05.

Results

Fledgling number and intake rates

Grasshopper sparrow nests in this study produced from 0 to 5 fledglings, although nests with 1 and 3 fledglings were represented by one nest each and are thus excluded from the ANCOVA. The one-tailed test detected a significant increase in prey provisioning rate with number of offspring fledged (p = 0.0460, Table 1, Fig. 1). Nests that fledged five young showed the highest provisioning rate.

The single prey loader model

The SPL model assumes a homogenous distribution of prey with distance from the nest. Of five nests sampled,

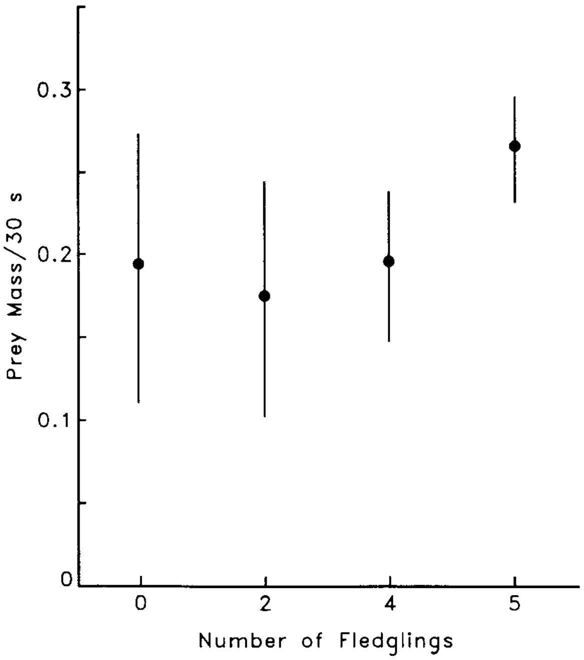

Fig. 1. Relationship between number of nestlings fledged and the rate of prey delivery. Values are least-square means, ± 1 standard error. "0" fledglings arise from predation or starvation which may occur at any nestling age and at any clutch size. Nests which fledge five fledglings receive a higher prey delivery rate.

Table 2. Test of the assumption that prey abundance (number of grasshoppers in each size category per 0.8 m^2) is constant with distance from the nest. Sample size, n, represents number of samples per distance. Probability value is generated from a Kruskal-Wallis test.

Nest	Prey size	Distance (m)				n	p
		5	10	20	40		
3g4	< 1 cm	1.0	0.8	1.3	2.0	4	0.6700
	1–2 cm	1.0	1.0	1.5	0.5	4	0.7351
	> 2 cm	0.0	0.0	0.0	0.3	4	0.3916
3g9	< 1 cm	0.7	0.7	0.3	0.3	6	0.8661
	1–2 cm	0.7	0.2	0.2	0.3	6	0.2296
	> 2 cm	0.3	0.2	0.2	0.0	6	0.5125
3g10	< 1 cm	1.8	3.3	4.2	4.7	6	0.3508
	1–2 cm	0.5	0.5	0.7	0.3	6	0.8881
	> 2 cm	0.0	0.0	0.0	0.0	6	–
3g12	< 1 cm	3.0	2.2	1.2	1.8	5	0.2871
	1–2 cm	1.6	1.4	1.4	1.0	5	0.8939
	> 2 cm	1.6	1.4	1.4	1.8	5	0.9858
4g3	< 1 cm	0.2	1.0	1.6	0.8	5	0.3028
	1–2 cm	0.0	0.2	0.2	0.0	5	0.5497
	> 2 cm	0.0	0.0	0.0	0.0	5	–

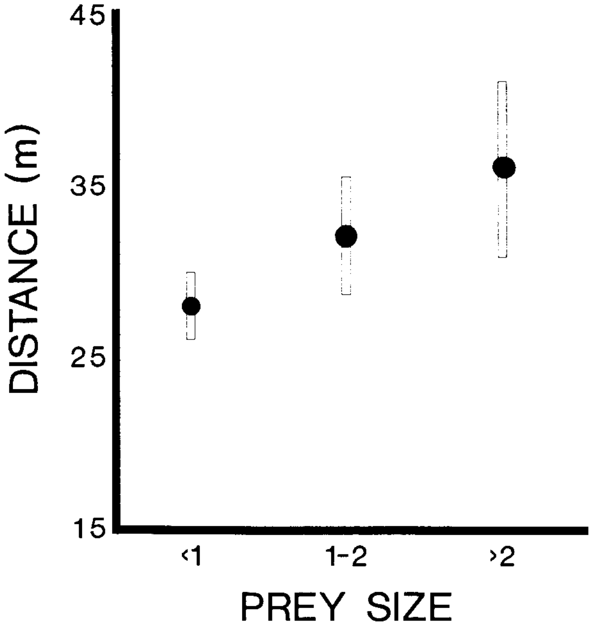

Fig. 2. Mean distance traveled back to the nest as a function of the size of prey fed to nestlings, ± 2 standard errors. Larger prey are delivered from a longer distance.

none showed differences in densities in three sizes categories of grasshoppers with distance from the nest (Table 2: Kruskal-Wallis test, $p > 0.2$ for all 15 comparisons).

The SPL model predicts that larger prey should be returned in single prey loads as the sparrows forage farther from the nest. This prediction was upheld ($p < 0.0014$, Table 3, Fig. 2). Individual birds foraged at different mean distances from the nest ($p < 0.0001$). However, the significant interaction term indicates considerable variability ($p < 0.0001$) between the 13 individuals ($p < 0.0001$) evaluated. Separate Spearman Rank Correlations show a positive trend between prey size and distance foraged from the nest for only 7 of the 13 individuals sampled. Thus, some individuals are more likely to return with larger prey than others.

The multiple prey loader model

Field observations supported the assumption of a negatively accelerated loading curve. The grasshopper sparrow's small bill brings prey longer than a centimeter directly into the bird's line of sight, likely hindering its ability to capture further prey. Subsequent prey, if spotted, are dealt with after the bird drops the prey it has already captured. This often necessitates a search for the first prey after capturing the second (pers. obs.). Both these factors would appear to decrease harvesting efficiency as more prey are loaded.

Grasshopper sparrows behaved as predicted by the multiple prey loader model: multiple loads are more likely to come from an increased distance from the nest ($p < 0.002$, Table 4, Fig. 3). Although individual birds forage at different mean distances from the nest as before ($p < 0.0001$), they follow the predicted rule uniformly (interaction term, $p = 0.15$).

Table 3. Two-way Analysis of Variance of distance foraged from the nest as it varies between birds and with size category of prey. See Fig. 2.

Source	df	Type III SS	p	$r^2=0.3088$
Prey size	2	3470	0.0014	
Between birds	12	21865	0.0001	
Size*Bird	24	15778	0.0001	
Error	470	122456		

Table 4. Two-way Analysis of Variance of distance foraged from the nest as it varies between birds and with load class (single versus multiple). See Fig. 3.

Source	df	Type III SS	p	$r^2=0.2162$
Load size	1	4.97	0.0016	
Between birds	12	40.15	0.0001	
Size*Bird	24	8.35	0.1531	
Error	536	263.31		

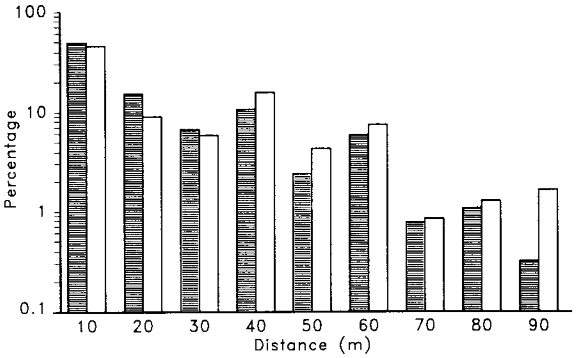

Fig. 3. Distribution of single prey loads (dark bars) and multiple loads (white bars) as a function of distance foraged from the nest. Multiple loads become more common at a distance of 40 m.

Load size: the effects of prey size and type

Single prey loads comprise a population average of 65% of provisioning trips (s = 18.5, range: 46–100). Two hypotheses have been proposed to explain when prey should be singly versus multiply-loaded. The Escape Syndrome hypothesis is falsified: both quiescent and actively-escaping prey are loaded with the same frequency: 82% of lepidoptera larvae versus 81% of grasshoppers (G-test $p < 0.45$, $n = 246$ and 873 respectively). Sparrows returning with multiple loads are likely to have selected smaller prey (Fig. 4) supporting the prey size hypothesis. Of 17 individuals analyzed with at least 5 single and multiple-load trips, 15 showed a trend toward smaller prey in multiple loads (binomial probability of 15/17: $p = 0.0012$). Furthermore, 6 of 17 sparrows, individually analyzed, show the trend significantly.

Discussion

Optimal foraging models begin with the core assumption that high intake rates are associated with higher fitness. Grasshopper sparrows in the Sand Hills prairie of western Nebraska meet this assumption over the course of this study: nests with higher prey delivery rates also yield more offspring.

Central Place Foraging models make two sets of predictions: both are upheld to varying degrees in this population. With increasing distance from the nest, grasshopper sparrows return with larger prey, but individual birds show considerable variability in this trait. The population is more uniform in their tendency to multiply-load prey as they forage farther from the nest. What factors underlie the significant between-bird variance in SPL's versus MPL's (i.e., distance-bird interaction term = 0.0001_{SPL} versus 0.15_{MPL})?

Most of the grasshoppers on Arapaho Prairie reach maturity and peak size in August, after grasshopper sparrow nestlings have already fledged. At 3 of the 5 nests sampled (all early nests), grasshopper distributions lacked almost any individuals in the largest (> 20 mm) size class. Grasshoppers < 10 mm in length were three times more common than grasshoppers in the next larger size category. Thus the prediction of the SPL model – return with larger prey farther from the nest – may be not be a viable tactic when large prey are scarce.

Competition and fluctuating environments

Food limitation in bird communities may be episodic both seasonally (Fretwell 1972, DuBowy 1988) and annually (Wiens 1977). Arapaho Prairie shows large between-year variation in both grasshopper and grasshopper sparrow numbers. Population densities of grasshopper sparrows on a 1×0.5 km plot – censused with the spot-flush technique (Wiens 1969) – varied between 14 and 16 pairs (Kaspari, unpubl. data) in 1981 through 1984. The 1985 population was over three times as dense (A. Joern and S. B. Gaines, pers. comm.). Grasshopper populations over the course of this study ranged between 2.6 and 3.0 grasshoppers m^{-2} (mean = 2.82, s = 0.16), whereas in 1979, two years before, they were 1.5 times as high (4.2 grasshoppers m^{-2}, all grasshopper densities from Joern and Pruess 1986).

However, despite this variability, the grasshopper sparrow population on Arapaho Prairie show patterns consistent with Martin's (1986) requirements for food-based competition. First, avian predators have been experimentally shown to depress grasshopper populations (i.e., resource depression, Joern 1986). Second, foraging intake is correlated with fledging success in the dominant insectivorous bird, suggesting food limitation.

Furthermore, contrary to Wiens and Rotenberry's

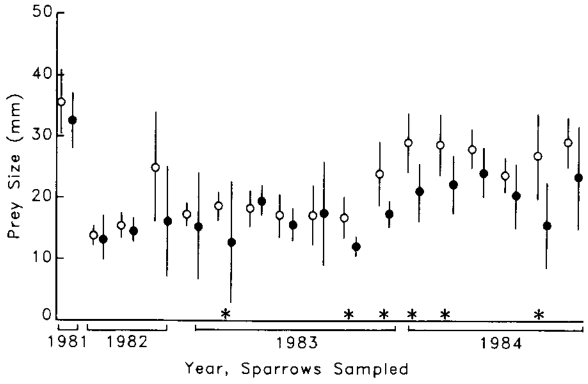

Fig. 4. Mean prey size (± 2 standard errors) for single prey loads (white dots) versus multiple prey loads (dark dots) for 17 grasshopper sparrows (separated by year). Fifteen show a trend toward smaller prey in multiple loads (binomial probability of 15/17: $p = 0.0012$). Six of 17, marked with asterisks, show the trend significantly.

(1979) analysis of a series of grassland systems, grasshopper sparrows are not opportunistic but follow rules of diet selection consistent with energy maximization models. Our different conclusions may stem from our different methods of analysis. The conclusions of Wiens and Rotenberry arise from the failure of models of limiting similarity (sensu MacArthur and Levins 1967) to produce consistent, statistically detectable patterns of diet segregation of species across multiple sites. The studies of Joern (1986) and Kaspari (this study) and Kaspari and Joern (unpubl. MS) at a single site have focused on the behavioral and population interactions between two trophic levels via experiments and tests of foraging models. Such a mechanistic approach, we believe, allows a more direct evaluation of the determinants of diet, leaving unanswered, for the moment, questions of community structure. Optimal foraging theory plays an important role in such a mechanistic approach, providing rigorous alternative models to contrast with the null model of dietary opportunism.

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