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Prey choice by three insectivorous grassland birds: reevaluating opportunism

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Assemblages of breeding grassland birds have typically been considered dietary opportunists. We studied prey selection by an assemblage of three breeding insectivores – grasshopper sparrows, lark sparrows, and western meadowlarks – in the Sandhills grasslands of Nebraska, USA and we contrast three foraging models with a null model of opportunism.

Handling times and %-chitin varied among prey taxa. The profitability (grams of non-chitin intake/handling time) of acridids, a major part of the diet of all three birds, declined with body size of grasshoppers. We measured Selectivities by comparing arthropods recovered from avian guts with those recovered from sweep sampling. Birds preferred some prey taxa (e.g., acridids, tettigoniids, small Coleoptera) over others (e.g., Homoptera, Hymenoptera, spiders). Small prey were avoided by all three bird species, intermediate-sized prey were more preferred, and preferences for larger prey increased with bird size. Two models based on pure energy maximization – the Classical model and the Central Place Foraging model – received some support: (1) profitability curves predicted the three species' size selectivity for 2 of 3 bird species; (2) diet breadth and selectivity for some alternate prey tended to decrease with the abundance of the most preferred prey; and, (3) nestlings received larger prey than were consumed by adults. Nutrient limitation is suggested for 2 of 8 prey types given the existence of partial preferences ($-1 < S$'s < 1), and the negative relationship between prey abundance and S.

These results suggest that prey selection in this assemblage of birds is a complex function of prey size, energy, and other nutrients. The similarity in profitability curves for the three species supports Rotenberry and Wiens' dismissal of limiting similarity in grassland birds. But our data fail to support their assertion that grassland birds are dietary opportunists. Regardless of how it is defined, the concept of opportunism requires the measurement of prey availability, and should yield predictions that are testable (i.e., falsifiable) in the field.

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Understanding the diet selection rules used by predators may help us predict and interpret prey morphology (Vermeij 1987) and behavior (Lima and Dill 1990). If prey are limiting and depletable, the rules used by predators to select prey should provide a mechanistic framework for the resulting competitive dynamics within the guild (Schoener 1984, Schluter and Grant 1984, Pulliam 1985, Martin 1986).

One concept fundamental to the discussion of diet selection is that of the dietary opportunist. Foragers are opportunists when the composition of their diet reflects the availability of their prey (Cody 1974, Rotenberry

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1980). Accounts of diet selection by grassland birds have concluded that these species are largely opportunists (Cody 1968, Fretwell 1972, Wiens and Rotenberry 1979, Rotenberry 1980, Wiens 1989a, b). Most evidence for this conclusion, however, is inferential. For example, Wiens and Rotenberry (1979) analyzed avian gut samples from a number of grasslands, using these data to evaluate models of limiting similarity (MacArthur and Levins 1967, Schoener 1974). They concluded that birds in these assemblages were foraging opportunistically given (1) the high diet overlap among co-occurring species, and (2) strong covariance among species in diet (see also Rotenberry 1980). These studies were particularly influential coming on the heels of Wiens' (1977) reevaluation of the importance of competition as a force structuring communities and guiding natural selection.

Yet these studies, important as they were in forcing us to re-evaluate models of limiting similarity, were less convincing as tests of the hypothesis that grassland birds are dietary opportunists. This hypothesis requires measures of prey availability and prey use; and prey availability measures were missing from Wiens and Rotenberry's work. When prey availability has been measured in diet studies, strong preferences are typically observed (Tinbergen 1981, Simon and Toft 1991 and references therein). Given the importance of the above studies to our understanding of avian assemblages, we return to the problem and attempt to build predictions from the bottom up, using simple models of diet selection (MacArthur and Pianka 1966, Pulliam 1975, Orians and Pearson 1979). Dietary opportunism becomes the appropriate null model.

Field studies, by necessity, do not allow for the careful controls and manipulations afforded by lab studies. We deal with this complication by evaluating assumptions to the extent possible and then comparing models that allow assumptions to vary in different, biologically reasonable ways. On the plus side, field studies of foraging tactics realistically test the robustness of behavioral models even at the expense of a lab's precision.

If models based on energy or nutrient maximization adequately predict diets, even under field conditions, we conclude that birds are not feeding opportunistically. However, if models of selective predation fare poorly, and diets mirror estimates of availability, we feel that our analysis combined with previous studies (above) support the claim that grassland birds feed opportunistically. This would be a powerful result, since very different approaches (e.g., community-based versus behaviorally-based theory) would converge on the same conclusion.

The study site

This study was conducted in 1982 and 1983 on and around Arapaho Prairie, a mixed grassland in the Sand Hills of Arthur County, Nebraska. The Sandhills grassland consists of large vegetated dunes. Grasses (e.g., *Bouteloua*, *Calamovilfa*, *Stipa*, *Andropogon*, and *Sporobolus*) dominate the landscape while forbs are more diverse comprising 80% of 200 plant species (Keeler et al. 1980).

We studied the grasshopper sparrow (*Ammodramus savanarrum*, 17 g), lark sparrow (*Chondestes grammacus*, 27 g) and the western meadowlark (*Sturnella neglecta*, 100 g). These are the three numerically dominant insectivorous birds on Arapaho Prairie (pers. obs). Other avian insectivores occasionally spotted on Arapaho Prairie were either more common on surrounding patches of short-grass prairie (horned lark, *Eremophila alpestris*; lark bunting, *Calamospiza melanocorys*), were aerial foragers (western kingbird, *Tyrannus verticalus*) or were rare (burrowing owl, *Athene cunicularia*). All three focal species overwinter elsewhere, with the meadowlarks returning in April, the lark and grasshopper sparrows returning in May, and the three leaving as early as late August. All three species often produce two clutches, the first occurring in May/June and the second in July/August.

The models

Here we present three diet models, focusing on relevant assumptions and predictions (for a complete discussion, see Stephens and Krebs 1986). We chose the models for their relevant assumptions (see below) and clear, field-testable predictions.

The Classical Model

This model was independently derived in various forms by MacArthur and Pianka (1966), Schoener (1971) and Pulliam (1974). Below we relate its critical assumptions and make operational its predictions.

Assumption 1: Rate of energy intake is correlated with fitness. The three birds in this study are small endotherms (17–100 g). These birds depress the numbers of grasshoppers on the site by up to 25% (Joern 1986). The grasshopper sparrow shows a positive relationship between intake rate and fledging success (Kaspari 1991a). Taken together, these data suggest ongoing selection for maximizing the rate of energy intake, at least in the grasshopper sparrow.

Assumption 2: Prey are encountered sequentially. Observations from field experiments (Joern 1986, 1988) confirm that the majority of prey are encountered sequentially.

Assumption 3: Prey are encountered randomly. Each prey encounter is assumed to represent an independent sample of environmental availability. Since availability is measured by the observer (in this case, by sweep-netting), we assume that our scale of insect sampling corresponds to that of the birds. This assumption is discussed in greater detail in the section *Measuring Selectivity's.*

Assumption 4: Handling is exclusive from searching. All three bird species often close their eyes, shaking and mandibulating prey after capture (Kaspari 1990, pers. obs.). It seems unlikely that birds obtain further information about prey distribution during handling.

Assumption 5: Foragers in a sample perceive the same prey abundance. Bird diets were estimated from gut samples. Each of seven estimates was collected over no more than three consecutive mornings, from the same habitat on and around Arapaho Prairie. So all birds on a sample date likely encountered the same prey.

Assumption 6: Handling times are constant within a species. Birds may adaptively vary handling time with changes in prey encounter rate and gut fullness (Kaspari 1990). However, grasshopper sparrows show no significant inter-bird variation in handling times (Kaspari 1990, this study, see also Pulliam 1985).

Assumption 7: Prey types are homogenous in energy content. Many studies treat broad groups of insect taxa (e.g., order or family), as single prey types. We constructed prey types in a two part process. First, prey were separated based on gross similarity in shape and/or taxonomic group (e.g., acridid, coleopteran, lepidoptera larvae). Second, these taxa were split into size categories uniform across taxa. The resulting prey types (e.g., acridids 5–15 mm, coleoptera larvae <5 mm) are more likely to be more homogenous in energy content.

Predictions of the Classical Model: The classical model makes four predictions:

1) Prey are ranked by their profitabilities (energy/handling time, or E/T) and added to the diet in rank order;
2) Prey are always either consumed when encountered or ignored, no partial preferences within a sample are found (e.g., the All or None Rule);
3) Diet breadth increases with decreasing abundance of preferred prey (i.e., a prey's probability of selection should be negatively correlated with the abundance of higher quality prey).
4) A prey's probability of selection should be independent of its own abundance.

The classical model has been tested in a variety of systems (see Stephens and Krebs 1986). Prediction 3 has been supported with two species of insectivorous birds (Davies 1977a, b). Prediction 1 has been supported for two species of insectivorous birds (Davies 1977a, Zach and Falls 1978).

Testing the Classical Model. The classical model and the others below predict which prey should be selected and which ignored given a distribution of prey types, handling times, and profitabilities. Since our data are in the form of gut samples and not direct observations of foraging, we need an index that describes how preferences change with the abundance of prey. We use Jacob's (1974) index of selectivity:

$$S = \frac{r-p}{r+p-2rp}$$

where r is the proportion of a prey type in the diet and p is its proportion in the environment. S starts at -1 (prey never consumed despite presence in habitat) and approaches 1 (prey consumed far more than that predicted by availability). S allows us to examine how preferences for prey types change with the abundance of that and other prey.

To test Prediction 1 we calculate E/T's over a size range of acridids, the chief arthropod prey of this assemblage. These data are summarized in a series of profitability curves that describe the relationship between a prey type's size and it's E/T (Werner 1974, Davies 1977a, Pulliam 1985). Even if S's are distributed bimodally (centered around -1 and 1 as per the All or None Rule), sampling diets over a range of prey availabilities, yielding different combinations of -1's and 1's, should provide a distribution of mean S's to prey size that mirrors the shape of the profitability curves.

To test Prediction 2 we examine the distribution of S's for each available prey type. If the All or None Rule is supported, these S-distributions should be bimodal and clustered around -1 and 1.

To test Prediction 3, we correlate diet breadth, the total number of prey types sampled in a bird species diet, with the abundance of preferred prey in the habitat at the time of the sample. The Classical Model again predicts a negative correlation. We also relate the S's of highly preferred prey (mean $S > 0.5$) to those with intermediate S's (-0.75 – 0.5, see below). The classical model predicts a negative correlation.

To test prediction 4, we relate the S's of prey with their own abundance. The Classical Model predicts no correlation.

The Central Place Foraging Model

Orians and Pearson (1979) modified the Classical model to describe a forager returning prey to a central place (e.g., a bird provisioning its brood in the nest). The question confronted by such a forager is which prey to consume on the spot versus which prey to carry back to the nest (adding to the prey the energy and time cost of the round trip from the nest). The Central Place model predicts that energy maximizers should select smaller prey for immediate consumption and carry larger prey back to the nest.

Numerous studies of insectivorous breeding birds have confirmed the other predictions of the Central Place Foraging Model (Stephens and Krebs 1986). For example, as grasshopper sparrows on Arapaho Prairie forage farther from the nest, they return with more prey (Kaspari 1991a). Tests of prey size in adults versus nestlings are

Tab. 1. Prey types recognized in this study. Prey types are taxa that are uniform in size and shape.

TAXA	Maximum length of prey (mm)					
	<5	15	25	35	45	>45
ORTHOPTERA						
Acridids	×	×	×	×	×	×
Tettigoniids	×	×	×	×	×	×
PHASMATIDS			×			×
COLEOPTERA						
Larvae	×	×	×	×	×	×
Adults	×	×	×	×		
HOMOPTERA						
Cicadellid	×	×				
Cercopid		×				
LEPIDOPTERA						
Larvae	×	×	×	×	×	×
Adults	×	×	×	×	×	
NEUROPTERA		×				
DIPTERA	×	×	×			
HEMIPTERA	×	×				
HYMENOPTERA	×	×	×			
SPIDERS	×	×	×			
OTHER ARTHROPODS	×	×	×	×	×	×
SEEDS	×					

rarer: prey fed to nestlings (and hence accruing a travel cost) are larger than those consumed by adult insectivores in at least two species (Davies 1977b, Krebs and Avery 1985).

The Nutrient Constraints Model

The Nutrient Constraints model (Pulliam 1975, Belovsky 1978) assumes that while maximizing energy intake, the forager must meet some minimum required intake of nutrients. If the diet that maximizes energy intake lacks the minimum titer of required nutrients, then Assumption 1 of the Classical model is incorrect and needs to be modified to include relationships between other prey qualities and fitness. These other requirements constrain the energy maximizing solution. Predictions then differ from the Classical model in a number of respects. The Nutrient Limitation model predicts partial preferences for prey that contain these limiting nutrients. Partial preferences violate Prediction 2, the All or None Rule. The Nutrient Model also predicts S's which are inverse functions of the prey's abundance. This results from the static r in the calculation of S (reflecting a constant nutritional requirement) in the face of an increasing p (prey abundance). This is contra Prediction 4, which states preferences should not be related to a prey's own abundance.

Nutrient limitation has been shown in only a few insectivores. Wolf spiders (Greenstone 1979) show partial preferences for three types of insects, optimally balancing the proportion of essential amino acids in the diet. Similarly, bee eater nestlings grow fastest when fed a mixed diet of insect prey, not a more restricted diet that maximizes energy intake (Krebs and Avery 1984). Juvenile lizards (genus *Anolis*) maintained constant fractions of certain prey in their diets despite fluctuations in abundance, suggesting minimal nutrient requirements (Stamps et al. 1981).

Opportunism

Opportunism, the null hypothesis, suggests that foragers consume prey in proportion to its relative abundance. In other words, $r=p$ for all prey, with the result that S for all prey should approach 0. Since no criteria are used for selection, then there should be no a priori relation between profitability or diet breadth and S.

Methods

The Classical model predicts that prey with higher E/T's should have correspondingly higher S's. Measures of S require data on both the abundance of prey and the types of prey selected.

Measuring selectivities (S)

Prey abundance. Twelve 100 m transects were sweep-sampled by M. K. with an insect net. In each sample one sweep of the net, parallel to the ground corresponded to one stride for a total of 40 sweeps. The contents were emptied into a large plastic bag and then frozen. We made seven collections: 11 June, 5 July, 24 July, and 7 August in 1982; and 21 June, 11 July, and 10 August in 1983. Arthropods collected in gut or sweep samples were sorted into prey types based on combinations of taxa and size. We first grouped taxa that were similar in overall morphology (e.g. acridids, Lepidoptera larvae, spiders). These taxa were then sorted to size (<5 mm, 5–1.49 mm, 1.5–2.49 mm, 2.5–3.49 mm, 3.5–4.49 mm, >4.49 mm). A total of 55 prey types were recognized (Table 1).

Sweep sampling captures arthropods clinging to vegetation or escaping in front of the net (Southwood 1966). The Sandhills prairie's low vegetation profile is structurally suited to sweep sampling. Although sweep sampling does not measure absolute prey density, it does realistically estimate relative abundance; total number of arthropods captured is correlated with absolute abundance (Southwood 1966, Evans et al. 1983, Thompson 1987). Many of the numerically dominant prey taxa (tettigoniids, Lepidoptera larvae, Hemiptera and many dominant acridids) reside exclusively on vegetation. The remaining acridids reside on the ground between feedings but leap and are captured as the sweep net approaches. We have observed foraging birds both in the field and in semi-natural aviaries (Joern 1988, pers. obs). Foraging birds walk slowly through vegetation, gleaning prey from

Tab. 2. Summary of Power Curve Regression of arthropod mass on percentage chitin, with least squares solutions. Solution is power function (i.e. % chitin = $e^{a+b*\text{ weight (g)}}$). Chitin percentage varies across taxa, and across body size.

Source	df	Type III SS	Pr>F	r
Taxa	11	39.27	0.0001	0.51
Dry weight	1	0.89	0.0392	
Weight*Taxa	11	13.16	0.0001	
Error	316			

Taxa	Mean % Chitin	Solution				
		n	Intercept	Slope	r^2	p
Lepidoptera adults	18	7	−2.16	5.89	0.53	0.0401
Acridids	20	97	−1.44	−0.74	0.13	0.0003
Spiders	25	19	−1.45	4.34	0.03	0.4826
Hemiptera	28	14	−1.16	−4.528	0.14	0.1766
Diptera adults	32	6	−0.14	−45.005	0.91	0.0008
Tettigoniids	32	14	−1.27	2.94	0.03	0.5670
Phasmatids	34	7	−0.09	−1.97	0.29	0.1713
Lepidoptera larvae	37	17	−0.797	−6.93	0.30	0.0197
Homoptera	42	19	−0.73	−24.52	0.01	0.5806
Coleoptera adults	44	102	−0.68	−1.594	0.34	0.0001
Hymenoptera	59	26	−0.42	−2.89	0.14	0.0572
Coleoptera larvae	60	3	0.26	−8.947	–	–

grass and forbs or occasionally flushing arthropods from the ground and either chasing them down or hawking them from the air (Joern 1988, unpubl. data). Thus foraging birds on Arapaho Prairie appear to sample arthropods in a fashion similar to sweep sampling.

Some taxa (gryllids, larval cercopids and larval Neuroptera) are found on or within crevices at ground-level and are likely under sampled by sweeping. We include them in the prey category "other" to avoid assigning spuriously high selectivities (see below). For the same reasons, seeds are not included in the calculation of selectivities.

Sampling insect prey abundance in the field, especially to reflect the predator's viewpoint, is a difficult task. Estimates are rarely absolutely accurate and various biases easily creep in. We proceed in our analyses using prey abundance estimates with such problems, but we have not blindly dismissed the problems. We sampled conscientiously with such problems in mind. As will be seen, the selectivity values that rely on our relative abundance estimates are bimodal so that implicit sampling error is unlikely to qualitatively alter our conclusions.

Adult diets. Adult birds were collected on and around Arapaho Prairie within 3–4 days of insect collections. Once collected, stomachs were injected with 70% ethanol. In the lab all contents in the esophagus, proventriculus, and stomach were removed and stored in 70% ethanol. We attempted to collect at least ten birds per species every sample period.

Gut contents were examined with a dissecting scope. Arthropods were typically fragmented. However, most sclerotized parts like mandibles, wings, or elytra could be identified to taxa and size using a reference collection. Numbers of individual prey in the gut represent minimum estimates based on paired hard parts.

Sampling diets from stomach analyses may bias selectivity measures against easily digested prey (Custer and Pitelka 1978). Although we cannot directly address this issue with data, soft-bodied prey like spiders and lepidoptera larvae have characteristic hard parts. We assume that our stomach contents diet samples are adequate diet representations for the avian species in this study.

Nestling diets. All three bird species nest on the ground. Nests were located through haphazard walking. Once located, we set up blinds 5 m from the nests and observed returning birds using a spotting scope. As adults often perch at predictable locations for a minute or more before feeding young, we could readily identify prey and assign them to size categories (see above) using the bird's bill size as a reference (Kaspari 1991a). Identification of prey was typically precise: grasshoppers were normally identified to species and sex.

A total of 22 grasshopper sparrow and 6 lark sparrow nests were observed for a total of 251 and 65 h respectively. Sampled nests were assigned to the collection date of adult birds.

Prey quality and profitability curves

We collected and froze arthropods from Arapaho Prairie in 1982 and 1983. Arthropods were measured with dial calipers for maximum length and width. Arthropods were freeze-dried then weighed. The arthropods were sorted to taxa and size, and 5–10 individuals of each prey were weighed.

Tab. 3. Handling time increases with the size of acridids consumed for 20 grasshopper sparrows and 2 lark sparrows tested.

Grasshopper sparrow Source	df	Type III SS	Pr > F
Bird	19	5.73	0.9586
Prey length	1	51.14	0.0001
Length*Bird	19	6.80	0.9073
Error	79		

Lark sparrow Source	df	Type III SS	Pr >F
Bird	1	0.36	0.4968
Prey length	1	18.44	0.0002
Length*Bird	1	0.12	0.6883
Error	17		

The exoskeleton of arthropods is largely chitinous and less digestible than the remaining tissue (Karasov 1990); birds often remove mostly chitinous parts before swallowing arthropods (Zach and Falls 1978, Sherry and McDade 1982, Kaspari 1990, 1991b). Since chitin appears to be an important general determinant of prey quality, we measured chitin content for different arthropod taxa common in sweep samples. The exoskeleton was isolated by immersing a pre-weighed arthropod into a solution of 3M NaOH for 3–5 d, then rinsing thoroughly, freeze-drying and re-weighing.

Given the enormous task of estimating E/T for all 54 arthropod prey taxa, we estimated profitability curves only for acridids. Profitability curves relate the length of prey of a particular taxon to its handling time (Werner 1974, Davies 1977a, Pulliam 1985). We focused on acridids because they constituted over a third of the arthropod diet of these birds, and show a wide variation in size. Handling times were measured by presenting acridids to captive birds. Twenty grasshopper sparrows, two lark sparrows and one western meadowlark were mist-netted and placed in cages. Birds were kept on ad lib diets of arthropods and water, fasted for two hours, then presented with acridids. Handling times, from capture through the disappearance down the throat, were measured at the time of the event or from audio tape records of the event, to the 0.1 s using a stopwatch. For further details see Kaspari (1990). For each size of acridid, we constructed proxies for E/T using the ratio of non-chitin dry weight to handling time.

We used an analysis of covariance to look for among-bird variation in handling times of different sized grasshoppers. Means for each combination of bird/grasshopper species were then calculated, and we compared height and shape of the profitability curves between bird species.

Results

Variation in prey quality

Arthropods sampled from Arapaho Prairie varied in dry weight by an order of magnitude, with the majority weighing less than 0.2 g. Percentage chitin, log-transformed and analyzed in an ANCOVA, varies both across taxa ($p = 0.0001$) and prey size ($p = 0.04$, Table 2). Phasmatids, Hymenoptera and Coleoptera were the most chitinous arthropods. Lepidoptera adults, spiders and acridids were the least chitinous (Table 2).

Six of eleven taxa also showed significant changes in chitin fraction with body size (Table 2). Five of these six were negative, relating the increased surface area to volume with decreasing size. However, Lepidoptera adults (the butterflies and moths) showed an increasing chitin fraction with body size.

Handling times and profitability curves

Assumption 6 of the Classical Model states that no intraspecific variation in handling times exists. Log-transformed handling times were positive, linear power functions of acridid size ($p < 0.0002$, Table 3, Kaspari 1990)

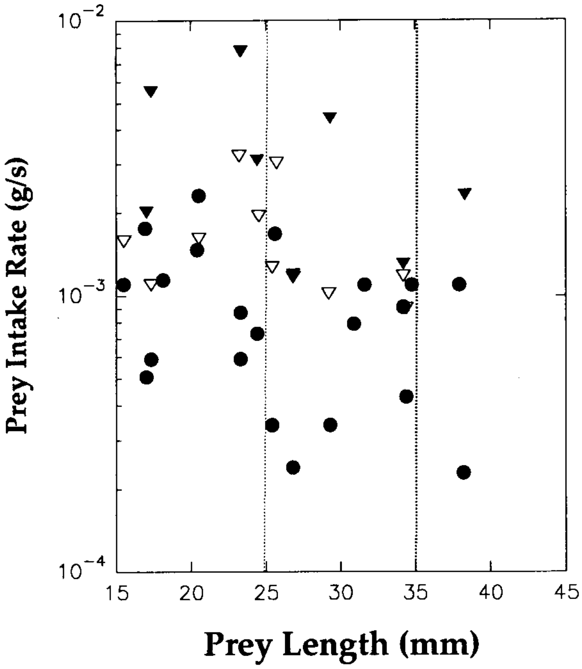

Fig. 1. Profitability (grams intake/second) of adult acridid grasshoppers for grassland birds (dark triangle: western meadowlark; light triangle: lark sparrow; dark circle: grasshopper sparrow). Prey size categories designated by dotted lines. An analysis of covariance suggests that E/T decreases with acridid size (Type 3 SS = 0.35, $F_{1,31} = 5.8$, $p = 0.02$), but neither the intercept nor the slope of this relationship varies across species.

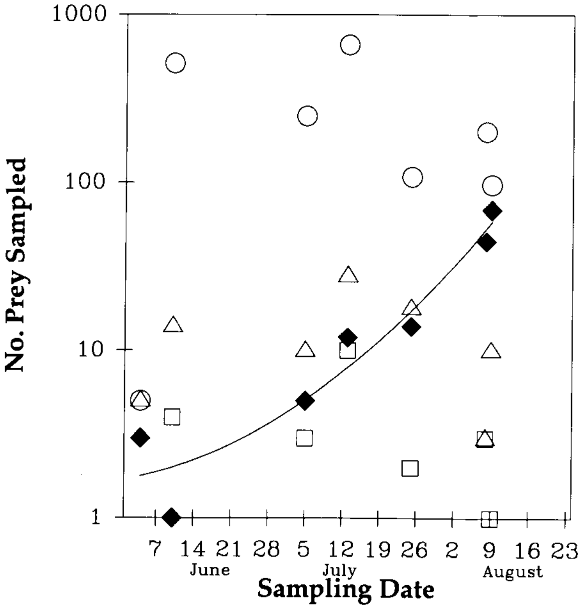

Fig. 2. Estimates of prey abundance from sweep netting in 1982 and 1983 vary considerably across taxa. Acridids 5–25 mm, the most preferred prey of the grassland birds, are dark diamonds connected by line. Squares are 5–15 mm spiders, triangles are 5–15 mm Coleoptera, prey of intermediate selectivities. The most abundant taxa, adult cercopids, was least preferred by the three species in this analysis.

for the two replicated species. The 20 grasshopper sparrows and 2 lark sparrows exhibited consistent handling times among individuals both in magnitude (p's <0.4) and slope (p's <0.6). In the following analysis, we use this result to justify representing handling time for each grasshopper taxon with a single mean per bird species. Note, we examined only a single meadowlark and can only assume no significant between-bird differences for this species.

A grasshopper's E/T was calculated for each bird using chitin-free dry weights/mean handling time for that species. Twenty acridid morphs of varying size were used to construct the curve, but not every acridid was tested with each bird species. Since we only used adult grasshoppers, we failed to sample the profitability curve in the two smallest size categories of acridids, which are represented only by nymphal instars. The largest size class is also missing, represented by a single rare morph on Arapaho Prairie. We restrict predictions from profitability curves to only those sizes estimated by the profitability curves.

We evaluated the effect of bird species and body size on E/T using Analysis of Covariance (Fig. 1). There was a decrease in E/T with prey size across all three species ($p = 0.02$, best linear fit, $\log(E/T) = -2.6-0.014[\text{acridid length, mm}]$). However neither the intercept nor the slope of this relationship varied across the three species ($p = 0.55$, $p = 0.70$). Adding a quadratic component to this analysis did not improve the fit. These results suggest that all three species should prefer the smaller acridids of the sizes offered.

Selectivities

Arthropod taxa differed considerably in absolute abundance in the field over the 1982–83 breeding seasons. Fig. 2 shows a sample of the taxa from Arapaho Prairie. Adult cercopids (small homopterans), often exceeded 100

Tab. 4. Sampling statistics for avian gut and nestling diet analysis.

	1982				1983		
	J11	JY5	JY24	A2	J21	JY11	A10
Grasshopper sparrow							
Number of birds	10	14	12	17	16	21	24
Number of arthropods	99	123	73	179	79	168	288
Number of taxa >1%	17	12	9	12	16	14	10
Lark sparrow							
Number of birds	–	13	4	4	15	20	11
Number of arthropods	–	132	42	41	64	139	109
Number of taxa >1%	–	13	9	8	10	9	9
Western meadowlark							
Number of birds	6	13	12	12	17	20	15
Number of arthropods	73	265	278	296	184	315	307
Number of taxa >1%	14	15	14	11	8	13	10
G. sparrow nestlings							
Number of parent birds	6	4			10		2
Number of arthropods	575	128			633		109
L. sparrow nestlings							
Number of parent birds		4			2		
Number of arthropods		234			188		

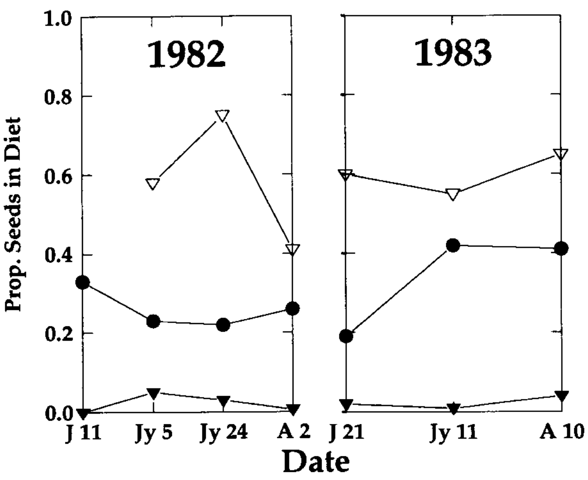

Fig. 3. Percentage of seeds (by number) in diet samples of 3 grassland birds from 1982 and 1983 (dark triangle: western meadowlark; light triangle: lark sparrow; dark circle: grasshopper sparrow). Percentage by biomass is likely much smaller. J = June, Jy = July, A = August.

individuals/sample, comprising over 50% of sampled taxa. Most other taxa were an order of magnitude less abundant. Some common prey (small coleopterans and spiders) tended to be relatively constant. In contrast, intermediate-sized acridids, the only prey with mean *S*'s >0.5 (see below), tended to increase from June through August (Fig. 2).

Adult diets. Grasshopper sparrows were the most extensively sampled bird species with a total of 114 birds and a range of 73–288 arthropods sampled per period (Table 4). We sampled 67 lark sparrows with 41–139 arthropods sampled per period. Lark sparrows were the rarest of the three species and none were collected during the first sample period. We sampled a total of 95 western meadowlarks, with 63–315 arthropods sampled per period. In all, 3 of the 20 bird collections are represented by sample sizes of <10 birds (Table 4).

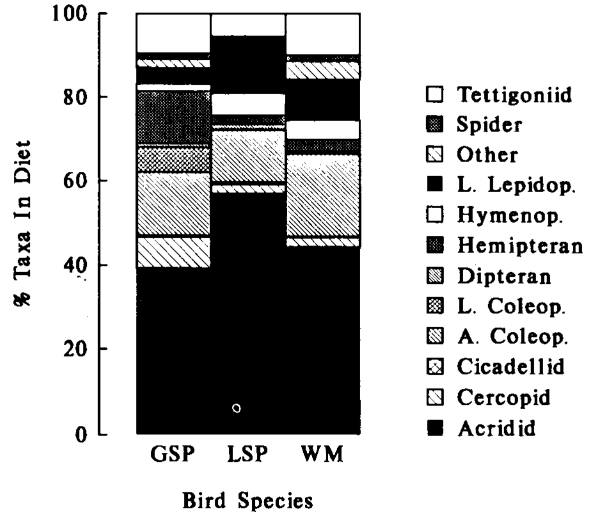

Fig. 4. Mean proportion of arthropod types in the diets of grassland birds in 1982 and 1982. Acridids, adult Coleoptera, and Lepidoptera larvae are dominant parts of all three species' diets. (GSP = grasshopper sparrow, LSP = lark sparrow, WM = western meadowlark. L. = larvae, A. = adults).

The three species differed greatly in the proportion of arthropods and seeds in their diets (Figs 3–5). Meadowlarks were primarily carnivorous, consuming no more than 5% seeds. The two emberizine finches included considerably more seeds. Seeds comprised on average 61% of the prey items in the lark sparrows' diet, 33% in the smaller grasshopper sparrow (Fig. 3).

A variety of arthropods composed the rest of the diet of all three species. In each species, acridids and adult Coleoptera were the numerically dominant arthropod prey (Fig. 4). Hemiptera were the next most common prey in grasshopper sparrow diets; Lepidoptera larvae held that place for lark sparrows and western meadowlarks. Lepidoptera adults, cicadellids and spiders were less common although each left behind characteristic hard parts (scales, probosci and mandibles).

Diets of all three species strongly co-varied over time in both years (Fig. 5). A dominant trend was the increase in proportion of acridids in the diet over the breeding season.

Selectivities (*S*) for all prey that occurred in at least one diet sample are summarized in Table 5. When prey were present in diet samples but absent in the sweep samples, those prey types were arbitrarily given frequencies of 0.001. Within each species' diet, mean *S*'s varied from −1 to approaching 1.

Species preferred most of the same prey. We compared *S*'s for 21 common prey – those found in at least 6 sweep samples. These *S*'s varied between bird species in 4/21 (19%) of the prey (Table 5). This appears to result from the larger western meadowlark preferring larger prey, and the smaller grasshopper sparrow showing higher *S*'s for smaller prey. Nine of 55 prey were consumed by one species: grasshopper sparrows were the only species to consume <5 and 15–25 mm coleopteran larvae; western meadowlarks exclusively consumed the largest sizes of five taxa and 5–14.9 mm coleopteran larvae (Table 5).

Prediction 1: Do selectivities mirror profitability curves?

For all three bird species, the selectivities, *S*, vary across the 6 size classes of acridids (Wilcoxon $\chi^2 > 16$, $p < 0.005$, Fig. 6 left). The birds uniformly avoid consuming the two smallest sizes (Fig. 6 left) and select intermediate sizes of prey. Some interspecific diet segregation occurs along the upper two sizes of prey, with the smaller grasshopper sparrow avoiding these two classes while the lark sparrow and western meadowlark show higher *S*'s.

Recall that profitability curves predict weak prefer-

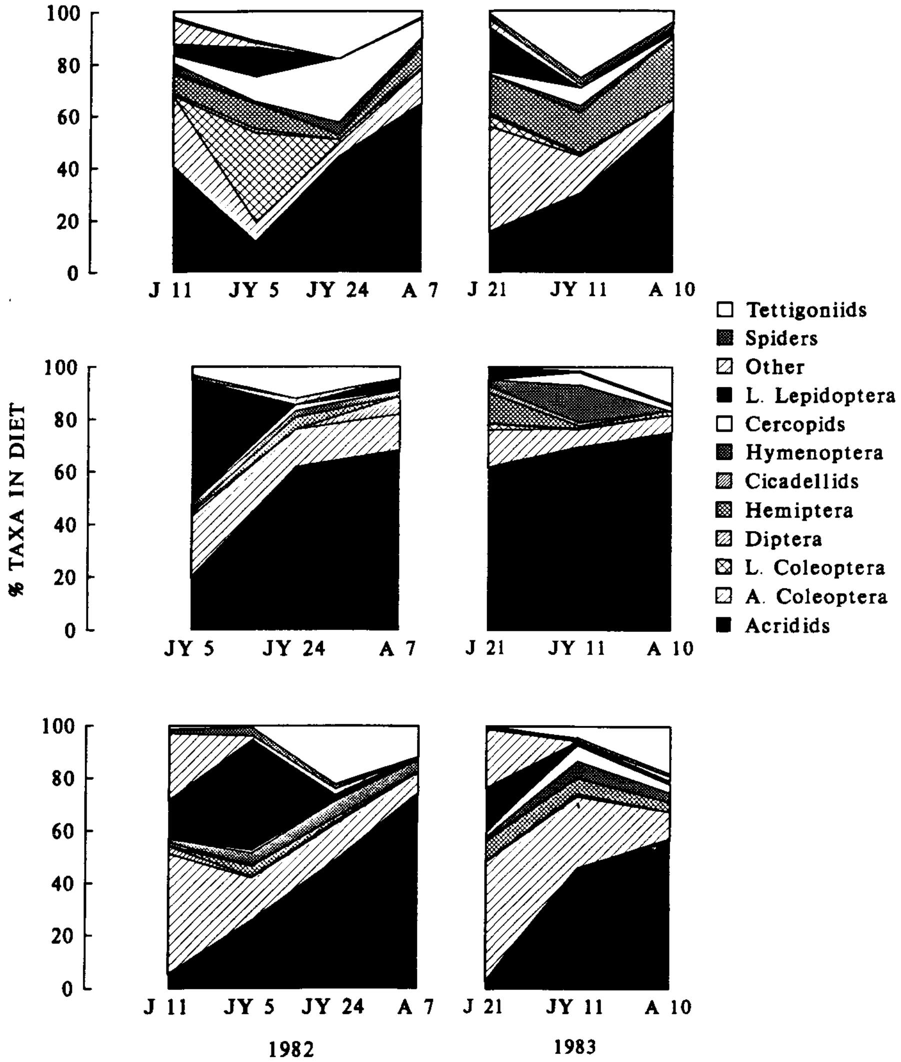

Fig. 5. Proportion of arthropods in the diets of grasshopper sparrows (top), lark sparrows (middle) and western meadowlarks (bottom). Left column is from 1982 samples, right column from 1983. Diet composition varies considerably between years and sample periods within the year.

ences for smaller acridids within the size range 15–45 mm for grasshopper sparrows and western meadowlarks, and 15–35 mm for lark sparrows. When only these sizes are compared, grasshopper sparrows (Wilcoxon χ^2 = 7.51, 1-tailed p = 0.012) and western meadowlarks (Wilcoxon χ^2 = 4.69, 1-tailed p = 0.047) showed decreased selectivities across the three size classes used to construct their profitability curves (Fig. 1). Lark sparrows, failed to show any differences in selectivities over the two intermediate size classes (15–35 mm, Wilcoxon χ^2 = 0.92, p = 0.36) from which we had profitability data.

When size selectivities are evaluated across all 54 arthropod prey (Fig. 6 right) similar patterns hold: avoidance of arthropods less than 15 mm in length, preference for prey between 15 and 35 mm, and increasing preference for prey exceeding 35 mm as a function of increasing size of the bird species (Wilcoxon χ^2's >32, p <0.0001).

Prediction 2: Testing the All or None Rule

The Classical Model predicts that prey should either always be included in the diet or always excluded, corresponding to S's approaching −1 and 1. The Nutrient Model predicts the existence of partial preferences for prey low in energy but containing limiting nutrients. Opportunism predicts constant S's approaching 0. For each species, when S's of all prey over all sample periods are pooled, they show a bimodal distribution with the modes centered at −0.95 and 0.95 (Fig. 7) as predicted. However, 30% of the grasshopper sparrow's S's, 25% of the lark sparrow's S's, and 35% of the western meadowlarks S's represent intermediate values. So against a background of strong preferences and aversions, many prey are partially preferred.

Tab. 5. Mean selectivities for three bird species from Arapaho Prairie. When 6–7 selectivities are available for each species, a Wilcoxon test looks for differences in selectivities between species (* = p <0.05). Number of diet samples, n, given for grasshopper sparrows and western meadowlarks.

Taxa	Prey (mm)	n	grasshopper sparrow		lark sparrow		western meadowlark	
			$\bar{x}$	(SD)	$\bar{x}$	(SD)	$\bar{x}$	(SD)
Acridids	<5	6	−0.81	(0.48)	−1.00	(0.00)	−0.72	(0.68)
	5–14.9	7	−0.63	(0.52)	−1.00	(0.00)	−1.00	(0.00)
	15–24.9*	7	0.72	(0.25)	0.77	(0.23)	0.67	(0.31)
	25–34.9	7	0.78	(0.22)	0.90	(0.09)	0.92	(0.07)
	35–44.9	4	−1.00	(0.00)	0.13	(1.02)	0.21	(0.89)
	>45	3	−1.00	(0.00)	−1.00	(0.00)	0.95	(0.01)
Tettigoniids	<5	6	−1.00	(0.00)	−1.00	(0.00)	−1.00	(0.00)
	5–14.9	6	−0.87	(0.31)	−0.89	(0.25)	−1.00	(0.00)
	15–24.9*	7	0.92	(0.11)	0.28	(0.73)	0.23	(0.87)
	25–34.9	5	0.00	(0.94)	−0.59	(0.82)	0.61	(0.73)
	35–44.9	2	−1.00	(0.00)	−1.00	(–)	0.98	(0.01)
Phasmatids	15–24.5	1	−1.00	(–)	−1.00	(–)	−1.00	(–)
	>45	3	−1.00	(0.00)	−1.00	(0.00)	−1.00	(0.00)
Coleopteran larvae	<5	1	0.99	(–)	−1.00	(–)	−1.00	(–)
	5–14.9	1	−1.00	(–)	(–)	(–)	0.98	(–)
	15–24.9	1	0.99	(–)	−1.00	(–)	−1.00	(–)
	35–44.9	3	0.32	(1.14)	−0.34	(1.15)	−0.35	(1.12)
Coleopteran adults	<5	7	0.09	(0.82)	−0.11	(0.89)	0.21	(0.55)
	5–14.9	7	0.46	(0.45)	0.29	(0.67)	0.45	(0.41)
	15–24.9*	7	−0.01	(0.51)	0.37	(0.17)	0.97	(0.08)
	25–34.9	3	−1.00	(0.00)	−1.00	(0.00)	0.96	(0.02)
Cicadellid	<5	4	−1.00	(0.00)	−1.00	(0.00)	−1.00	(0.00)
	5–14.9	7	−0.45	(0.79)	−0.78	(0.38)	−0.51	(0.72)
Cercopids	5–14.9	7	−0.85	(0.20)	−0.97	(0.03)	−0.74	(0.58)
Neuroptera	5–14.9	3	−0.34	(1.40)	−0.00	(1.41)	−0.39	(1.05)
Lepidoptera larvae	<5	7	0.39	(0.95)	0.16	(0.18)	0.23	(0.89)
	5–14.9	4	−1.00	(0.00)	−1.00	(0.00)	−1.00	(0.00)
	15–24.9	6	0.05	(0.85)	−0.39	(0.84)	0.20	(0.94)
	25–34.9	4	−0.18	(0.95)	−0.05	(1.10)	−0.07	(1.07)
	35–44.9	5	0.19	(1.09)	−0.50	(1.00)	0.58	(0.88)
	>45	2	−0.00	(1.41)	−0.26	(1.04)	0.97	(0.03)
Lepidoptera adults	5–14.9	1	−1.00	(–)	−1.00	(–)	−1.00	(–)
	15–24.9	4	−1.00	(0.00)	−1.00	(0.00)	−1.00	(0.00)
	25–34.9	2	−1.00	(0.00)	−1.00	(0.00)	0.97	(0.01)
	35–44.9	1	−1.00	(0.00)	−1.00	(0.00)	0.97	(0.00)
Diptera	<5	6	−0.96	(0.09)	−1.00	(0.00)	−1.00	(0.00)
	5–14.9	7	−0.37	(0.67)	−0.61	(0.64)	−0.46	(0.66)
	15–24.9	3	−1.00	(0.00)	−0.34	(1.15)	0.16	(1.02)
Hemiptera	<5	7	0.56	(0.39)	0.02	(0.58)	0.02	(0.67)
	5–14.9*	7	−0.27	(0.78)	−1.00	(0.00)	−0.91	(0.24)
	15–24.9	1	−1.00	(–)	−1.00	(–)	0.97	(–)
Hymenoptera	<5	7	−0.66	(0.74)	−0.19	(0.78)	−0.33	(0.69)
	5–14.9	7	−0.47	(0.68)	0.44	(0.63)	0.06	(0.56)
	15–24.9	3	−0.01	(1.14)	−1.00	(0.00)	0.19	(0.97)
Spiders	<5	7	−1.00	(0.00)	−1.00	(0.00)	−0.91	(0.25)
	5–14.9	7	−0.19	(0.56)	−0.64	(0.57)	−0.11	(0.50)
	15–24.9	5	−0.60	(0.89)	−1.00	(0.00)	0.50	(0.85)

Prediction 3: How does diet breadth vary with abundance of good prey?

To test the Classical Model's prediction of decreasing *S*'s with increasing abundance of high quality prey, we chose as our high quality prey those that meet the criteria of: 1) occurring in at least 6 of the 7 sweep samples and, 2) with mean *S*'s >0.5. (The former assures large sample sizes, the latter sufficient potential variation in which to detect correlations). These criteria yielded two prey types: 15–25 and 25–35 mm acridids. Note by inferring high prey quality from large *S*'s we are allowing the birds to define their own high quality prey. This was a necessary simplification, since we could not measure E/T for all 55 size classes of prey for all three bird species.

Different birds had different mean sample sizes. In particular, lark sparrows were less intensively sampled late in 1982. This might confound the prediction of decreasing diet breadth with increasing abundance of high quality prey, since acridids hit their peak late in the

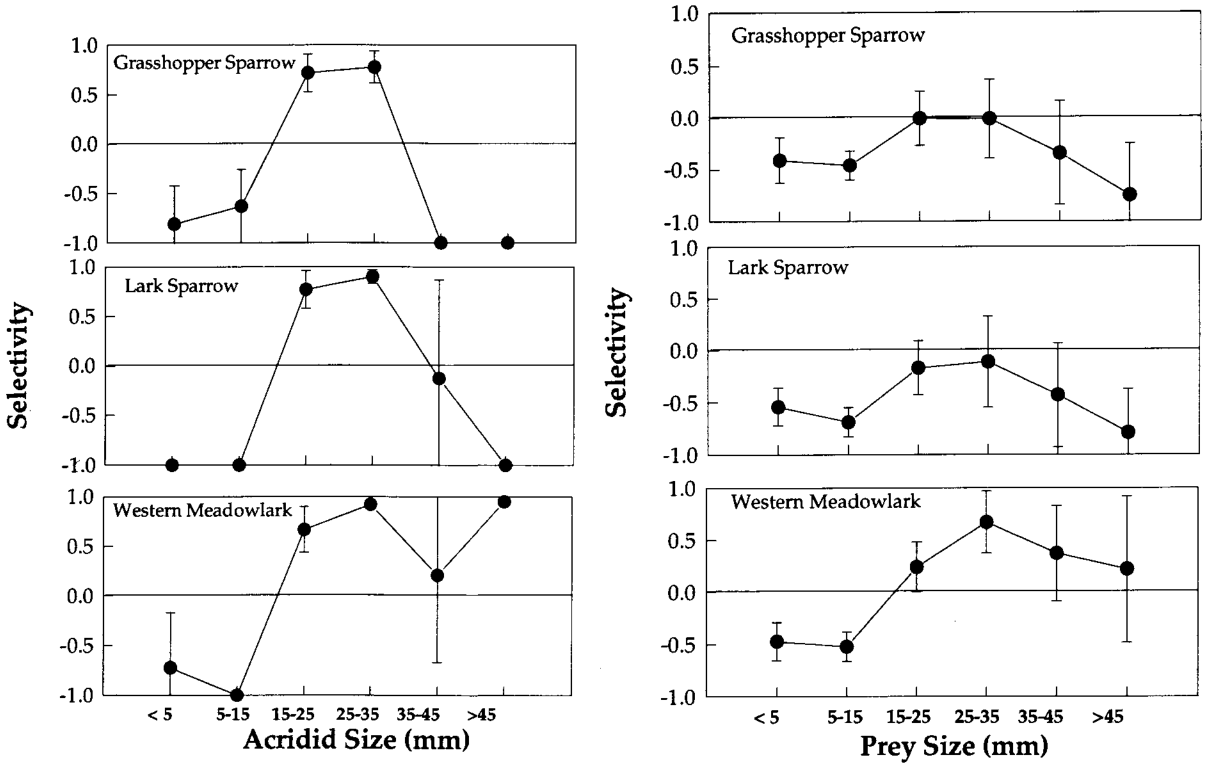

Fig. 6. Mean selectivities (±2 standard errors) of three grassland birds for (left) acridids, and (right) all prey, as a function of size. Small prey are avoided by the three bird species and intermediate sized prey are preferred while preferences for large prey increase with the larger lark sparrow and western meadowlark.

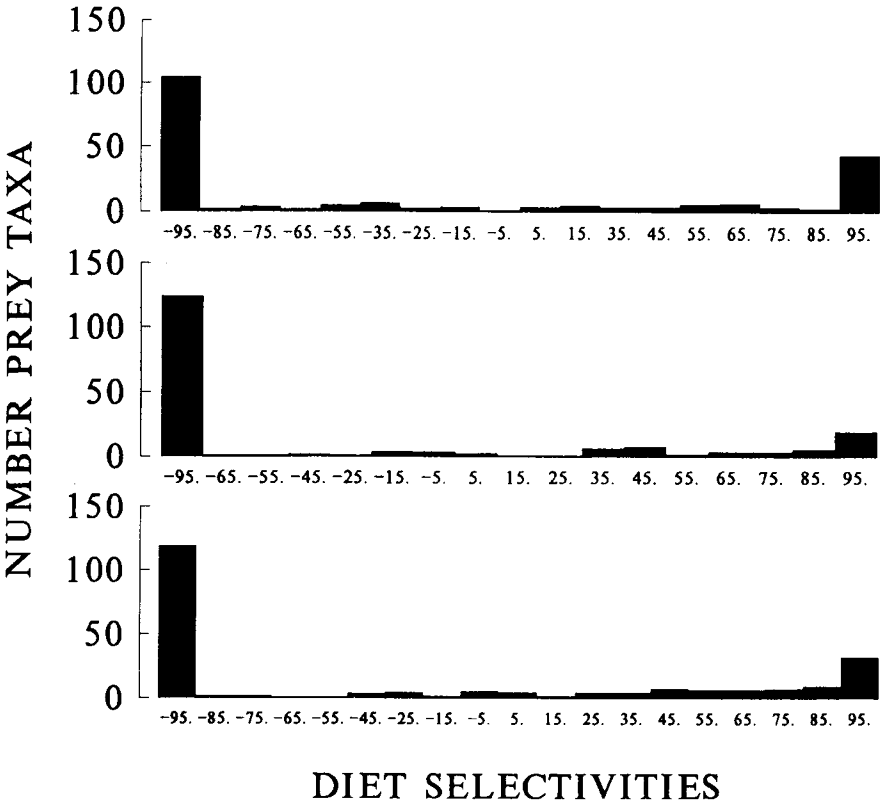

Fig. 7. The distribution of selectivities is bimodal for three grassland birds (top = western meadowlark, middle = lark sparrow, bottom = grasshopper sparrow).

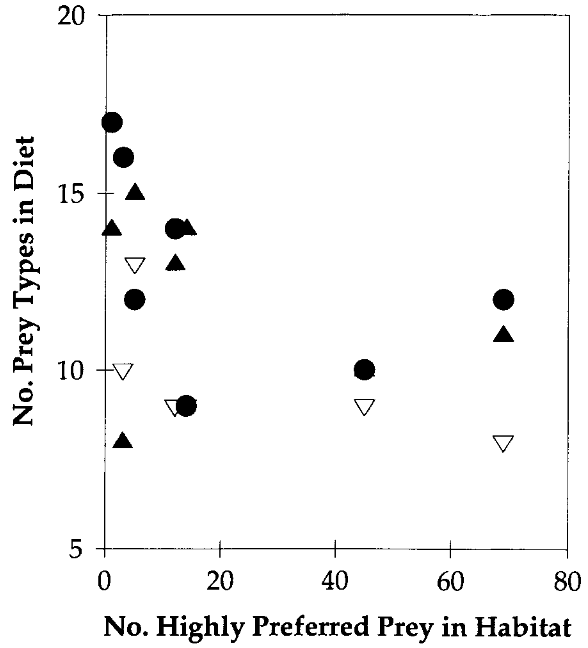

Fig. 8. Diet breadth (number of prey taxa >1% of the diet) decreases as the abundance of highly preferred ($S > 0.5$) prey in the habitat increases (dark triangles = western meadowlark, clear triangle = lark sparrow, dark circle = grasshopper sparrow).

season (Fig. 2). To evaluate diet breadths, we focused only on prey that made up >1% of the prey in any sample period. This decreases the effect of rare taxa, decreasing the importance of variable sample sizes of bird species.

All three birds exhibited the predicted negative relationship between the abundance of high quality prey and diet breadth, although the meadowlark response was not significant (One-tailed Spearman Rank Correlation: grasshopper sparrow r = -0.75, p = 0.043; lark sparrow r = -0.88, p = 0.02, meadowlark r = -0.252, p = 0.58, Fig. 8).

Predictions 3 and 4: How does selectivity for a prey type vary with its own abundance and the abundance of high-quality prey?

The Classical model predicts that a prey type's S should decrease with the abundance of high quality prey, and that there should be no relationship between a prey's own abundance and it's S. In contrast, the Nutrient Model predicts decreasing S's as the abundance of prey with limiting nutrients increases.

If diet shifts of the three species are considered separately, small sample sizes (7 for grasshopper sparrows and western meadowlarks, 6 for lark sparrows) introduces the strong likelihood of Type II error. We pool S's across bird species for each prey taxa when 1) there are 6–7 samples per species; 2) S's did not vary between the species; and, 3) the taxa showed intermediate mean S's $(-0.75 < S < 0.5)$. These 8 prey types thus provide the best opportunity for statistically detecting trends between S and abundance of various prey. We performed a 2-way regression, in order to evaluate how S's vary with the abundance of high quality prey and the prey's own abundance. We used Type III Sums of Squares to remove the effects of the other factor.

The eight prey fall into four groups of two prey each (Table 6). In group 1 (the <5 mm Lepidoptera larvae and 5–15 mm Hymenoptera) S's do not systematically vary with changes in their own abundance or that of highly preferred prey.

In group 2 (Coleoptera and Hymenoptera <5 mm) S's increased with the abundance of highly preferred prey. As highly preferred prey increased in the samples, the birds increasingly preferred small Coleoptera and Hymenoptera.

In group 3 (Coleoptera and spiders 5–15 mm) S's did not vary with their own abundance, but increased with the declining abundance of the preferred prey. This matches the predictions of the Classical model of energy maximization.

Tab. 6. Regressing a prey type's selectivities (S) against its abundance and the abundance of prey with S's >0.50, using Type III Sums of Squares. Data pooled for all three species. Only prey 1) having 6–7 samples per bird species, 2) showing no differences in S's between species and 3) with $-0.75 < S < 0.50$, are used. P-values for the predicted negative slope between good prey and S are 1-tailed.

Prey Taxa	Size	Mean		Regression against Good Prey		Regression against Abundance	
		S	n	Slope	p	slope	p
Lep. larvae	<5 mm	0.26	19	0.000	NS	0.058	NS
Hymenoptera	5–15 mm	−0.28	19	0.002	NS	−0.018	NS
Coleoptera	<5 mm	0.28	19	0.021	0.035	0.053	NS
Hemiptera	<5 mm	0.19	19	−0.011	0.006	−0.029	0.003
Coleoptera	5–15 mm	0.40	19	−0.009	0.033	−0.011	NS
Spiders	5–15 mm	−0.30	19	−0.010	0.045	0.043	NS
Diptera	5–15 mm	−0.47	19	−0.014	0.005	−0.058	0.010
Hymenoptera	<5 mm	−0.40	19	0.018	0.003	0.001	NS

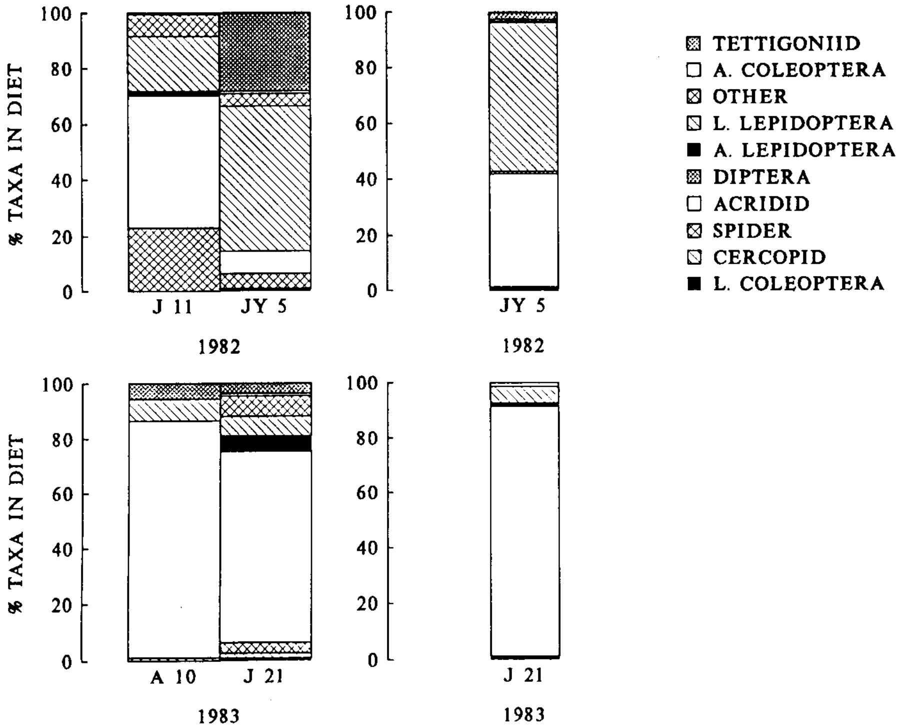

Fig. 9. Diet composition of nestlings of grasshopper sparrows (left) and lark sparrows (right) in 1982 (top) and 1983 (below). Not represented are homopterans, hemipterans and hymenopterans (found in one of six diet samples), and cicadellids (found in 2 of six diet samples).

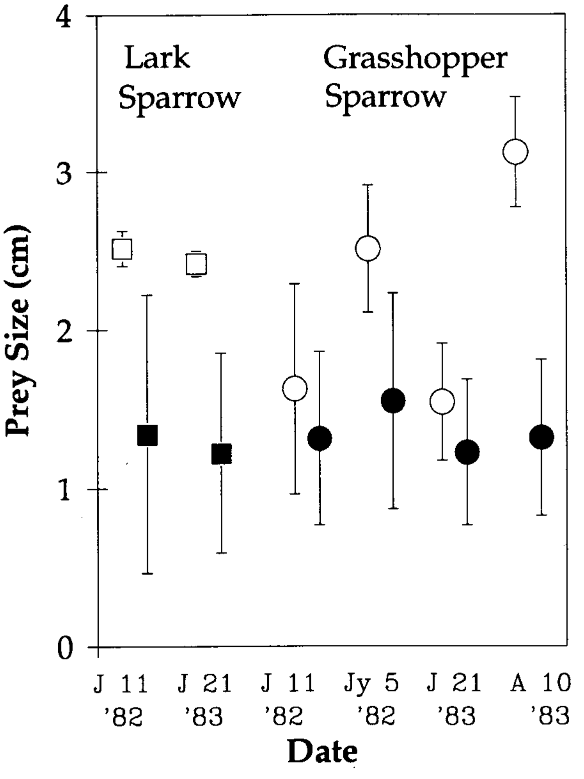

Fig. 10. Mean prey size (±2 standard errors) of adult birds (dark symbols) tends to be smaller than nestling birds (clear symbols).

Finally, in group 4 (the <5 mm Hemiptera and 5–15 mm Diptera) *S*'s declined both with the abundance of preferred prey, and with their own abundance. This matches the predictions of the Nutrient model.

Prediction 5: Does adding a travel cost restrict the diet to larger prey?

Over 4 collection periods, we sampled between 2–10 grasshopper sparrow individuals feeding nestlings (Table 4); we sampled lark sparrows over two periods, yielding 2 and 4 individuals feeding young. Diets fed to nestling lark and grasshopper sparrows differed from adult diets in

Tab. 7. Prey size consumed by adult grasshopper and lark sparrows differs from that fed to nestlings.

Source	df	Grasshopper sparrow Type III SS	*p*
Date	3	7.163	0.0001
Age	1	9.551	0.0001
Date* Age	3	7.523	0.0079

Source	df	Lark sparrow Type III SS	*p*
Date	1	0.047	0.7613
Age	1	6.273	0.0013
Date* Age	1	0.000	0.9808

a number of respects. Nestlings received few seeds (included in the "other" category of Fig. 9) in contrast to the 3–61% composition of adult diets. Acridids, Lepidoptera larvae and tettigoniids were more represented, at the expense of adult Coleoptera. Diets also varied across years (Fig. 9): Lepidoptera larvae, a conspicuous prey late in 1982 was less represented in 1983.

The Central Place Foraging model predicts that prey items returned to a nest, and thus having an additional travel cost, should be larger than prey without such a cost. The diets of nestling lark and grasshopper sparrows are more restricted, dominated by acridids and Lepidoptera larvae at the expense of taxa like Coleoptera and Hemiptera (contrast Fig. 5 with Fig. 9).

A two-way ANOVA compared adult versus nestling prey sizes while controlling for sample date. A sample consisted of the mean size of prey in a gut sample or mean size of prey returned to a nest by a single bird. Nestling diets of lark and grasshopper sparrows contained larger prey than their adult counterparts ($p < 0.002$, Fig. 10, Table 7). In lark sparrows, where two sample dates were compared, mean prey sizes did not differ with date ($p = 0.76$), nor did the extent of difference between adult and nestling diet sizes vary with date ($p = 0.98$).

In grasshopper sparrows, where four sampling dates were compared, the results were more complex (Table 7). The size of prey consumed by adults and nestlings differed between sample periods ($p < 0.0001$) and although there was a significant effect of nestlings versus adults ($p < 0.0001$), there was also a significant interaction term ($p = 0.0079$). T-tests comparing adult/nestling prey size for each sample date reveal no differences on 11 June 1982, ($p = 0.32$), but significantly larger prey for nestlings in the remaining samples (p's < 0.02).

Discussion

The birds of Arapaho Prairie encounter a wide range of arthropod taxa during the breeding season. These arthropods compose a large fraction of the prey items eaten by adult birds, from 97% of the western meadowlarks diet to 67 and 33% of the items in the diet of the grasshopper and lark sparrow (Fig. 3). Contribution of arthropods by mass is certainly much higher since all seeds consumed are in the smallest size category. Arthropods are virtually the sole prey item fed to nestlings. Since these birds can depress at least some of the arthropods by up to 25% (e.g., acridids Joern 1986, 1988) and since feeding rates increase with fledging rates in at least the grasshopper sparrow (Kaspari 1991a), understanding prey selection rules should help us understand how avian predators influence both their own populations and those of their prey.

The great variety of prey sizes and taxa in the diets of these birds precluded an exhaustive inventory of E/T's. However, estimates of chitin fraction, a component of the arthropod exoskeleton less digestible than others (Karasov 1990) varied considerably across taxa. For example, the long and thin phasmatids (walking sticks) and hymenoptera average over 50% chitin by dry weight, compared to the acridids, spiders, and adult lepidopterans, which average below 25% (Table 1). This variation did not appear to translate directly into differences in selectivity: Lepidoptera adults were not more preferred than Hymenoptera (Table 5). However, the declining chitin fraction with prey size in many prey taxa may begin to explain the avoidance of small prey in the diet (see below).

Selectivities

All three species of birds are selective both in the taxa they consume and the sizes of prey within those taxa (Table 5, Fig. 6). For instance, acridids appear to be the most preferred insect taxa, more so than the numerically dominant Homoptera (cercopids and cicadellids) which represented the majority of arthropods in sweep samples. Other taxa, like the tettigoniids, small Coleoptera, and small Lepidoptera also showed relatively high S's compared to the Hymenoptera, adult Lepidoptera, and Diptera.

Prey size also helped to determine preference. In general, the two smallest size classes showed low S's, intermediate prey sizes showed higher S's, and the larger prey were exclusively preferred by the largest bird, the western meadowlark.

Why are prey <15 mm so avoided when they constitute most of the prey items in the Sandhills (Table 1)? Smaller prey may simply be less conspicuous, and thus less likely to be detected (e.g., O'Brien et. al. 1976). However, it is difficult to picture how this would produce the sharp discontinuity in S's for the acridids.

The answer may also lie in the chitin. Grasshopper sparrows go to great lengths, often tripling handling times, to remove chitinous prey parts (Kaspari 1990). The most chitinous prey parts are removed to increase room for more prey, postponing gut limitation and concentrating nutrients in the remaining prey (Kaspari 1991b). Small prey, which often have a larger chitin fraction per weight than large prey (Table 1) may not only have less energy, but a diet of small prey would also fill the gut with less nutritious chitin more quickly. Preferences for large prey may arise because birds want to postpone filling their gut. Put another way, chitinous exoskeletons are "second-class nutrients" that the birds avoid by 1) avoiding small prey and 2) removing chitinous prey parts from large prey.

Evaluating the optimal diet models

Classical model. The Classical model of pure energy maximization receives mixed support in this study. We constructed profitability curves – expressing the relationship between energy/handling time and prey length – for intermediate-sized adult acridids. These curves predicted a weak preference for smaller acridids. This prediction was supported for grasshopper sparrows and western meadowlarks.

The Classical model also predicts the decrease in diet breadth with increasing abundance of preferred prey for all three species, two significantly. As acridids 15–35 mm increased toward the end of the breeding season, the birds concentrated increasingly on these prey and dropped others from their diet.

However, evidence argues against a pure energy maximizing strategy. Although distributions of S were distinctly bimodal, as predicted by the All or None rule, between 25% and 35% of S's fell between –0.90 and 0.90, suggesting partial preferences. Furthermore, of the 8 prey with intermediate S's, only half showed decreased S's with increasing abundance of the preferred prey.

Central Place Foraging model. Prey from the stomach samples of lark and grasshopper sparrows were smaller than prey fed to young by adults in the same period. Thus when travel costs were added to prey, the sparrows selected larger prey as predicted by the Central Place Foraging model. Grasshopper sparrows loaded more prey the farther they foraged from the nest (Kaspari 1991a), further supporting the model.

Taken together, the results from the tests of the Classical and Central Place Foraging models suggest that energy maximization is a partial explanation for the diet selectivity shown by this assemblage. Left unexplained are the existence of partial preferences for many taxa.

Nutrient Constraint model. The Nutrient model posits that foragers maximize energy intake while obtaining non-substitutable nutrients from the fraction of prey in which they occur. Foragers must minimally consume some number of these prey. This results in high selectivities when the prey are rare and low selectivities when those prey are abundant. This negative relationship between a prey's S and its abundance is supported for 2 of 8 prey: 5–15 mm Diptera and <5 mm Hemiptera. What nutrients these prey may contain is unclear.

Two more prey, Hymenoptera and Coleoptera <5 mm, show a positive correlation between the abundance of the highly preferred 15–35 mm acridids and their S's. This pattern was unexpected, and may represent nutrient complementarity (Rapport 1980) between the acridids and these taxa, or some other phenomena not yet explained.

A complex picture of diet selection begins to emerge, driven in part by the maximization of energy, but with evidence for minimal nutrient requirements and even complementarity among some dominant prey taxa . Insectivorous *Anolis* lizards in California also showed partial preferences and decreasing selectivities with increasing abundance of preferred prey (Stamps et al. 1981), suggesting nutrient limitation. However, these dietary dynamics are as yet intriguing patterns without mechanism. We have yet to understand the nutrients required by these vertebrate predators and their distribution in available prey.

We do know that insects can vary significantly in the fraction of various amino acids required by the spiders that prey upon them (Greenstone 1979). Our study clearly shows differences in chitin, a negative nutrient, over taxa and prey size for an arthropod assemblage. Some predators capitalize on such differences: mixed diets outperform pure energy maximization in a bird (Krebs and Avery 1984), a spider (Greenstone 1979) and a protozoan (Rapport 1980).

Ecologists studying herbivory have recognized and convincingly modeled herbivore behavior using the distribution of nutrients across plants, and the nutrient requirements of foragers (e.g., Belovsky 1978, 1981). Similar studies up the food chain are needed. The range of arthropod prey in Table 5 include sap feeders, chewing herbivores, granivores, folivores and carnivores. Perhaps a line of exploration linking insect diets to their nutrient content would be fruitful.

Studying diets: what is opportunism?

Studies of avian assemblages often conclude, or proceed from the assumption, that the birds are dietary "opportunists". What does this mean? Cody (1974) states

> "As birds seem to be largely opportunistic in what they feed on *every food item encountered and found to be manageable will be incorporated into the diet and none such is likely to be passed over* (italics ours).

Likewise, Wiens and Rotenberry (1979) suggest opportunistic foragers are

> "eating by and large whatever they encounter".

We used these definitions to suggest a simple criterion to operationalize the concept of opportunism: for the range of potential prey encountered by the forager (as necessarily defined by the investigator) a forager opportunistically selects among these prey if it's S's for these prey are uniform and approach 0. Our definition, we have learned, does not match the intent of Wiens and Rotenberry (pers. comm.). They suggest, and we concur, that foraging decisions are likely a hierarchical process. First, some prey are too noxious or too large to ever be consumed. Second, the subset of remaining prey are subject to predator choice. In order for this approach to be useful, it must be subject to falsification. High levels of diet overlap between co-occurring bird species (Wiens and Rotenberry 1979) can support, but not falsify, the hypothesis of opportunism.

Our approach to the problem of avian diet selection differs from Wiens and Rotenberry (1979) and allows us to address both levels of diet selection. First, we estimated prey availability and prey selection. We found that some prey taxa and some prey sizes were uniformly excluded from the diets of some bird species of Arapaho

Prairie. This uniform avoidance corresponds to the first level of the diet selection hierarchy. This is not a trivial result, since some large prey were avoided by grasshopper sparrows and preferred by western meadowlarks. Next, we approached the second level of diet selection – choice among palatable prey types – by contrasting different models of optimal diet against the null hypothesis of opportunism. We found some support for diet rules predicted by energy maximization. It would have been difficult to address the null hypothesis of opportunism at any behavioral level without estimating prey availability and contrasting diet patterns against those predicted by alternate hypotheses.

Diets, competition, and the structure of grassland bird communities

Regardless of differences in approach, our Sandhills grassland parallels the Shrubsteppe in many ways. Both habitats are dominated by grass and low shrubs where three insectivores are abundant. Diets of the assemblage appeared roughly comparable: Orthoptera, Lepidoptera larvae and seeds are common. The western meadowlark, found in both habitats, consumes few seeds and more large (>35 mm) prey than the other birds. In both habitats, the intermediate-sized insectivore (lark sparrows and horned larks) consume large quantities of seeds, with the smallest (grasshopper and sage sparrows) lying somewhere intermediate in the mix of arthropods and seeds. In both habitats, dietary overlap was high and diets tended to covary over time. Thus it is not surprising that we also share some of the same conclusions of Wiens and Rotenberry (1979) to a point: competition has not produced highly segregated diets among species in either system.

High diet overlaps, however, do not preclude competition. Populations may diverge in diet in response to competition, as MacArthur and Levins (1966) and Schoener (1974) point out, but this is but one possible response. Optimally foraging competitors may segregate foraging habitats (MacArthur and Pianka's 1966 Compression Hypothesis) and still maintain high dietary overlaps. On Arapaho Prairie, lark sparrows appear to nest in habitats different from grasshopper sparrows and western meadowlarks (Kaspari and Joern, unpubl. data). Such nesting segregation will promote some degree of segregation in foraging patches for distance reasons alone. Grasshopper sparrows and western meadowlarks, on the other hand appear to nest in the same habitat.

Populations may also compete precisely because they have failed to diverge. The profitability curves constructed for the most preferred prey (acridids) predict high overlaps except for the larger, rarer size classes. On Arapaho Prairie, avian predators can depress grasshopper populations by up to 25% (Joern 1986); grasshopper sparrows produce more offspring in nests with higher prey delivery rates (Kaspari 1991a). Taken together, these data suggest the existence of competition in the avian assemblage of Arapaho Prairie (Martin 1986). Wiens (1989a, unpubl. data) argues that food limitation and depression is lacking in the Shrubsteppe. If the Shrubsteppe birds are indeed opportunistic predators – and measures of prey availability and prey selection would greatly help to address this question – then this would provide a strong link between an ecological process (competition for food) and an evolutionary result (the evolution of optimal foraging).

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