

AN ABSTRACT OF THE THESIS OF

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Title: Ecological Relationships among Shrubsteppe Passerine

Birds: Competition or Opportunism in a Variable Environment?

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Abstract approved: \_\_\_\_\_

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Tramer (1969) has suggested that "regulation" of species diversity occurs through variation in either its richness or evenness component with the former occurring in predictable, non-rigorous environments, and the latter under the opposite conditions. This hypothesis is tested by examining the variation in components of bird community diversity along a derived gradient of climatic variability and rigor.

The gradient consists of the first axis of a principal component analysis of fifteen weather variables recorded at stations throughout the Pacific Northwest, and accounts for 53.8% of the total variation in those variables. Factor loadings of the original variables suggest that the gradient represents a cline from the mild, moist, uniform weather of the Oregon and Washington coast, to the severe, arid variable climate of interior southern Oregon and Idaho.

Correlations of avian community attributes (diversity, richness, and evenness) with their geographic position along

the derived gradient show that species diversity decreases significantly along the gradient from mild-moist-stable to severe-arid-unstable climates. Unlike several other studies, however, diversity changes as a result of variation in its evenness rather than its richness component, supporting Tramer's hypothesis.

The results are consistent with the suggestion that in less stable environments resource limitation and subsequent interspecific competition may be relatively unimportant in determining bird community structure. This aspect is explored more fully by examining in some detail the dietary relationships within a guild of three ground-foraging passerine birds (Horned Lark, Sage Sparrow, and Western Meadowlark) in the shrubsteppe of southeastern Washington, which lies well toward the severe-arid-unstable end of the derived gradient.

General dietary analysis indicated a strong temporal component to the organization of bird diets: different species collected at the same time ate the same things while the same species collected at different times ate different things. This pattern is reinforced by cluster analysis and stepwise discriminant analysis. Similarities in diet extended to other components as well. Dietary diversities tended to be the same for contemporaneous collections of birds, as did average prey sizes, although the latter evidenced a few statistically significant exceptions.

Theoretically predicted relationships between diet and trophic structure morphology emerged only at the grossest level, and even then were not always observed. In general, differences in body size or bill length were insufficient to account for variation in prey sizes, although meadow-larks did on occasion take significantly larger items than the other, smaller species. Average prey size was significantly correlated with the proportion of seeds in the diet and varied seasonally as seed consumption varied.

Simulation model estimates of energy flux indicated a total annual energy demand of  $2.91 \text{ kcal m}^{-2} \text{ yr}^{-1}$  by the entire passerine avifauna during 1974, with daily demands varying from 0.0025 to  $0.0260 \text{ kcal m}^{-2}$ . Coupling energy requirements with estimates of arthropod availability implies (at a rather crude level of analysis) that bird demands on the insect standing crop never exceed 0.7% per day of that standing crop during the breeding season or summer. Overall, the bioenergetic estimates suggest that these birds play a relatively unimportant role in ecosystem processes.

Several aspects of this study indicate that shrub-steppe passerines are largely opportunistic rather than optimal in their foraging and diet selection, and that the apparent absence of "fine-tuning" to their competitive milieu is most likely a function of the variable environment in which they coexist.

Ecological Relationships Among Shrubsteppe  
Passerine Birds: Competition or Opportunism  
in a Variable Environment?

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ECOLOGICAL RELATIONSHIPS AMONG SHRUBSTEPPE PASSERINE BIRDS:  
COMPETITION OR OPPORTUNISM IN A VARIABLE ENVIRONMENT?

I. INTRODUCTION

The following thesis is divided into two distinct but related parts. This structure largely reflects the preparation of each part as a separate manuscript. The first part is an attempt to test a hypothesis that deals with the "regulation" of species diversity (Tramer 1969). Among other things, the results suggest that the principles underlying community organization vary as a function of environmental variability and harshness, and that as variability and harshness increase, resource limitation and subsequent interspecific competition are reduced in importance.

In the second part, the effects of potentially reduced resource limitation are investigated in a guild of ground-foraging birds of the southeastern Washington shrubsteppe, an area which can be shown to exhibit elements of climatic variability and harshness. Focusing on diet selection, I examine avian utilization patterns along their food niche dimension. The results appear consistent with the notion that opportunism, not competition-induced optimization, plays a major role in the food selection process.

## II. COMPONENTS OF AVIAN DIVERSITY ALONG A MULTIFACTORIAL CLIMATIC GRADIENT

The causes of gradients in species diversity have been the subject of considerable speculation (for review see Pianka 1966, Whittaker 1975), a substantial amount of which is concerned with the role of environmental variability. This variability may be expressed by such forms as spatial heterogeneity (Simpson 1964, MacArthur 1965) or climatic irregularity (Klopfer 1959, MacArthur 1965), but it has generally only been correlated with observed diversity patterns and rarely used to make testable predictions about community structure. A model proposed by Tramer (1969), however, suggests that diversity within a collection of communities might vary as a function of changes in either its richness component (number of species) or its evenness component (distribution of relative abundances of the species), each of which represents an alternative response. Tramer expected variations in richness to occur in predictable, non-rigorous environments, with variations in evenness to occur under the opposite conditions. Without regard to the mechanistic details of the model (which will be discussed later), I sought a system that might yield an appropriate test of these predictions.

One approach often taken to examine the effects of environmental variation on community structure is to sample

communities along some abiotic gradient. Although such gradients may involve variation in a single factor such as temperature (e.g. Kullberg 1968), more often than not they reflect a multifactorial environmental complex. Such gradients may be illustrated by changes in elevation (Terborgh 1971, Whittaker 1969), latitude (Pianka 1969, Tramer 1974), or time (Odum 1950). It is usually assumed that the multiplicity of factors contained in such gradients varies in some reasonably consistent manner. I will consider a number of large-scale climatic variables that may vary in a variety of directions with respect to one another, and combine them into a derived gradient that reflects a logically consistent pattern. Once the gradient has been derived I will examine its relations with a few simple avian community attributes in a manner that allows appraisal of Tramer's predictions.

## METHODS

Avian Community Analysis

Bird community data were taken from all North American Cooperative Breeding Bird Surveys (Robbins and Van Velzen 1967) conducted in Oregon, Washington, and Idaho between 1968 and 1974. This region was selected on the basis of both a familiarity with its avifauna and the qualitative observation that it probably included a climatic range sufficient to generate a gradient with the desired attributes. The data consisted of 348 roadside counts distributed among 87 sites. Since most of the sites were sampled for several years, these years were averaged to yield a single representative census for each site.

The major reason for the use of these samples is the relatively large area covered by each census ( $25.4 \text{ km}^2$ ); such a census should reflect bird community composition on a scale consistent with that of the macro-climatic variables to be examined, whereas smaller (but more precise) censuses would more likely be sensitive to microclimatic or micro-habitat changes. Although there are sampling problems inherent in the roadside technique (references summarized in Rotenberry and Wiens 1976), there is no reason to expect potential errors or biases to be systematically or non-randomly distributed throughout the three-state region, particularly with respect to the climatic gradient to be

derived.

A species diversity index was calculated according to Simpson (1949), then converted to the equivalent number of equally common species by applying a reciprocal transformation. Thus, in the notation of Hill (1973), diversity becomes

$$N_2 = 1 / \sum p_i^2$$

where  $p_i$  is the relative abundance of the  $i^{\text{th}}$  species. This represents diversity as the number of equally abundant species occurring in a sample that would produce the untransformed index previously calculated for that sample. This has the obvious advantage of expressing diversity with "species" as the basic unit (rather than "bits" of information or other such elusive terms), yet including the evenness component of species abundance patterns as well as the richness component (Peet 1974). Further, it is a mathematically tractable measure (Hill 1973), allowing more straightforward comparisons among communities with different diversities and sample sizes, and Stander (1970) has shown that the Simpson diversity value for a sample converges rapidly to the true population value with sample sizes as low as 25 individuals. An additional property of  $N_2$  recommends its use with these data: as Peet (1974) pointed out,  $N_2$  is more sensitive to variations of the abundant species than of the rare ones. Robbins and Van

Velzen (1967) have indicated that the cooperative surveys more likely reflect the true relative abundances of the more common species while being much less accurate for the rare ones.

Richness ( $N_0$ ) was expressed as the number of species observed in a sample. Evenness was calculated using a ratio proposed by Hill (1973):

$$E = N_2 / N_1$$

where

$$N_1 = \exp (-\sum \underline{p_i} \ln \underline{p_i}).$$

The quantity  $N_1$  is essentially the equivalent number of equally common species derived from the information theory measure for species diversity, and Hill (1973) suggests that this ratio stabilizes to a true community value of evenness with increasing sample size more readily than either  $N_1 / N_0$  or  $N_2 / N_0$ .

### Climatic Analysis

There are clearly a variety of climatic conditions that act either directly or indirectly to influence the distribution of birds. The 15 variables I chose to use (Table 1) were selected on the basis of their availability from various U. S. Weather Service sources and their potentially important effects on birds. All are yearly averages representing from ten to sixty years of records. These

variables were also chosen to reflect elements of both the absolute quantity and temporal variation of precipitation and temperature. For example, the absolute amount of rainfall (variable 9) might be important in driving factors influencing bird distributions, but its variability, particularly the occurrence of "bad years" (variable 12), may also be critical. Quantity and variability during the biologically important rainfall periods of the spring and fall (variables 10, 11, 13, and 14) might be especially influential.

For thermal values it seems reasonable that the extremes (variables 1 and 2) and their variation (variables 3 and 4) are much more likely to be important in limiting distributions of birds than average values. Further, thermal extremes are likely to exert their effects even more directly than precipitation patterns (Salt 1952, Johnston et al. 1972, Jenkins et al. 1965). These extremes are expressed in a more general way by the number of very hot days and the date of the first frost (variables 5 and 6). Likewise, frost-free days and number of days with snowpack (variables 7 and 8) may indirectly contribute to population limitation.

The value of each particular climatic variable at each census site was determined by plotting the location of that site on a map containing isopleths for that variable. Each variable was then standardized to zero mean and unit

variance, and principal component analysis (Cooley and Lohnes 1971) used to isolate the various concurrent climatic trends expressed by the resulting 87 sites x 15 climatic factors matrix. This analysis takes the original 15 variables and extracts the patterns of correlations by creating 15 new components. Since the total variability in the original data set is unequally partitioned among the components, one can ignore those components that account for what one may consider an insignificant proportion of the total variation, thus considerably reducing the number of dimensions with which one need be concerned. If, in fact, the first component (which has the maximum variance) alone contains a substantial amount of the total variation, one can then treat it as a multidimensional gradient much like elevation or latitude, but with the relationship of each variable to the gradient perhaps more precisely known. By examining the correlations between the new components and the original variables (factor loadings), one can infer which of the original variables contribute the most to the physical interpretation of each component.

White and Lindley (1976) have shown that the longer the interval over which weather data are averaged (e.g. monthly vs. weekly averages) and the longer the period over which those data are accumulated, the greater the proportion of the total variation accounted for by the first principal component. They interpret this to mean that the first component



becomes an increasingly better descriptor of the overall climate. Furthermore, since the first component contains the largest variance, it is reasonable to interpret it as that linear combination of the original variables that maximally discriminates among the sites, a sort of "internal discriminant analysis" (Harris 1975).

The location of each site along the derived gradient is represented by its factor score for the first component, the factor score being determined from the interrelations of the original site-specific climate variables and the new component (Cooley and Lohnes 1971). Factor scores are then used in correlation analysis with other site properties (e.g. community attributes) to examine the relationship between these properties and the gradient.

## RESULTS

The first principal component alone accounts for 53.8% of the total variation in the original climatic data set; the second only 16.9%, and the rest even less. As over half the original variability is contained in the first component, it seems justifiable to treat that component as representing a real environmental gradient, thus reducing from 15 to one the number of dimensions that need be considered.

Examination of the factor loadings (Table 1) shows that this component is highly correlated with a number of original variables and that these correlations form a logical pattern. At one extreme there are high positive loadings for those variables indicating climatic severity and large temporal variation: high daily July maxima, a large number of days over 32°C, wide daily July and January ranges, and a high frequency of annual rainfall less than 85% of average. At the other extreme there are high negative loadings for variables expressing amount of rainfall and winter mildness: warm and cool season precipitation, total precipitation, daily January minimum, date of first freeze, and number of days without frost. The observation that the latter three temperature-related variables have negative factor loadings implies that they express higher values at one end of the gradient than at the other, which

translates into comparative winter mildness: warmer January lows, the first freeze comes later in the autumn, and there are more days without frost. Summers are milder, too, since daily July maxima and days over  $32^{\circ}\text{C}$  attain their high values at the other end of the gradient. Taken together, the loadings suggest that the first principal axis describes a cline between moist, mild, relatively uniform weather, and a severe, dry, much more variable climate.

By using the factor scores of the 87 census areas for the first principal axis, each census can be placed into its position along the environmental gradient, thus ordering the sites both with respect to the gradient and with respect to each other. Rather than presenting the numerical value for each site, I have chosen to plot contour lines showing unit isopleths of these factor scores relative to their geographic position (Figure 1). The relationships between the site factor scores and the original climatic variables with respect to the first principal component are summarized in Table 2. This derived gradient clearly expresses the cline between the mild, moist Oregon and Washington coast and the severe, arid interior of southern Oregon and Idaho.

Variation in community attributes with respect to the gradient was examined by calculating their product-moment correlation coefficients with the site factor scores for the first principal axis. Diversity, the attribute of

most concern, shows a statistically significant decline along the gradient from mild-stable to severe-unstable ( $r = -0.33$ ,  $\underline{P} < 0.01$ , 85 df). Interestingly, this decline is not associated with a decline in richness, but instead parallels a decrease in the evenness of the distribution of abundances, which also shows a significant decline ( $r = -0.27$ ,  $\underline{P} < 0.05$ ). Since variability in evenness may be associated with variability in either sample size (Peet 1975) or richness (Sheldon 1969), the observation that the number of individuals and species in each census do not vary significantly along the gradient ( $r = 0.09$  and  $-0.20$ , respectively; both N. S.) suggests that these results reflect a real change in community structure.

## DISCUSSION

Although the first principal climatic axis accounts for only about 11% of the total variation in the diversity measure ( $r^2 = 0.109$ ), it is the pattern of variation in the components of diversity that is most instructive. These results strongly suggest that, although the number of species and the number of individuals remain relatively constant, these individuals become increasingly concentrated in a smaller proportion of the species as communities are ordered from mild, moist, less variable to severe, dry, more variable climates. In other words, evenness decreases. This contrasts with other attempts to relate both aspects of diversity (richness and evenness) to environmental variability (e.g. Kricher 1972, for birds; Kushlan 1976, for fish; Uetz 1975, for spiders; and implied by Pianka 1967, for lizards), which suggested that diversity changes are mediated by changes in richness. Except for Pianka's study (which was rather general in nature), these investigations were geographically quite localized, which may account for the difference in these observations.

Using censuses distributed over a wide area of North America, Tramer (1969) also observed that bird species diversity changed through its richness component, although he did not investigate this phenomenon with respect to a gradient of environmental stability. However, he did propose

a mechanism for variation in diversity that appears consistent with the results obtained here. Comparing birds to plankton, he observed that diversity differences in predictable, non-rigorous environments (territorial birds in their breeding season) were associated with changes in richness, whereas these differences were associated with differences in evenness under the opposite environmental conditions ("opportunistic" lacustrine plankton). The former occurs when most populations in the community are near equilibrium, which is possible because the physical environment and resource levels are stable from year to year. Hence, fluctuations in relative abundances are minimized and variation among areas depends on the addition or substitution of additional species as basic resources vary geographically. Populations in variable environments, on the other hand, are often held below equilibria during unfavorable times, and numbers may increase considerably in response to ameliorating conditions. The mechanism by which variation occurs will likely be different from species to species, but in any event should create enough variability in population numbers to consistently affect the distribution of relative abundances. Therefore community diversities arrayed along a gradient of environmental stability are expected to change in response to changes in evenness; diversities along a gradient of resource abundance or limitations should reflect changes in richness.

Although anticipating that within-habitat diversity would vary as a result of changing richness, Wiens (1974) proposed that the same sort of phenomenon (reduced diversity through climatic instability) is of common occurrence in grasslands and, indeed, is one of the major features determining community structure among grassland birds. Pulliam et al. (1968) also discussed a possible relationship between variations in community evenness and resource-related equilibria. They suggested that high evenness values are to be expected under conditions of resource limitation and subsequent intense interspecific competition, whereas lower values should occur when populations are regulated outside their resource base (e.g. by predation). These arguments all suggest that while interspecific competition may be an important and sufficient variable for determining community structure, it is by no means a necessary one, particularly as environmental variability increases.

Perhaps, as Pianka (1967) suggests for lizards, climate expresses its effects on community structure only indirectly, mediated by its more direct effects on vegetation physiognomy. However, most studies on the effects of habitat structure on bird species diversity (see especially Willson 1974, Roth 1976) indicate that changes in physiognomy are more often correlated with changes in richness, primarily

by the addition or subtraction of individual species or even entire guilds. Such a trend is not consistent with the results presented here. It is feasible that rather than affecting vegetation structure in the strict physiognomic sense (e.g. percent coverage values, foliage height diversity), increasing climatic variability acts to reduce, on a large scale, the degree of spatial heterogeneity or habitat patchiness. In such a case, the framework provided by McNaughton and Wolf (1970) to investigate "dominance" might be applicable, although the results here are consistent with a conclusion different from that they reached. In their view, community richness is a measure of the number of exploitation zones available within a system. They concluded that the dominant species in a community are generalists while subordinants appear to be specialists less through physiological requirements than through being excluded from areas they would ordinarily occupy by the superior competitive ability of the dominants. In such a competition-dominated system, however, one expects to observe changes in richness along gradient in spatial heterogeneity. If, on the other hand, most species are more or less specialists, the relative abundances of species reflect the relative abundances of their specialties. This implies that habitat patchiness and spatial variability in the resource base are the driving forces behind community structure, and that community differences along a hetero-



geneity gradient should reflect evenness differences.

Unfortunately, quantitative descriptions of vegetation composition, structure, and heterogeneity along the gradient I investigated are lacking; given the nature and extent of the study area, such data would be difficult to generate. The question becomes, which contains more "heterogeneity" on a scale of about 25 km<sup>2</sup>, the Thuja - Tsuga - Pseudotsuga forests of western Oregon and Washington, or the Artemisia-dominated shrubsteppe of eastern Oregon and Idaho? If it is, in fact, the forests, the data presented here are consistent with the assertion that habitat patchiness or spatial heterogeneity, driven in part by climatic variability, may be relatively more important than competitive interrelationships in determining bird community structure, particularly as patchiness and heterogeneity decrease.

This is certainly not to say that competition is unimportant; indeed, since we are observing the change in community structure along a gradient, it is not unreasonable to expect a change in the balance of any two factors which would separately influence species' distributions. However, there may be pitfalls in assuming that any particular biotic relationship determines community structure throughout a wide range of environmental conditions.

The methods employed here have considerable potential beyond the investigation of species diversity patterns. Once

communities have been ordered, gradient analyses of a variety of other structural or functional attributes, which theories predict may be correlated with climatic variability (such as biomass distributions, generalist/specialist ratios, amount of real or expected interspecific competition) may be undertaken. The problems lie more in the quantification of the attributes than in the construction of the gradient. Examination of single-species' abundances along a principal component axis may provide insight into species/climate relationships, and the correlation of a species' abundance pattern with an interpretable component may suggest appropriate variables for predictive model-building by multiple regression techniques (e.g. Hinds and Rickard 1973).

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Table 1. Climatic variables and their factor loadings for the first principal component. Variables that attained their highest loadings on the first component italicized.

Variable <sup>1</sup>	Attribute <sup>2</sup>	Factor Loading
Temperature		
1. Daily January minimum	A	<u>-0.807</u>
2. Daily July maximum	A	<u>0.789</u>
3. Daily January range	V	<u>0.870</u>
4. Daily July range	V	<u>0.914</u>
5. Number of days > 32°C (90°F)	A	<u>0.607</u>
6. Average date of first freeze	A	<u>-0.704</u>
7. Number of days without frost	A	<u>-0.764</u>
8. Number of days with snow cover	A	<u>0.565</u>
Precipitation		
9. Total annual precipitation	A	<u>-0.832</u>
10. Warm season precipitation (April - September)	A	<u>-0.711</u>
11. Cool season precipitation (October - March)	A	<u>-0.853</u>
12. Frequency of annual precipitation less than 85% of average	V	<u>0.722</u>
13. Frequency of October precipitation less than 50% of average	V	0.383
14. Frequency of May precipitation less than 50% of average	V	0.278
15. Relative humidity (July)	A	<u>-0.873</u>

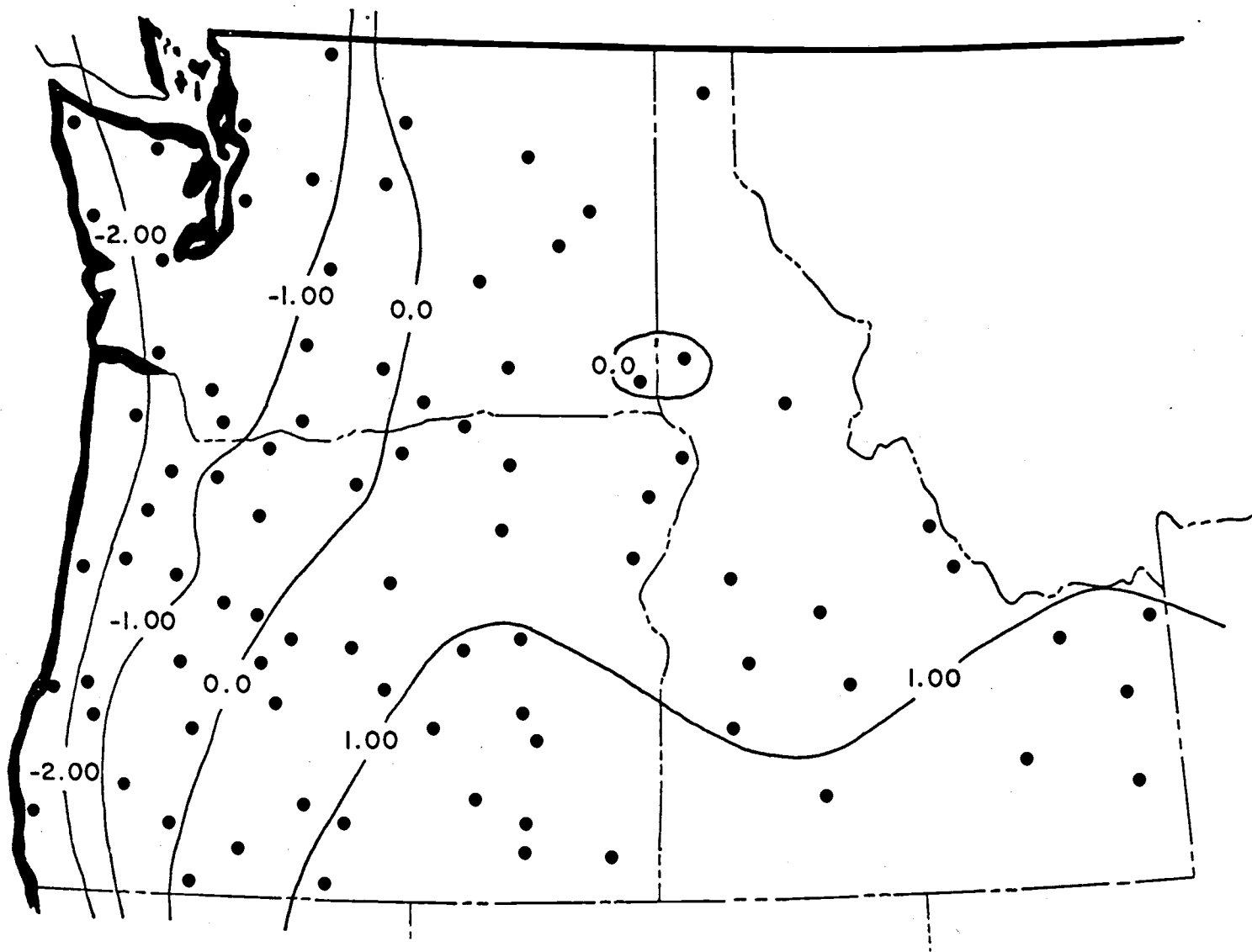
<sup>1</sup> Climatic variables taken from Baldwin (1968), U. S. Dept. Commerce (1959, 1960a, 1960b), Kincer (1922, 1928), and Reed (1918).

<sup>2</sup> A : absolute quantity  
V : temporal variation

Table 2. Relationship between climatic variables and bird survey site factor scores for the first principal component.

Positive Site Factor Scores	Variable	Negative Site Factor Scores
low	1. Daily January minimum	high
high	2. Daily July minimum	low
high	3. Daily January range	low
high	4. Daily July range	low
many	5. Number of days > 32°C (90°F)	few
early	6. Average date of first freeze	late
few	7. Number of days without frost	many
many	8. Number of days without snow cover	few
low	9. Total annual precipitation	high
low	10. Warm season precipitation	high
low	11. Cool season precipitation	high
high	12. Frequency of annual precipitation less than 85% of average	low
high	13. Frequency of October precipitation less than 50% of average	low
high	14. Frequency of May precipitation less than 50% of average	low
low	15. Relative humidity (July)	high

Figure 1. Contour lines showing unit isopleths of site factor scores in their relative geographical locations. Factor scores indicate positions of sites on a climatic gradient ranging from mild-moist-stable (negative values) to severe-dry-unstable (positive values). Dots indicate positions of sample sites.



III. DIETARY RELATIONSHIPS AMONG SHRUBSTEPPE  
PASSERINE BIRDS: COMPETITION OR OPPORTUNISM  
IN A VARIABLE ENVIRONMENT?

Analysis of the dietary relationships withing an assemblage of organisms can provide information on a variety of ecological processes. Insofar as food at times may be a limiting resource, it might be expected that food supply plays a major role in determining the structure of any community it supports. To the extent that food is limiting, it may represent a niche dimension especially prone to competitive adjustments between and within populations. At a higher level, the basic structure of an ecosystem is largely determined by its energy fluxes and nutrient cycles, and these in turn are direct results of the food selection exercised by the organisms within that system and the niche adjustments that influence their diets. Thus a knowledge of trophic relationships and the nature of energy and nutrient transfers between trophic levels is necessary to understand ecosystem processes fully. It is the purpose of this study to examine the trophic patterns within a small community of organisms at two levels: first, I hope to relate observed patterns of resource utilization to the question of competition between populations within the community; and second, I seek to define what roles these organisms may play in the processes within their ecosystem.

The interplay between competition and diet selection (i.e. resource utilization) has been extensively investigated by ecologists, resulting in a vast number of theoretical models, predictions, and subsequent "tests" of those predictions. The major concept about which these models have been constructed has come to be called "optimal foraging theory" (see Pyke et al. 1977, for review), and consists of four sub-categories: optimal diet, patch choice, allocation of time to patches, and the foraging path. Of the four, optimal diet is of the greatest proximate importance to ecosystem processes, and this discussion will be restricted to that aspect.

Most explicit formulations of optimal foraging assume that natural selection is operating to produce an optimal diet, that is, a diet composition that maximizes fitness (Pyke et al. 1977). Although often left unstated, it is clear that competition is seen as the driving force behind that selection. After all, fitness is a relative thing, and if competition were non-existent it seems unlikely that selection would act against individuals that deviated from their theoretically-defined optima (Wiens 1977a).

The optimal diet of an organism is considered in different terms by different investigators. In a theoretical context, it is the diet that maximizes the net rate of energy intake (e.g. Schoener 1971, Pulliam 1974, Charnov 1976), although it has been tested in this specific form by few (e.g.

Menge and Menge 1974, Emlen and Emlen 1975, Charnov 1976). In most field applications, however, the optimal diet is that which helps to minimize the overlap between two or more potentially competing species and consequently allows them to coexist (e.g. Cody 1968, 1974; Zaret and Rand 1971; Lack 1971). Indeed, many comparative studies of two or more coexisting species are undertaken strictly to demonstrate that their diets are different, thus presumably accounting for their continued coexistence (e.g. Marti 1974, Allaire and Fisher 1974, Beaver and Baldwin 1975, Brown and Lieberman 1973).

In the resource partitioning approach to species coexistence, similarity of species' utilization patterns along one niche dimension should imply dissimilarity along another if resource use is to be sufficiently distinct (Schoener 1974). Thus differences are expected, if not in the actual prey taxa taken, then in such things as prey sizes (e.g. Hespenheide 1971, 1975; Mares and Williams 1977) or in foraging microhabitats (e.g. Brown and Lieberman 1973; Cody 1968, 1974). Such expectations have resulted in a substantial body of literature that attempts to relate various aspects of "trophic morphology" (body size or bill size in birds, for example) to the size or type of prey taken (e.g. Pulliam and Enders 1971, Schoener 1968b, Allaire and Fisher 1975). The relationship between the morphologies of a community's members and the structure of that community

has also been addressed (Diamond 1975, Karr and James 1975).

Birds in grassland or steppe ecosystems were originally considered ideal for testing many of the theories about habitat selection, foraging behavior, and population ecology (Cody 1968, Wiens 1969). The structural simplicity of the vegetation, coupled with communities of few species and low diversities (Cody 1966), suggested an environment where ecological and behavioral relationships were much more detectable and amenable to study than other more complex habitats. Indeed, the original thrust of the present study was to examine in some detail the relationships among a species-poor community of birds in the northwestern shrub-steppe to ascertain what mechanisms allowed the birds to coexist.

The pervasive role of competition in determining community structure and ecosystem processes, however, is increasingly coming under question (e.g. Connell 1975, Menge and Sutherland 1976, Wiens 1977a). In particular its role seems reduced as a function of increasing environmental variability (Wiens 1974, 1977a), a view which has been empirically supported (Rotenberry, in press). In this light then, the shrubsteppe becomes an especially interesting system to study as it has clearly been demonstrated to exhibit at a high level the three components of "temporal heterogeneity" (Menge and Sutherland 1976): environmental instability, environmental stress (Rotenberry, in press), and



environmental unpredictability (Wiens 1974).

With this in mind, I seek to do the following:

- (1) Describe in considerable detail the diet of the dominant members of a guild of birds in the arid Pacific Northwest shrubsteppe;
- (2) Examine the dietary similarity within and among all species on both a seasonal and yearly basis;
- (3) Examine relationships between prey size and bird morphology, especially to test predictions from ecomorphological theory;
- (4) Estimate the energy requirements of the avian community and compare this demand with estimates of arthropod abundance, both quantitatively and qualitatively.

The first three points should allow some assessment of the degree to which competition and optimization principles determine the consumption of food by these birds and consequently what role these factors play in determining community structure. The fourth will permit a preliminary evaluation of the relative "importance" of birds in overall ecosystem function.

## STUDY AREA AND AVIFAUNA

The data presented below were collected on the Arid Land Ecology (ALE) Reserve, a 300 km<sup>2</sup> portion of the U. S. Department of Energy's Hanford Reservation. ALE lies on the western edge of the Lower Columbia Basin in southeastern Washington, and ranges in elevation from 140 m to 1100 m. The dominant vegetation throughout the region is the sagebrush/bunchgrass shrubsteppe (Artemisia tridentata/Agropyron spicatum) (Daubenmire 1970), although local variation in the relative cover of the two major species is apparent. This variation reflects past disturbances, primarily due to fire, with increasing coverage of Artemisia indicating the time since disturbance (Daubenmire 1970; W. H. Rickard, pers. comm.).

The present study was confined to a 40 km<sup>2</sup> area (20 km x 2 km) averaging around 370 m in elevation. Average rainfall for ALE at this elevation is 25 cm yr<sup>-1</sup>; average daily maximum and minimum temperatures range from 14°C and -16°C in January to 44°C and 10°C in July (Thorp and Hinds 1977). The short-term (1 month to 1 yr) unpredictability of precipitation here has been demonstrated by Wiens (1974) using patterns of serial autocorrelation of monthly rainfall. Using multivariate techniques, I have shown (Rotenberry, in press) the long-term (10-60 yr) irregularity in overall climatic patterns throughout the northwestern shrubsteppe in

general.

Since 1971, data on vegetation structure and bird densities have been collected on three 9-ha plots within the general study area in each of the three major habitat types typified by the local variation on the general shrub-steppe vegetation theme. Although too detailed to be presented here in their entirety, the data for the percent cover of Artemisia and Agropyron are summarized in Table 1A, while those for the average breeding densities of the three dominant bird species are given in Table 1B. Not shown in Table 1 is how clearly dominant the Horned Lark (Eremophila alpestris), Sage Sparrow (Amphispiza belli), and Western Meadowlark (Sturnella neglecta) really are: from 1971 through 1977 they have never constituted less than 85% of the total breeding population (25 censuses) and rarely less than 95% (23 censuses). Also absent from Table 1 is an indication of how much between-year variation exists for density values of each species. Population estimates for any of the dominant species may either halve or double from one year to the next (Rotenberry and Wiens 1978; Rotenberry, unpubl. data), although most variation is on the order of 10-20%. There are no detectable compensatory changes in the densities of other species.

These three species all belong to the same foraging guild; all feed extensively on the ground in between and at the base of the bunchgrasses and sagebrush, and to a much

lesser extent in the lower branches of sagebrush (Wiens and Rotenberry, unpubl. data). Diurnal activity patterns are also similar, with foraging bouts scattered throughout the day, but accounting for a higher proportion of the time budget during the morning. Although interspecific aggression is occasionally observed, all these species' territories are broadly overlapping on plots where all three occur. Horned Larks and meadowlarks nest on the ground; Sage Sparrows generally nest in sagebrush, but may occasionally construct ground nests.

The great deal of similarity in these species with respect to habitat utilization and activity patterning suggests that if resources are being partitioned, it is most likely to occur along the food dimension. Indeed, given the relatively simple structure of the habitat, coupled with the high interspecific overlap in territories, it seems that food selection is the only niche dimension that demonstrates sufficient variation to observe possible partitioning in the classical sense (Schoener 1974).

The only other passerine regularly found on the study area is the Vesper Sparrow (Pooecetes gramineus), but its low density ( $\sim 20$  individuals / km<sup>-2</sup>) results in only sporadic appearance on any of the 9-ha sample plots. Other birds typically quite abundant in the Great Basin shrubsteppe [e.g. Sage Thrashers (Oreoscoptes montanus) and Brewer's Sparrows (Spizella breweri)] are very uncommon at

ALE. During the non-breeding season Horned Larks are still present in considerable (but reduced) numbers, with meadowlarks and White-crowned Sparrows (Zonotrichia leucophrys) constituting the bulk of the remaining birds. During a short period of spring migration Song Sparrows (Melospiza melodia), Savannah Sparrows (Passerculus sandwichensis), Robins (Turdus migratorius), and Common Flickers (Colaptes auratus) are temporarily and locally abundant.

## METHODS

Diet Analysis

Individuals were collected for dietary analysis by shotgun from throughout the study area. Collections were made of breeding birds during 1971 and 1972, and throughout the year from late 1973 through 1974, when collection activity was most intense. Insofar as possible I attempted to equalize the number of specimens taken during any one sampling period with respect to sex and time of collection (morning or evening). Immediately upon collection, each bird was injected with 0.4 ml of 5% formalin. Within 6 h the specimen was weighed and various morphological features were measured. The proventriculus and gizzard were removed and preserved in formalin for subsequent analysis. Any food items found in the mouth or esophagus were also saved.

Analysis of stomach contents began with the opening of the proventriculus and gizzard whose contents were then washed into a petri dish. Using a dissecting microscope with an ocular micrometer, plant items (all seeds) were sorted, identified (to family, if possible), counted, and measured to the nearest millimeter. Because of substantial fragmentation, however, animal items (arthropods) proved much more difficult to sample accurately. Most identifications were made on the basis of characteristic legs, mandibles, heads, elytra, or occasional entire individuals.

When possible, identification was carried to the family level. Items which could not be readily identified by comparison with voucher specimens were referred to qualified entomologists. The minimum number of individuals per taxon was estimated from the fragment counts (e.g. counting mandibles, which were usually well preserved, and dividing by two).

The length of each individual prey item was estimated by comparing the size of characteristic body fragments (particularly jaws and elytra) with voucher specimens of known body length. The length of each item was then converted to dry weight using the series of taxon-specific length/weight regression equations provided by Rogers et al. (1977) for a wide range of shrubsteppe invertebrates collected on the ALE Reserve. Most of the regression models reported were power equations, and those few that were not could be converted with only a slight ( $\sim 5\%$ ) reduction in their coefficients of determination. Equations for grass and forb seeds were taken from Wiens et al. (1974). Thus the contribution to total dietary biomass for each dietary item could be estimated once its size was known.

Biomass estimates were not corrected for digestion rate differentials (e.g. Custer and Pitelka 1975) because of the absence of correction factors for either the birds or prey items found in the present study. In this case, the data are biased toward prey types that remain recognizable in

the digestive tract longer than others. In the absence of such correction factors it must be assumed that the observed stomach contents are a random sample of the diet actually selected by an individual over some unknown time interval.

Although each prey item was identified as far as possible, it became clear that not all could be taken to the same level. Final prey categories were based on all taxa, regardless of rank, that occurred in at least 5% of all stomachs examined. Taxa that did not meet this criterion were lumped under the next higher taxonomic level that did. The resulting 23 categories are in Tables 2-5. In addition, each prey category was classified into one of the broad functional groups phytophagous, predaceous, or "other" (i.e. omnivorous, scavenging) to help assess the role of birds in ecosystem processes a little more realistically (see Appendix for classifications).

### Morphological Measurements

Although measurements of a variety of external morphological features were taken from all specimens collected (Wiens and Rotenberry, MS), only the five generally linked with foraging ecology and diet selection will be considered here. Body weight (e.g. Schoener 1968a, 1968b) was recorded in the field to the nearest 0.1 g immediately following collection. Three bill measurements (e.g. Hespenheide 1971; Cody 1968, 1974; Allaire and Fisher 1975) were taken to the



nearest 0.1 mm as follows: length, from the anterior border of the nares to the tip of the culmen; height, culmen height at the anterior edge of the nares; width, culmen width at the anterior edge of the nares. Tarsus length (e.g. Cody 1968, 1974; Grant 1971) was recorded as the length of the tarsometatarsus to the nearest 0.1 mm. As absolute lengths of prey items were used in this study, absolute sizes of morphological features were used rather than being scaled as ratios of body weight (e.g. Karr and James 1975). Variability in morphological measures was indexed by the coefficient of variation (Grant 1967). As the collection process inevitably damaged a few birds, only those specimens that were complete for all measurements were included in the morphological analyses.

### Statistical Techniques

Most relationships between sets of variables were examined using either product-moment correlation coefficients or Spearman rank correlation coefficients (Fritz 1973). Levels of significance were taken from Rohlf and Sokal (1969); a level of  $P < 0.05$  is hereafter denoted as "significant" or "\*", and a level of  $P < 0.01$  is denoted as "highly significant" or "\*\*". Often these comparisons led to large matrices of coefficients and subsequent problems in interpretation. Out of, say, 100 correlations, five are expected to indicate a significant relationship by chance

alone. Rather than examine each correlation in such a matrix on a case-by-case basis, it seems much more reasonable to look for patterns of significance. Patterns were detected by comparing confidence limits of observed percentages of significant correlations versus those expected by chance (Rohlf and Sokal 1969: 208).

Because of the heterogeneity inherent in data such as these, the  $t'$ -test (which makes no assumptions concerning homogeneity of variances nor requires equal sample sizes) was used for all tests of equivalence of means (Sokal and Rohlf 1969: 374). Prey size distributions were normalized, however, by transforming prey lengths to  $\log_2$  values.

Dietary diversity [the "niche breadth" of Levins (1968), Pianka (1969), and others] was calculated according to Simpson (1949), then converted to the equivalent number of equally common prey taxa by applying a reciprocal transformation. Thus

$$\text{dietary diversity} = 1 / \sum \underline{p}_i^2$$

where  $\underline{p}_i$  is the relative biomass of the  $i^{\text{th}}$  taxon in the sample. This measure has several advantages: (1) it can be derived from sampling theory, and before transformation expresses the probability that two randomly selected items from the same sample belong to the same taxon; (2) after transformation its units become "number of taxa," although still retaining the evenness component of taxa abundance

patterns (Hill 1973, Peet 1974); and (3) sample values quickly converge to the parametric value they estimate, even with small sample sizes (Stander 1970).

Dietary similarity between any two collections was calculated using Stander's community correlation index (Stander 1970, Pianka 1973)

$$\text{SIMI} = \frac{\sum \underline{x}_i \underline{y}_i}{\sqrt{\sum \underline{x}_i^2 \sum \underline{y}_i^2}}$$

where  $\underline{x}_i$  is the relative biomass of taxon  $i$  in one sample and  $\underline{y}_i$  is its relative biomass in a second sample. It has obvious similarities with the diversity index above and is analogous in structure to the product-moment correlation coefficient (Stander 1970). It represents the probability that two individuals, each drawn from a separate population, will be of the same taxon, scaled as the square root of the probabilities of drawing each taxon separately (see also May 1975 for an alternative interpretation of SIMI as the competition coefficient  $\alpha$ ).

The information content of similarity or correlation matrices expressing the relationships among diets or between diets and morphology was extracted using a variety of multivariate techniques. Relationships among the diets of all collections of birds were initially defined by weighted pair-group cluster analysis (Sokal and Sneath 1963),

which produced agglomerative hierarchical groups of closely-related samples. The resulting groups were then subjected to stepwise discriminant analysis (Dixon 1976), which served to evaluate the effectiveness of the cluster analysis in producing distinct groups and to define the diet variables (prey taxa) most responsible for producing the groups. Patterns of covariance between diet and morphology were extracted by means of canonical correlation (Cooley and Lohnes 1971).

#### Bioenergetics/Arthropod Abundance

Knowledge of the role of avian consumers in ecosystem processes would be incomplete without some estimation of energy fluxes through their populations. Further, this information must be coupled with estimates of energy fluxes or standing crops of the other trophic levels with which birds may interact. While standing crops may be sampled with relative ease, measurements of energy demands in free-living organisms are more often than not extremely difficult to obtain. The alternative approach, followed here, is to estimate bird energy requirements using a computer simulation model, such as that provided by Wiens and Innis (1974). In this study a recent updating of their model was employed.

Basically, the model couples population density changes for each age class of a species with ambient temperature

regimes and various metabolic functions (Kendeigh et al. 1977) to generate age-class specific bioenergetic demands through time. By knowing the proportion of each prey class in the diet and the caloric value ( $\text{kcal g}^{-1}$ ) of each class, the model estimates consumption rates ( $\text{g m}^{-2} \text{ day}^{-1}$ ) of each prey taxon. Full details of the structure, assumptions, and operation of the model are given in Wiens and Innis (1973, 1974; see also Wiens and Dyer 1977).

The basic life history attributes of each species required to calculate population density fluxes in the model (e.g. onset of immigration, clutch size, length of incubation period) were either determined from direct field observations (1971-1977) or gleaned from Bent (1942, 1958, 1968). Breeding densities used were those given in Table 1B, scaled to the relative proportion of each of the three major habitat types in the study area as a whole. The simulation was performed on the temperature regime of 1974, the year in which most of my specimens were taken.

Lee Rogers of Batelle-Northwest kindly made available to me drop-trap estimates (Huddleston et al. 1969) of arthropod abundances made during 1974 on the ALE Reserve within my study area. The data consisted of the biomass of each arthropod order taken per  $\text{m}^2$  of each vegetation type sampled (bunchgrass, sagebrush, etc.) on five census dates from late February through early September. These were converted to absolute abundances by multiplying each sample

biomass by the percent cover of the vegetation type from which it came. Coverage values were seasonally adjusted for variations due to plant growth (Rotenberry, unpubl. data) and scaled to their relative abundances in the three major habitat types (Table 1A). The values for each order were then summed over all vegetation types to yield the average abundance or standing crop of arthropod taxa ( $\text{g m}^{-2}$ ) throughout the study area. No estimates of turnover rates of these standing crops are available.

## RESULTS AND DISCUSSION

General Diet Description

During this study 22 dietary collections (a collection being 2-23 individuals of a species taken over a short period of time) were made, consisting of 284 sampled individuals of 5 species. Horned Larks constituted the bulk of the samples, with 11 collections of 179 birds taken throughout the seasons of the year (Table 2). Sage Sparrows (68 individuals, 5 collections; Table 3) and meadowlarks (23 individuals, 4 collections; Table 4) were collected only during the breeding season. Vesper Sparrows (5 individuals, 1 collection) were taken only during the 1974 breeding season (Table 5); they had not been locally abundant in prior years of this study. White-crowned Sparrows (9 individuals, 1 collection) were taken during the winter (Table 5). Collections were made on about the same date one year apart twice with Horned Larks and once with meadowlarks and Sage Sparrows.

Several overall patterns are apparent from the data. All four breeding species were highly insectivorous throughout the breeding season (February through August), including even the Sage and Vesper sparrows, possessors of deep, conical bills presumably adapted for the efficient handling of seeds. Except for the August Horned Lark sample, all collections during the breeding season contained at least

70% arthropods (Fig. 1). During the non-breeding season, however, there was a substantial shift to seed consumption. In the fall seeds constituted 60-70% of Horned Lark diets, while later on in the winter their proportion rose to 80-100%. However, even in November and December a few birds managed to find arthropods.

The most common insect prey early in the breeding season were coleopterans, particularly weevils (Curculionidae) and beetle larvae (Tables 1-5). Ants (Formicidae), wasps, caterpillars, small spiders and hemipterans, and grasshopper nymphs were consistently found in these samples but even combined generally contributed less than the beetles. An abrupt shift, however, took place during the latter half of the season (June - August); grasshoppers became much more abundant in the diets, particularly for Sage and Vesper sparrows and meadowlarks (Tables 4-5). In the latter two species orthopterans often accounted for over half of their diet at this time.

Seasonal variation was most apparent in Horned Lark diets (Fig. 2). The shift from seeds to arthropods and back to seeds as the seasons progressed is most likely a response to temporal variation in their availability. On a finer scale, however, there were also dietary shifts within each of the main categories. For example, grass seeds increased in abundance in the diet between February and March, and were maintained at a fairly high level through



October (Fig. 2B), when forbs became increasingly important. In the middle of winter (January), forb seeds constituted almost all of Horned Lark diets. While several explanations for this pattern are plausible, I suspect that it reflects the changing availability of the two seed resources. The dominant gramoids on the ALE Reserve shrubsteppe, Agropyron spicatum and Poa sandbergii, are cold season grasses whose seeds begin germinating in the fall (W. H. Rickard, pers. comm.) and hence become increasingly unavailable to birds as winter progresses. On the other hand, most of the forbs, especially the chenopod Salsola kali, which forms the greater proportion of the forb seed diet of Horned Larks, do not begin germinating until early spring. It is early in the spring, too, that Poa begins to set seed, again making grass available to the birds. The seasonal patterns of arthropod contributions to Horned Lark diets (Fig. 2C) are also likely reflections of their abundance in the environment. The major beetle prey, weevils, are common from spring through early summer, while grasshoppers, which dominated the "other" portion of the diet, become abundant during the warmer parts of the summer and persist into early fall.

Although the samples taken here do not permit resolution of seasonal variation in the other dominant species, some general observations are possible. Sage Sparrows, abundant only in the breeding season, showed approximately

the same patterns as Horned Larks (Table 3, Fig. 1B) for the same period of time: highly insectivorous throughout, with a switch from beetle-dominated to grasshopper-dominated diets occurring in June. Consumption of seed was greatest in June, shortly after Agropyron has set seed, although their relative contribution declined thereafter. Western Meadowlarks proved to be the most insectivorous of the species sampled, with seeds never contributing more than 5% to the total consumption (Table 4, Fig. 1C). Although curculionids and grasshoppers comprised a substantial portion of their diets, other beetles, particularly Tenebrionidae, were relatively more important than in the smaller birds. A large irruption of periodical cicadas (Okanogana utahensis) in June 1974 made up about 30% of the birds' diets during that period.

The high reliance on arthropods by all these species suggests it might be fruitful to examine their contribution in more detail. The proportions of phytophagous, predaceous, and "other" arthropods (see Appendix) in the birds' diets are given in Fig. 3. The general clustering of points in the lower righthand corner of each trimat clearly indicates the dependence on phytophagous forms by all bird species. The three Horned Lark samples with less than 50% relative abundances of phytophagous arthropods (winter collections 5, 6, and 12) also contained very low absolute abundances of arthropods in general.

The distinct seasonal patterns in Horned Lark prey consumption are paralleled by seasonal variation in the length of those prey items. Comparisons of average Horned Lark prey lengths (Table 6A) with the diet patterns in Fig. 2A suggests that prey size varied as a function of the relative proportion of plant and animal items and, indeed, the correlation between percent of diet attributable to arthropods and average prey length ( $\log_2$ ) is highly significant ( $r = 0.93$ , \*\*, 9 df). This observation is not unexpected as, on the average, seeds are smaller than insects. Prey sizes of Sage Sparrows (Table 6B) were generally commensurate with those of Horned Larks for the same periods, although they are higher than larks in August, a reflection of the reduced contribution of seeds to the sparrow diets. The average length of meadowlark prey items increased substantially between May and June (Table 6C), no doubt as a function of the relatively greater size of cicadas and grasshoppers over the beetles that comprised the bulk of early season diets.

Analysis of diets may also elucidate some components of species' niche variation, both within and between phenotypes. This variation is generally expressed as trophic diversity (Hurtubia 1973) or "niche breadth" (sensu Levins 1968). Unlike prey selection and sizes, however, easily-discernable seasonal patterns are not detectable. In Horned Larks, for

example, although dietary diversity peaked during the warmer parts of the year (Table 7A), probably reflecting the greater diversity of available arthropods, several samples from the colder times (e.g. February 1974 and November 1972) were nearly as high. The converse is true, too; there were low values in both summer and winter.

An interesting comparison can be made between the dietary niche breadth of an individual Horned Lark with that of the sampled population as a whole (Table 7A). Such a comparison allows assessment of the between-phenotype component of niche breadth (Roughgarden 1972), as each individual generally uses a smaller range of resources than the overall population. For example, in May 1972, 17 prey taxa were discovered in the diets of all Horned Larks combined, but each individual, on the average, had only four taxa (24% of total). The average for all Horned Lark samples was 30%, suggesting in general terms of niche theory (Roughgarden 1972) that between-phenotype variation accounts for about a third of the total variation in this dimension (i.e., individual Horned Larks have a dietary niche breadth roughly one-third that of the species as a whole). This picture changes, however, when one samples niche breadth based on dietary diversity, which includes information not only on the number of taxa but also on the relative abundances of those taxa. For the same May 1972 sample the dietary diversity of both the total population and the individuals

in it are identical. On the average, individual diversities were 70% that of the population, a more than two-fold increase when compared to the number of taxa alone. (Both percentages are uncorrelated with sample size.)

Dietary diversity patterns in Sage Sparrows closely paralleled those of larks, particularly with respect to individual/population comparisons: an individual contained about a third of the total taxa but over two-thirds the total diversity of the population. Sage Sparrows, too, showed a fair amount of temporal variation in all the niche breadth measures calculated.

About half the prey taxa present in the meadowlark sample as a whole were likely to be found in any one individual's stomach, and individual dietary diversity was nearly 80% that of the population. These diversities both showed a substantial drop coincident with the shift to orthoptera/homoptera domination of the diet.

Variation in dietary diversity of a species may also be examined within the framework of optimal foraging theory, but again the absence of any clear-cut patterns confounds interpretation. With respect to the diversity drop in meadowlarks just mentioned, one might enquire: Has dietary diversity decreased as a result of increasing food availability, particularly in the larger packets offered by big grasshoppers and cicadas (e.g. Emlen 1966, Schoener 1971), or

are the birds encountering and opportunistically eating from a prey taxa pool of reduced diversity? One might also expect dietary diversity to increase during the winter as overall food abundance decreases -- the birds must take what they can get rather than pick and choose among acceptable items. Examination of the Horned Lark data (Table 7A) supports no such expectation.

Although it is impossible to assess variation in the diets of those species which were collected only once, a brief description may be made of each. The diet of Vesper Sparrows (Table 5, Fig. 1C) seemed little different from the other contemporaneous collections -- mostly arthropods, most of which are phytophagous (Fig. 3C). Although grasshoppers constituted over half the biomass, the numerical domination by grass seeds (88% vs. 4% of the prey items) reduced the length of prey in the average individual substantially. The dietary diversity of both the total sample and its individuals were very close, although any individual only contained about half the total prey taxa.

The collection of White-crowned Sparrows revealed a preponderance of seed in the diet (Table 5, Fig. 1C), which was much like that of the Horned Larks taken during the same winter period. Further, these seeds were mostly chenopods (Salsola), probably for the same reasons as suggested for the larks. The few arthropods found were divided between weevils and predaceous ground beetles (Carabidae). The

abundance of seed was also reflected in the rather low average prey size (Table 6).

In summary, this general description of diets has produced several salient features that bear close attention. First, there appears to be a great deal of similarity between the diets of species taken during the same period of time; warm season samples reflected high insectivory, cool season high granivory. Do these similarities persist when examined at a finer level? Second, there appear to be substantial overlaps in prey sizes taken by the different species at certain times of the year. How is prey size selection coupled with morphological variation? Third, patterns of dietary diversity, as well as those points just mentioned, do not appear consistent with predictions from optimal foraging theory. What do they imply with respect to the role of competition in diet selection? These and other points will be examined in greater detail shortly.

### Similarity Analysis

Within species. Before the question of what sorts of differences or similarities exist between species can be addressed, the patterns within each species must be identified. An initial attempt at defining these intraspecific patterns is given in Table 8. The average similarity between all individuals of a collection indexes the homo- or heterogeneity within the sample much like a variance measure,

and provides a point of reference for subsequent comparisons. It also reflects within-phenotype variability (Roughgarden 1972) of the sampled population in that it compares an individual's resource utilization to that of the sampled population as a whole.

Several of the within-sample comparisons are of interest. It has been suggested that in some cases the diets of males and females should be different (Selander 1966), especially in sexually dimorphic species. Differences are expected to arise from selection to reduce intraspecific competition and increase population niche breadth. In highly insectivorous species such as these, one might also expect dietary differences in specimens collected in the morning and evening, reflecting dissimilar activity patterns among different prey taxa. Also, hunger level may be different between the two periods, birds probably being more hungry in the morning after a long period in which foraging is not possible. Insofar as the level of satiation influences the type and diversity of prey items selected (e.g. Holling 1959, 1965; Emlen 1966), there should be daily temporal differences in the observed diets. And finally we can examine to what extent the diets of morphologically and behaviorally different juveniles differ from those of adults.

Horned Larks showed a substantial and highly significant range in sample heterogeneity that apparently varied as a function of total sample dietary diversity (Table 7;



$r = -0.84$ , \*\*, 9 df). In other words, the more diverse the diet as a whole, the less likely are any two individuals to be highly similar. This trend was the same for all species ( $r = -0.86$ , \*\*, 18 df). In all cases, Horned Lark females differed little from males, even when the sample as a whole demonstrated substantial variability; similarity between all males and all females was always greater than among all individuals. Morning/evening comparisons (Table 7) paralleled this trend and, except for two cases, were even higher than male/female similarities. In one case (May 1971), a shift occurred from a morning diet of grass seeds and weevils to an evening one with substantial numbers of coleopteran larvae. In the other case (November 1973), however, the shift was merely between seed types: grasses in the morning and chenopods in the evening. For what few data there are it seemed that, in general, the diet of juveniles was very similar in composition to that of adults.

The patterns observed in Horned Larks were recapitulated in each of the other species for which there were sufficient individuals (two or more in each category) to estimate similarity. Basically, variation among individuals of a species seems unassociated with distinctive groups within the species, and increasing individual variation is associated in turn with increasing overall population dietary niche breadth.

These inter-group similarities extended to prey size

selection as well. Examining the 26 combinations presented in Table 8 where dimorphism might play a role showed that in only one set (adult/juvenile Sage Sparrows taken in August 1974) was there a significant difference in average prey length per individual bird. In view of the dimorphism to be demonstrated later, this suggests that the size of a prey item may be less important than its taxa in its selection by the birds.

There also appeared to be few differences in the average individual trophic diversities between groups within collections (Table 8; 5 out of 38 tested), and no clear pattern is evident from those differences that were significant (Horned Lark males/females in November 1972 and 1973; Sage Sparrow morning/evening in May 1971 and 1972; Sage Sparrow adults/juveniles in June 1974). In all, males were no more likely to have greater diet diversity than females, mornings greater than evenings, or adults greater than juveniles, as one would otherwise predict from consideration of size difference (Emlen 1973) or presumed levels of satiation (Emlen 1966). These observations seem sufficient justification for lumping these groups within each collection for all analyses.

Between species. It is clear from the information presented in Figs. 1 and 3 that there is substantial similarity between the diets of populations of different species col-

lected at the same time, in some cases even more than among samples of the same species collected at slightly different times. These relationships are summarized in Fig. 4. Except for the high degree of granivory shown by Horned Larks in August 1974, the clustering of bird diets based on broad prey categories according to time rather than species is evident (Fig. 4A). Lest it seem that these categories are too broad and obscure substantial variation at a finer level, Fig. 4B, which is based upon major functional groups of arthropod prey, is offered. Except for the November 1973 White-crowned Sparrow and Horned Lark collections that contained few arthropods, all of the samples appear closely grouped. Finally, breaking down the phytophagous arthropods into their three dominant taxa (which contributed 92% of the biomass of the phytophagous forms and 40% of the biomass of all diet items sampled) shows that even near the limits of resolution of this study contemporaneous samples demonstrate an extremely high degree of similarity regardless of species (Fig. 4C).

Although much too large to be shown here, the Spearman rank correlation matrix of the diets for all collections contains a pattern which statistically reinforces the observed similarity among contemporaneous samples. Of all 231 coefficients calculated, 17 are between collections of different species made at the same time; 10 of these 17 (59%) are significantly different from zero, and none are signifi-

cantly negative. To place this in perspective, only 10 of the remaining 214 coefficients (5%) achieve positive significance, about that expected from random samples. Patterns of significance in negative correlations will be discussed below.

The most interesting relationships are revealed by cluster analysis of all dietary collections. The results, based on the relative biomass of each prey taxon, are graphically presented in Fig. 5. With a few exceptions, one pattern is overwhelming: the major clusters are formed not on the basis of species but on the basis of time of collection. Since the level at which clusters can be defined is arbitrary, it is worthwhile to examine in some detail the nature of the paths and bifurcations represented by the dendrogram.

An overview of the dendrogram suggests that there are three major clusters (defined at a similarity level of 0.34), two of which may be readily divided into two minor groups. It is clear from examining the members of each major cluster that they represent samples taken in the spring, summer, and non-breeding seasons. The "spring" group consists of all birds taken in February, April, and May, and no others. The "non-breeding season" group is made up of all birds taken from October through January, but also includes the August sample of Horned Larks, while the "summer" group con-

tains all the June and August birds except the August larks. The non-breeding season birds' diets differ from the other two groups primarily because of their high content of plant material (Fig. 1A,B; 4A), while spring and summer groups differ on the basis of coleopterans (abundant in spring) and orthopterans (abundant in summer).

The non-breeding season cluster breaks down into two subgroups rather quickly (0.40 similarity) which appear distinguishable largely on the basis of the relative abundance of grass seeds vs. forb seeds. The large quantity of grass in the August Horned Larks accounts for their inclusion here. In the spring cluster the May 1971 meadowlarks are set apart from the other collections at a similarity level of 0.51. This sample contained carabids and tenebrionids in much greater proportion than in the others, hence the separation of the spring cluster into two subgroups.

The time-oriented basis that underlies the overall pattern of the dendrogram is nowhere more evident than within the large subgroup on the spring cluster. Since the clustering algorithm used is agglomerative (Sokal and Sneath 1963), it is reasonable to consider this cluster in that manner. The first group formed (SIMI = 0.99) consists of the two May 1972 samples of Horned Larks and Sage Sparrows. This is joined by May 1971 Horned Larks (SIMI = 0.95) and May 1971 Sage Sparrows (SIMI = 0.94) to form a

distinct "May" group of small birds, irrespective of year of collection. At a level of .92 the April 1971 collections combine, although they then do not join the May sample for some time.

The May cluster is augmented first by May 1972 meadowlarks ( $SIMI = 0.76$ ), thus including all May samples but one, then by February 1974 Horned Larks. Interestingly, the February sample is more similar to those of May rather than the temporally adjacent April ones, which shortly combine ( $SIMI = 0.67$ ) to complete the large spring subgroup. The major cluster is completed with the addition of the May 1971 meadowlarks which, although fairly distinct from the rest of the members of the cluster, are nonetheless more closely related to them than any of the others.

This pattern of collections being sorted by time rather than bird species persists throughout the other major groups, too, but is not quite as neat as in the spring group. The overall theme is apparent in any event; although time of collection was not the criterion on which clustering was based, the result would have been little altered. Birds of different species taken at the same time are eating the same things; birds of the same species taken at different times are eating different things.

Although it is difficult to statistically verify the relationships resulting from the cluster analysis, examina-

tion of the entire matrix of Spearman rank correlation coefficients for all diet collections reveals some patterns that appear to be definitely non-random. For example, of 72 possible within-cluster comparisons (i.e. collections compared only with other members of their major group), 17 (24%) are positively significantly different from zero; 14% are highly significantly different. Both of these percentages are much greater (\*\*) than that expected by chance alone. By contrast, only 3% of the remaining 159 comparisons appear positively correlated, not unexpected as a matter of chance. The picture changes, however, for negative correlations. While 19% and 13% of all correlations are significant and highly significant in a negative direction for between-cluster comparisons (much greater than chance expectation; \*\*), only one of 72 is negative within clusters. Thus, to summarize, the diets of collections within the major groups are, on the average, significantly correlated with one another, but not with those from other groups. Conversely, diets between groups tend to be significantly negatively correlated, but not those within groups.

Nonetheless, all the patterns detected above are based upon cluster analysis, and one of the recognized drawbacks of cluster analysis, particularly hierarchical types such as that used here, is that they make clusters out of data regardless of whether such clusters really exist or not

(Williams 1971, Pielou 1977). Therefore it is important that the results be checked to insure that some distinctness is manifested by the resulting groups. The approach used here is to examine the groups formed by the clustering with stepwise discriminant analysis (del Moral 1975). The technique indicates (1) the relative importance of each diet taxon in discrimination among groups, (2) the probability, based on group means, that a sample belongs in either its designated group or some alternate group, (3) canonical correlation coefficients, and (4) an arrangement of samples along canonical axes that are based upon the most effective combination of variables for distinguishing among samples. This last step essentially results in an ordination of a classification (del Moral 1975).

As the five groups produced at the 0.55 similarity level (Fig. 5) seemed intuitively reasonable, the discriminant analysis was performed on them. The results yielded excellent separation of the groups, with no collection having a posterior probability of less than 1.00 of being classified into the correct group based upon the discriminant function. The canonical correlations (the maximum correlation between a linear function of the prey data and group membership for each sample) was 0.9998 for the first canonical axis and 0.9987 for the second. The first axis accounted for 86.4% of the total variability in the original classified data set, while the first two combine to explain



98.8% of that variance.

In order of importance in discriminating between groups of samples in a step-wise manner were chenopod seeds, orthoptera, grass seeds, scarabs, crucifer seeds, and lepidoptera larvae. It should be pointed out, however, that because discrimination proceeds in a step-wise manner, one of two variables that are highly correlated will not be valuable for discrimination (hence it will not enter into discriminant function construction until much later) if the other variable is included first. This problem is alleviated to some extent by correlating the relative abundance of each prey taxa for each sample with that sample's position along the first canonical axis. These correlations show that, in addition to those taxa mentioned above, curculionid abundance is also significantly associated with this axis, reinforcing the qualitative observations from the cluster analysis that they are important in distinguishing among the five groups.

The overall similarity analysis, buttressed by the clustering and discriminant functions, generally indicates that most individuals, regardless of species, are eating the same few things at any point in time. That is, there is no apparent niche separation on the basis of food types. The question that arises now is: are these common prey items the same size (i.e. do the different sized birds eat different sized items)?

Morphology/Diet Relationships

The presumed relationships between diet and morphology have been discussed extensively (for review see Hespenheide 1975, Wiens and Rotenberry MS) and several of those are testable with the data collected for this study. These relationships generally fall into a natural dichotomy: those dealing with patterns in mean values of morphology or diet and those dealing with patterns in variation. Both presume that the traits of organisms are molded in their details by natural selection, and that competition between species provides the impetus for that selection, at least for patterns within communities of ecologically similar species. The parallel to optimal foraging theory discussed in the introduction should be obvious.

One of the most persistent themes in ecomorphological investigation is the relationship between the size of the trophic apparatus (e.g. bill size in birds) and size of the prey eaten (Schoener 1968b, Grant 1968, Hespenheide 1973). If bill size and prey size are closely attuned, as suggested, this correlation should be apparent both within and between populations. For each collection (except May 1971 meadow-larks, which had two specimens) I calculated the correlation between each morphological variable measured (weight, tarsus length, and bill length, height, and width) and average length of seeds, arthropods, and all items combined found

in the stomach of each individual bird. Of the 315 resultant correlations (21 collections X 5 characters X 3 prey lengths), only 15 (4.8%) were significantly different from zero, about the number expected by chance; 1.9% were highly significant. To guard against the possibility that one or more of the traits measured might be inappropriate and, hence, reduce the proportion of significant correlations spuriously, each trait was tested separately. For no trait was there any suggestion of non-randomness, and the few correlations that were significant were well-divided among all five traits.

A statistically significant pattern does emerge for bill length, however, when the data for all individuals of a species are combined. In both Horned Larks and Sage Sparrows larger individuals tended to eat larger overall prey items than smaller individuals ( $r = 0.52^{**}$  and  $0.47^{**}$  respectively, 141 and 37 df). But, curiously, there is no correlation between prey size and bill length in the highly dimorphic (see below) meadowlark ( $r = -0.32$ , N. S., 18 df).

The distribution of the prey sizes selected by each species are given in Fig. 6, which shows the relative proportion of each size class in the diet for all prey taxa combined. The fact that the range of each class doubles the one before it is equivalent to a  $\log_2$  transformation applied to the raw data. In only two cases does one species

deviate markedly from the others: meadowlarks in June and August 1974 took relatively more large items than the other species, which were very similar among themselves. This observation might best be rephrased, however, to suggest that instead of taking more larger items, meadowlarks were taking fewer small items (i.e. seeds) than the others. Again it is apparent that increasing average prey length is associated with decreasing proportion of the diet devoted to seeds (Table 6 and Fig. 2). In June 1974, for example, in the smaller bird species seeds constituted from 77.6% to 88.9% by numbers (which are used in generating prey distributions and average lengths) but only 30.0% and 32.6% by weight. If prey sizes for June 1974 are replotted to include only the arthropod items (Fig. 7), the distributions more nearly overlap. However, meadowlarks do in fact take statistically larger animal items than the others in both this sample and in the August one.

Since only adult specimens were included in this analysis much of the size variation present is a function of sexual dimorphism. The degree of dimorphism for all species is indexed by the Intraspecific Character Ratio (ICR -- Rothstein 1973), which is the ratio of male to female values for a given character (Fig. 8). For every trait the meadowlark is more dimorphic than any of the other species, thus rendering the lack of any prey/bill size correlation sur-

prising. According to current theory, dimorphism may facilitate prey size differentiation which in turn leads to diet differentiation and reduced intraspecific competition (Selander 1966). It has been demonstrated elsewhere (Wiens and Rotenberry MS) that meadowlarks are more dimorphic in body size characters (e.g. weight, wing length, tail length) than trophic (= bill) characters. This suggests that sexual selection may play a more important role in driving polymorphism in this species than trophic niche divergence. The lack of trophic niche divergence is reinforced by the results of the intraspecific similarity analyses (Table 8).

The canonical correlation analysis allows, among other things, an estimate of the amount of variation in one data set which is "explained" by another. This measure is called "redundancy" and is simply a scaling of the canonical coefficient of determination by the relative contribution of each of the canonical factors (Cooley and Lohnes 1971). This analysis was performed for the three major species in an attempt to associate the variation in prey sizes with variation in morphology. The amount of redundancy is low for each species: 24% in Horned Larks, 28% in Sage Sparrows, and 38% in meadowlarks. This means that in general about 30% of the variation in prey sizes selected could be accounted for by variation in metric trophic structures.

Most general theories of ecomorphology, however, were meant to be applied to all members of a community at once

rather than to each species separately. When analyzed in this fashion, the data do evidence some significant prey size/character size patterns. Table 9 clearly shows that there is a very strong association between all the feeding-related structures and average arthropod and total prey lengths. Seed size, however, is either uncorrelated or negatively correlated with all structural measurements, even the bill dimensions for which there is a supposed close relationship (e.g. Hespenheide 1966, Pulliam and Enders 1971).

Examination of the canonical factor structure generated when all species are lumped together shows there to be a strong "body size" component (cf. Johnston and Selander 1972, Niles 1973) that accounts for about 80% of the total variation in the morphological data set. This is not surprising, as the set includes 110-g meadowlarks and 20-g Sage Sparrows. Variation within the prey size data set, however, is not as concentrated, being distributed among the three canonical factors (42%, 32%, and 21%). Each diet factor generally shows a high correlation with only one of the prey categories, the first being associated with average total prey length. Despite the within-data set patterns, the redundancy is still only 29.8%, about the same as that for each species separately.

Theoretical elaboration of the prey size/body size theme suggests that variability in trophic dimensions is

associated with variation in the sizes of prey consumed (Schoener 1968b, Grant 1967). These data should show, then, a correlation between the coefficient of variation in, say, bill length, and the coefficient of variation in total prey length. Neither the 11 Horned Lark, 5 Sage Sparrow, nor 4 meadowlark collections demonstrate this correlation, though, nor was it discernable when all 22 collections were combined ( $r = 0.13$ , N. S., 20 df). If prey size diversity (calculated on the basis of the relative abundances of prey items in each of the octaves plotted in Fig. 5 and 6) is substituted for variation in total prey length, the outcome is the same as before, both within and among collections (among  $r = 0.02$ , N. S., 20 df). Species populations with greater variability in bill sizes did not eat more variable-sized prey.

Since these birds span almost a five-fold difference in weight and over a three-fold difference in bill length, they should be suitable for testing the hypothesis that smaller animals should exhibit greater dietary specialization than large animals (Gwynne and Bell 1968, Emlen 1973). Pooling all collections shows no correlation between body weight and either the number of taxa in the diet ( $r = 0.27$ , N. S., 20 df) or dietary diversity ( $r = 0.12$ , N. S., 20 df). Likewise, tests of association between bill length and number of taxa ( $r = 0.33$ , N. S., 20 df) or bill length and diet diversity ( $r = 0.19$ , N. S., 20 df) imply no significance. Small

birds appear no more specialized than large birds.

If the data in Table 7 are rearranged so that comparisons may be made between the individuals of each species taken during the same period one finds that in virtually all cases neither the number of taxa taken nor the dietary diversity can be statistically distinguished between pairs of species. The few exceptions are somewhat contradictory: in May 1972 an "average" meadowlark contained significantly more taxa than either an "average" Horned Lark or Sage Sparrow (which were the same), while in June 1974, Sage Sparrows had a greater dietary diversity than meadowlarks. In the latter sample, there were otherwise no differences among the four species studied.

The final morphology/diet comparison is suggested by Grant (1967) and Hespenheide (1973), who propose that diets should be more variable in populations with more variable bill morphology. Comparisons of bill length coefficients of variation with both the number of prey taxa and the overall trophic diversity for each collection reveals, in both cases, no significant correlation ( $r = 0.06$  and  $-0.10$ , both N. S., 20 df). Dietary "generalists" are no more variable than dietary "specialists."

General ecomorphological studies in birds (Diamond 1975, Pulliam 1975), mammals (Brown 1975), and reptiles (Schoener 1970) have also suggested that selection (competition) has produced regular distributions of body sizes or other



trophically-related structures among sympatric members of the same foraging guild of the type considered here. For birds, minimum ratios of adjacent guild members are suggested to approximate 1.3 (Hutchinson 1959, MacArthur 1972) or 1.5 (Diamond 1975); Pulliam observed "an amazingly constant average ratio" of 1.10 for bill sizes. The calculations in Fig. 9 show neither consistency nor conformance to expectations. In both body and bill sizes there is a large hiatus between Horned Larks and meadowlarks, a pattern consistently found in other sets of shrubsteppe and grassland species (Wiens and Rotenberry MS). With respect to body size, the ratios are either larger or smaller than expected depending upon (1) inclusion or exclusion of the intermittently abundant Vesper Sparrow, or (2) the theoretical ratio applied. In bill size comparisons the order of species ranking is different from those for weight.

Many past authors have found it convenient to estimate resource differences using morphological characters that presumably indicated the position of a species' utilization on a resource dimension (Schoener 1974). The commonest indicator in birds has been the size of the feeding structures, generally bill (e.g. Hespenheide 1971, 1975) or tarsus length (Cody 1968). This implies a strong functional relationship between utilization and phenotype, relations which presumably constrain resource partitioning. It now seems clear from this and the preceeding section that this

assumption can be largely invalid, depending on the system for which it is invoked. Such relationships emerge only at the grossest level of analysis -- indeed, they are absent among the morphologically similar small species, precisely where theory would predict fine-tuning would be required for coexistence.

### Bioenergetics/Arthropod Abundances

Energy flow. The results of model estimation of energy demands for each of the three dominant bird species and the avian community as a whole are presented in Fig. 10. Although current SI usage expresses energy in joules, the results given here are in calories ( $1 \text{ cal} = 4.19 \text{ joules}$ ) to facilitate comparisons with previous bioenergetic studies. Individual species' energy requirements varied substantially throughout the entire year (Fig. 10A), as much as an order of magnitude in meadowlarks. In general, the cumulative energy requirement of each species for the entire year was in proportion to their relative abundances throughout the year. Horned Larks required about  $1.16 \text{ kcal m}^{-2} \text{ yr}^{-1}$ , while Sage Sparrows only needed a little more than half that,  $0.70 \text{ kcal m}^{-2} \text{ yr}^{-1}$ . Although peak demand for meadowlarks was 30% greater than either of the other two species (which in turn were very close to one another), their total yearly consumption,  $1.05 \text{ kcal m}^{-2} \text{ yr}^{-1}$ , was less than that of Horned Larks. Overall, the temporal patterns of energy flow in the

three major species were very similar.

The temporal distribution of the demands of the total avian community (Fig. 10B) was highly variable, ranging from a low of about  $0.0025 \text{ kcal m}^{-2} \text{ day}^{-1}$  from November through February to a peak of over  $0.026 \text{ kcal m}^{-2} \text{ day}^{-1}$  during mid- to late May. The peak corresponds to the time of maximal reproductive output in all species. Although all three species are usually double-brooded at ALE (pers. obs.), there appears to be no bimodality in energy demand. This is likely attributable to both the lack of synchrony among the major breeders and the low success rate of second broods due to increased predation (Rotenberry, unpubl. data). The total annual energy demand of the entire passerine avifauna was about  $2.91 \text{ kcal m}^{-2} \text{ yr}^{-1}$ .

It is possible to compare the estimates generated here to those for other systems. For example, Holmes and Sturges (1975) calculated a total avian community consumption rate of  $7.39 \text{ kcal m}^{-2} \text{ yr}^{-1}$  in a northeastern hardwood forest, about 2.5 times that observed in the shrubsteppe. Unfortunately, few other estimates have been generated for the entire year, most being restricted to the breeding season. The length of such a season, of course, is highly variable from system to system, and estimates generated over such variable time spans cannot be readily compared. One can compare estimates of peak daily demand, however, as these will be independent of the time span of the study (provided,

of course, that the peak does occur within that time span). For example, Wiens and Nussbaum (1975) using the same simulation model estimated peak demands of 0.08 to 0.15 kcal  $m^{-2}$  day $^{-1}$  for northwestern coniferous forest breeding birds, 3 to 6 times greater than those generated here. Peak demands at a variety of grassland sites, however, were lower, ranging from 0.011 to 0.019 kcal  $m^{-2}$  day $^{-1}$  (Wiens and Dyer 1975, Wiens 1977).

Food consumption rates. The energy estimates of the foregoing section must now be placed in their proper perspective with respect to other parts of the ecosystem. Birds do not just consume kilocalories, but search for, pursue, capture, and eat individual prey items. Thus, what follows is an attempt to couple the dietary demands of the entire guild with estimates of prey standing crops. Because of the many simplifying assumptions that will become apparent as the analysis proceeds, this attempt must be regarded as only a coarse approximation.

Basically, information on the relative biomass of each prey taxon in the diet (lumped to the ordinal level) and caloric value of each taxon (kcal  $g^{-1}$ ) are coupled with model projections of caloric demands (kcal  $m^{-2}$  day $^{-1}$ ) to estimate the prey consumption rate for each taxon ( $g$   $m^{-2}$  day $^{-1}$ ). Daily estimates may be summed to give total yearly consumption by taxon ( $g$   $m^{-2}$  yr $^{-1}$ ). The accuracy of these

estimates depends on (1) variation in the caloric value of prey types, (2) variation in diets between sampling periods, and (3) the accuracy of diet determinations.

The results of the simulation run for 1974 are given in Table 11, which lists the total yearly consumption of each prey taxon by each bird species. Taken at face value, the data in Table 10 clearly demonstrate the overall importance of seeds, beetles, and orthopterans in the diets of these birds. The importance of orthopterans is especially interesting as their availability is confined to only a limited portion of the year. Their maximum contribution to the diet occurs simultaneously with their maximum density, however (see below, Table 11). The pattern of total dietary niche breadth estimated for each species for the entire year on the basis of prey consumption again demonstrates that the larger birds do not appear more generalized than the smaller ones; sage sparrows have a third again as great a dietary diversity as meadowlarks. This most likely reflects the relatively low seed consumption by meadowlarks throughout most of the year.

Similarities between estimated yearly diets seem equally as high as those demonstrated in Fig. 7. The two most similar are the Sage Sparrow and meadowlark (SIMI = 0.92), certainly a surprising combination considering expectations based on their general morphology. Sage Sparrows

were also fairly similar to Horned Larks (SIMI = 0.81), and Horned Larks were less similar to meadowlarks (SIMI = 0.55). These broad patterns based on estimated prey consumption are in general agreement with those seen from direct enumeration of prey items (e.g. Fig. 7).

Since the BIRD model generates its estimates of energy demand and prey consumption on a day-by-day basis, the estimates for any one day may be compared with point samples of the abundance of potential prey items. It must be constantly borne in mind, however, that this comparison does not take into account the large number of physical, physiological, and behavioral filters interposed between the arthropods observed in the field and those sampled by birds (Bryant 1973, Ellis et al. 1976). Nonetheless it represents a "ball park" estimate of the degree of inter-relatedness of birds and their arthropod prey and allows an initial assessment of the limitations of birds by their food and the potential impact of birds on lower trophic levels.

The results, presented in Table 11, allow a direct comparison between estimated consumption rates and observed arthropod abundances. If one takes these results at face value, several patterns and absences of patterns appear. Foremost is the uniformly low proportion of the arthropod standing crop necessary to support the avifauna, never more than 0.7%, even when bird demand is at its peak (31 May).

In fact, it appears at all points sampled arthropod standing crops are greater than total arthropod consumption by birds estimated for the entire year ( $0.1469 \text{ g m}^{-2}$ , Table 10). These estimates do not take into account prey turnover, however, which will be discussed below.

The similarity between birds and drop-traps in sampling the arthropods is quite variable, running almost the entire gamut of possible values. Even with this range of variability, no patterns are readily apparent. If diets become more opportunistic as prey become scarcer or more limiting (Emlen 1966), then one expects to observe either a positive correlation between BIRD/INSECT similarity coefficients and percent of standing crop required by birds or a negative correlation between this similarity and total arthropod biomass. Both correlations cannot be distinguished from zero, most likely due to the small sample size ( $r = 0.01$  and  $0.75$ , respectively, both N. S., 3 df), but neither appears promising in any event. Dietary diversity, too, is uncorrelated with arthropod biomass ( $r = -0.20$ , N. S., 3 df), but at least varies in the direction predicted by theory. Changes in dietary diversity were, however, weakly correlated with changes in prey diversity ( $r = 0.82$ ,  $0.10 > \underline{P} (r > 0) > 0.05$ , 3 df), perhaps reflecting an element of opportunism in prey selection.

## CONCLUDING COMMENTS

The results of this study are in general agreement with those described in geographically broader treatments of the same general topics in North American grassland and shrubsteppe avifaunas (Wiens and Dyer 1975, Rotenberry and Wiens 1978). Other studies of diet/morphology relationships (Wiens and Rotenberry MS) and bioenergetics (Wiens 1977b) also indicate an apparent lack of close coupling between birds and their biotic environments in these ecosystems. This has implications both for the importance of birds in ecosystem functioning and for the importance of resource-based competition in determining community structure.

For example, Wiens (1977b) suggested that avian seasonal consumption varied between 0.02% to 0.11% of the total net primary production in a wide variety of grasslands, and Holmes and Sturges (1975) estimated consumption at 0.17% primary production in a northeastern hardwoods forest. While estimates of total primary production at ALE are currently unavailable, comparison with just the peak harvest yield of just Agropyron spicatum for 1974 ( $38.6 \text{ g m}^{-2}$ ; W. H. Rickard, pers. comm.) indicates total yearly consumption by the avifauna (Table 10) to be only 0.6% of that point sample. The observation that the birds are generally primary carnivores (eat mainly herbivores), coupled with a



simple 10% trophic efficiency, would predict consumption of about 1% of the annual net primary production. As pointed out previously (Table 11), the consumption of arthropods by birds appears to be but a small fraction of that potentially available.

There are, of course, a variety of factors mitigating the usefulness of estimates such as those just presented. For one thing, the entire plant or insect standing crop measured is certainly not available to birds. The temporal activity patterns and micro-habitats of many insects render them completely unavailable for consumption. Many insects are either unpalatable, much too large to be subdued, or energetically uneconomical to pursue. Further, bird diets are not restricted to insects and seeds on an "either/or" basis. All these factors imply that birds could conceivably "impact" their prey populations to a much greater extent than the percentage estimates suggest. On the contrary, these factors are offset by a battery of other factors that imply even less impact than the percentage figures. Most important of these is the lack of consideration of population turnover or recruitment rates in the prey. When this rate is high prey populations may sustain considerable predation with little effect. Such measures of turnover are virtually absent from terrestrial studies, although estimates for freshwater invertebrates range from 2.5 - 5.0

(Waters 1969) to over 100 (Allan 1951, cited in Benke 1976) for ratios of production to biomass during a season. On the whole it seems quite likely that birds in the shrub-steppe play only a small role in reducing the numbers of invertebrates substantially, and that any "important" effects in ecosystem functioning are subtle at best.

The results of these diet observations and model simulations do suggest, however, the sorts of things one might look for in subsequent studies designed to elucidate the subtleties of avian involvement in ecosystem processes. For example, one of the serious limitations of this study was the absence of information on seed production and subsequent availability. Further, the method of arthropod sampling underestimates the standing crop of grasshoppers (L. E. Rogers, pers. comm.); given the apparent importance of orthopterans in the diet, data dealing with their density and turnover would be most valuable. Indeed, if birds exert any effects on ecosystems at all it is most likely as "controllers" of the dynamics of arthropod populations through which a much greater bulk of energy and materials pass (Wiens 1977, Wiens and Dyer 1975, Kendeigh et al. 1977, Holmes and Sturges 1975).

If these birds are not limited by food, then why do they eat the things they do? At this point one of the conceptual problems of optimal foraging theory becomes apparent:

how does one distinguish between a bird that is foraging optimally and one that is foraging opportunistically? Under circumstances of high abundances of "preferred" items both birds take the same prey items in roughly the same proportions. Indeed, under conditions of food superfluity it is difficult to imagine why a bird should forage optimally [i.e. what fitness penalty is paid for foraging "suboptimally" (Wiens 1977a)], although optimal foraging strategies have been invoked under just such circumstances (e.g. Wilson 1976). The fact that such disparate birds as Sage Sparrows and Western Meadowlarks have such similar diets (not expected from optimality considerations given the difference in body sizes and consequent energetic requirements) suggests that prey availability may be more important than prey "suitability" in determining its inclusion in the diet. The generalist (= opportunistic) feeding habit in the sort of variable habitat the shrubsteppe represents may be predicted from other aspects of niche theory quite apart from optimality constraints (e.g. Levins 1968, MacNaughton and Wolf 1970).

Several aspects of the data presented here affirm the notion of dietary opportunism. For example, the between-phenotype analysis showed that while individual birds were picking up a few odd taxa that other individuals were missing, all individuals were concentrating on the same few taxa. Prey size certainly did not seem a criterion either; often

the prey size distributions of all three major species appeared identical. Finally, the patterns of clustering of diet collections clearly argues for all species tracking changing availability, resulting in the observed seasonal co-variation in prey consumption.

This is certainly not to say that theoretical constructs based upon optimality constraints, resource partitioning, and competition are wrong; indeed, they often represent the quality of deductive modelling required to generate sound ecological predictions. However, as with most models that simplify nature, they are based on certain limiting assumptions (often merely implicit and not specified) to which a specific natural system may not conform. To the extent that non-conformance occurs, conceptual generalizations or confirmation of theoretical predictions from investigation of such a system may be in error.

My results clearly show too the pitfalls of "one-shot" studies, be they of niche breadth, prey size selection, or ecomorphological relationships. Each of these parameters demonstrates substantial variation, both within a single species throughout the year or among a suite of species sampled during different seasons. In fact, some inequalities between two species are reversed at different times of the year.

If birds in the shrubsteppe are, in fact, not "important" in an ecosystem context, it seems legitimate at this

point to speculate on why this may be. I would suggest that the apparent "decoupling" of birds from this ecosystem is primarily a result of the relative instability of the shrub-steppe climate and its subsequent effect on community structure. This instability has been clearly demonstrated with respect to both short-term predictability (Wiens 1974) and long-term variability (Rotenberry, in press). Theoretical predictions of a few dominant species that appear regularly but in substantially varying numbers under such environmental conditions (Tramer 1969) are fulfilled (Rotenberry, in press; Rotenberry and Wiens 1978). This implies that periodic "bottlenecks" occur through which few species can pass, resulting in a community which is "non-saturated" in the face of an apparent resource abundance (Wiens 1974, 1977a). In the absence of equilibrium species conditions (a necessary prerequisite for the predictions of competition theory to be expressed), it is not surprising that many of the conditions expected from theoretical considerations of resource partitioning and optimization are not apparent. This certainly points out in the strongest possible way the need for recognizing that the organizing principles behind community structure are likely to vary from community to community (Menge and Sutherland 1976; Rotenberry, in press), and that before investigating predictions from one set of principles one should be sure the system investigated is appropriate.

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Table 1. Summarization of significant biological features of the three major habitat types on the ALA Reserve. Types are coded by the names of the dominant vegetation. Numbers in parentheses are the relative abundance of each type throughout the 40 km<sup>2</sup> study area. A. Percent coverage of dominant vegetation. B. Approximate breeding densities of dominant birds.

	Habitat Type		
	<u>Agropyron</u> (40%)	<u>Agropyron/ Artemisia</u> (30%)	<u>Artemisia</u> (30%)
A. Percent Coverage			
<u>Artemisia</u>	0-1	5-10	25-30
<u>Agropyron</u>	50-60	50-60	10-20
B. Breeding Density (#/km <sup>2</sup> )			
Horned Lark	100	100	20
Sage Sparrow	0	100	200
Western Meadowlark	30	35	40

Table 2. Dietary composition of Horned Lark populations on the ALE Reserve, 1971-1974. Values are the percent of total sample dry weight for each collection.

Prey Taxon	Collection Date										
	Jan. 74	Feb. 74	Apr. 71	May 71	May 72	June 74	Aug. 74	Oct. 73	Nov. 72	Nov. 73	Dec. 73
ANGIOSPERMAE											
Graminae	1.3	21.0	15.7	8.8	0.7	29.1	56.3	48.4	16.6	65.4	50.0
Chenopodiaceae	98.4	5.0	0.1			0.3	7.3	3.6	41.3	19.5	23.5
Cruciferae		0.1	0.1		0.1		0.1	2.6		0.4	0.2
Misc. Forbs	0.3	14.1	0.6	2.5	0.3	2.9	3.8	5.2	8.4	7.7	17.9
ARACHNIDA											
Araneida		4.7	1.1	2.1	2.8	0.3	0.3	0.2	3.9		0.2
Solpugida						2.2		4.7			0.2
INSECTA											
Coleoptera											
Curculionidae		28.7	15.5	50.5	73.1	2.6	1.1	0.3			
Tenebrionidae		3.2				2.3	2.4		2.9		
Scarabaeidae		2.9	1.5		4.1	0.4	0.2	9.0	1.5		0.1
Carabidae		2.9	9.5	1.5	0.2		0.4			0.4	
Larvae		6.9	26.7	8.0		10.3	0.2	4.3			3.8
Misc. Coleoptera		3.6	2.1	0.1	0.7	0.4		0.8	1.5		0.1
Hymenoptera											
Formicidae		0.4	1.3	0.8	0.2	1.2	6.9	0.2	0.2	0.1	0.1
"wasps"		2.5	0.1	0.3	0.3	0.1	0.4	0.3	0.6		
Lepidoptera											
Larvae		2.7	9.3	18.8	14.0	6.0	0.4	0.1		1.0	0.1

Table 2. Continued.

Prey Taxon	Collection Date										
	Jan. 74	Feb. 74	Apr. 71	May 71	May 72	June 74	Aug. 74	Oct. 73	Nov. 72	Nov. 73	Dec. 73
Diptera											
Asilidae					0.6	4.6	1.7	14.5			
Misc. Diptera					0.7				3.2	0.1	
Neuroptera		1.0	0.6			0.4		4.8			
Hemiptera		0.2	1.1	2.1	1.2	0.6	2.9	0.3	0.1	0.9	
Orthoptera			13.7	4.2	0.5	27.9	15.7		19.1		
Homoptera											
Cicadidae					0.3	8.4					
Misc. Homoptera		0.1	1.1	0.1	0.3	0.1		0.7		0.1	
Other Insecta			0.2	0.3		0.1	0.1	0.1	0.8	4.4	3.8
Number of specimens	16	16	8	12	22	23	22	16	19	9	16
Total sample dry wgt. (g)	1.013	2.086	1.295	1.583	3.891	10.293	8.011	3.296	1.294	0.063	2.064
Dry wgt. per specimen: $\bar{x}$	0.063	0.130	0.162	0.132	0.177	0.448	0.364	0.206	0.068	0.071	0.129
S.D.	0.020	0.066	0.077	0.063	0.096	0.208	0.188	0.137	0.075	0.035	0.065
Number of taxa	3	17	18	14	17	20	17	18	13	11	12
Dietary diversity	1.10	6.20	6.35	3.25	1.80	5.29	2.81	3.64	4.08	2.11	2.94

Table 3. Dietary composition of Sage Sparrow populations on the ALE Reserve, 1971-1974. Values are the percent of total sample dry weight for each collection.

Prey Taxon	Collection Date				
	Apr. 71	May 71	May 72	June 74	Aug. 74
ANGIOSPERMAE					
Graminae	18.9	2.7	0.1	31.1	13.2
Chenopodiaceae				0.2	2.5
Cruciferae				0.2	0.1
Misc. Forbs	4.4	0.3	1.1	1.2	1.3
ARACHNIDA					
Araneida	5.3	2.4	1.0	0.5	
Solpugida				0.9	0.6
INSECTA					
Coleoptera					
Curculionidae	17.2	42.0	67.9	2.9	3.9
Tenebrionidae				12.0	22.5
Scarabaeidae			1.8	0.1	0.3
Carabidae		1.5		1.0	0.1
Larvae	18.5	0.9	0.8	2.5	
Misc. Coleoptera	0.5	1.3	6.5	0.4	0.4
Hymenoptera					
Formicidae	2.7	0.5	0.2	0.7	5.9
"wasps"		2.6	1.0	0.4	0.2
Lepidoptera					
larvae	5.4	23.9	6.0	3.6	0.1
Diptera					
Asilidae			2.1	3.6	1.0
Misc. Diptera	1.2	0.3	0.5		
Neuroptera	2.6	8.4	2.4	0.7	0.6
Hemiptera	1.0	1.0	2.0	0.3	1.0
Orthoptera	16.2	11.3	4.8	32.8	46.5
Homoptera					
Cicadidae				2.4	
Misc. Homoptera	2.5		1.4	0.1	

Table 3. Continued.

Prey Taxon	Collection Date				
	Apr. 71	May 71	May 72	June 74	Aug. 74
Other Insecta	3.6	0.9	0.5	2.5	
Number of specimens	4	12	20	18	14
Total sample dry wgt. (g)	0.563	1.399	2.929	9.025	6.712
Dry wgt. per speci- men: $\bar{x}$	0.141	0.117	0.146	0.501	0.479
S.D.	0.061	0.040	0.078	0.237	0.229
Number of taxa	14	15	17	22	17
Dietary diversity	7.31	3.90	2.11	4.46	3.44

Table 4. Dietary composition of Western Meadowlark populations on the ALE Reserve, 1971-1974. Values are the percent of total sample dry weight for each collection.

Prey Taxon	Collection Date			
	May 71	May 71	June 74	Aug. 74
ANGIOSPERMAE				
Graminae			2.7	3.7
Chenopodiaceae				
Cruciferae				
Misc. Forbs				1.1
ARACHNIDA				
Araneida	2.0	0.3	0.2	0.2
Solpugida				2.3
INSECTA				
Coleoptera				
Curculionidae	19.4	37.8	0.1	2.0
Tenebrionidae		28.1	8.9	20.6
Scarabaeidae	14.4	5.0	0.1	1.1
Carabidae	21.1	8.0	0.6	0.5
Larvae	1.3		0.9	0.2
Misc. Coleoptera		3.1		
Hymenoptera				
Formicidae	0.6	5.4	0.3	2.1
"wasps"	3.1	2.4	0.4	0.2
Lepidoptera				
Larvae	34.4	0.8	5.9	
Diptera				
Asilidae			0.3	1.1
Misc. Diptera		0.8	0.1	0.1
Neuroptera	2.8		0.2	
Hemiptera	1.0	1.8	0.4	1.3
Orthoptera		5.2	49.5	63.7

Table 4. Continued.

Prey Taxon	Collection Date			
	May 71	May 72	June 74	Aug. 74
Homoptera				
Cicadidae			29.5	
Misc. Homoptera		1.3		
Other Insecta				
Number of specimens	2	3	10	8
Total sample dry wgt. (g)	0.918	1.037	13.15	8.389
Dry wgt. per spe- cimen: $\bar{x}$	0.459	0.345	1.301	1.049
S.D.	0.181	0.043	0.495	0.468
Number of taxa	10	13	17	15
Dietary diversity	4.47	4.19	2.90	2.22



Table 5. Dietary composition of Vesper and White-crowned sparrow populations on the ALE Reserve, 1974. Values are the percent of total sample dry weight for each collection.

Prey Taxon	Vesper Sparrow June 74	White-crowned Sparrow Jan. 74
ANGIOSPERMAE		
Graminae	29.5	8.9
Chenopodiaceae		56.0
Cruciferae		
Misc. Forbs	0.5	14.5
ARACHNIDA		
Araneida	0.1	0.3
Solpugida	2.8	
INSECTA		
Coleoptera		
Curculionidae	4.8	6.0
Tenebrionidae	2.1	
Scarabaeidae		
Carabidae	1.4	9.4
Larvae	0.9	
Misc. Coleoptera	0.3	0.4
Hymenoptera		
Formicidae	0.1	0.2
"wasps"		0.5
Lepidoptera		
Larvae	1.4	
Diptera		
Asilidae	2.4	1.2
Misc. Diptera		
Neuroptera		
Hemiptera	0.2	2.7
Orthoptera	53.6	

Table 5. Continued.

Prey Taxon	Vesper Sparrow June 74	White-crowned Sparrow Jan. 74
Homoptera		
Cicadidae		
Misc. Homoptera		
Other Insecta		
Number of specimens	5	9
Total sample dry wgt. (g)	2.837	0.428
Dry wgt. per specimen: $\bar{x}$	0.567	0.048
S.D.	0.238	0.034
Number of taxa	14	11
Dietary diversity	2.64	2.81

Table 6. Average length of prey items per individual for bird populations on the ALE Reserve, 1971-1974. Measurements given in linear millimeters and  $\log_2$  mm. Standard deviations in parentheses. Sample sizes are the number of birds averaged.

Species	Date	Sample Size	Linear mm		$\log_2$ mm	
A. Horned Lark	Jan. 74	16	2.07	(0.17)	1.03	(0.08)
	Feb. 74	16	4.05	(0.87)	1.82	(0.39)
	Apr. 71	8	6.39	(2.01)	2.41	(0.47)
	May 71	12	5.57	(1.53)	2.33	(0.39)
	May 72	22	7.06	(1.07)	2.69	(0.31)
	June 74	23	5.18	(2.84)	1.86	(0.77)
	Aug. 74	22	2.95	(1.15)	1.22	(0.52)
	Oct. 73	16	3.44	(0.81)	1.46	(0.33)
	Nov. 72	19	2.48	(0.75)	1.11	(0.41)
	Nov. 74	9	2.89	(1.26)	1.32	(0.61)
	Dec. 73	16	2.77	(0.73)	1.32	(0.39)
B. Sage Sparrow	Apr. 71	4	5.19	(1.71)	2.14	(0.50)
	May 71	12	6.20	(0.96)	2.47	(0.20)
	May 72	20	7.32	(0.96)	2.79	(0.19)
	June 74	18	4.18	(1.88)	1.59	(0.45)
	Aug. 74	14	4.58	(1.88)	1.59	(0.45)
C. Western Meadowlark	May 71	2	8.23	(0.58)	2.88	(0.07)
	May 72	3	7.66	(0.58)	2.89	(0.11)
	June 74	10	14.62	(3.24)	3.54	(0.43)
	Aug. 74	8	12.51	(2.84)	3.41	(0.42)
D. Vesper Sparrow	June 74	5	3.52	(0.55)	1.41	(0.17)
E. White-crowned Sparrow	Nov. 74	9	2.54	(0.67)	1.18	(0.37)

Table 7. Dietary diversity of entire collections (all individuals pooled) and the average individual within each collection for bird populations on the ALE Reserve, 1971-1974. Figures in parentheses are the average individual expressed as a percent of the entire collection. See text for methods of calculation of diversity indices. Sample sizes as in Table 6.

Species	Date	Entire Sample		Average Individual	
		No. Prey Taxa	Dietary Diversity	No. Prey Taxa	Dietary Diversity
A. Horned Lark	Jan. 74	3	1.10	1.38 (46)	1.14 (104)
	Feb. 74	17	6.20	6.25 (37)	3.00 (48)
	Apr. 71	18	6.35	7.63 (42)	4.06 (64)
	May 71	14	3.25	4.83 (35)	2.22 (68)
	May 72	17	1.80	4.09 (24)	1.80 (100)
	June 74	20	5.29	6.91 (35)	2.57 (49)
	Aug. 74	17	2.81	5.86 (34)	2.48 (88)
	Oct. 73	18	3.64	5.06 (28)	2.33 (64)
	Nov. 72	13	4.08	2.42 (19)	1.72 (42)
	Nov. 73	11	2.11	3.56 (32)	1.66 (79)
	Dec. 73	12	2.94	3.50 (29)	1.83 (62)
B. Sage Sparrow	Apr. 71	14	7.31	7.00 (50)	3.62 (50)
	May 71	15	3.90	6.00 (40)	2.67 (68)
	May 72	17	2.11	4.40 (26)	1.94 (92)
	June 74	22	4.46	8.00 (36)	2.91 (65)
	Aug. 74	17	3.44	6.43 (38)	2.66 (77)

Table 7. Continued.

Species	Date	Entire Sample		Average Individual			
		No. Prey Taxa	Dietary Diversity	No. Prey Taxa		Dietary Diversity	
C. Western Meadowlark	May 71	10	4.47	7.50	(75)	3.52	(79)
	May 72	13	4.19	7.67	(59)	3.48	(83)
	June 74	17	2.90	6.40	(38)	1.96	(68)
	Aug. 74	15	2.22	6.00	(40)	1.94	(87)
D. Vesper Sparrow	June 74	14	2.64	7.20	(51)	2.57	(97)
E. White-crowned Sparrow	Nov. 74	11	2.81	3.44	(31)	2.26	(80)

Table 8. Similarity (SIMI).within collections (the average similarity between all possible pairs of individuals) and between groups within collections (the similarity between pooled data for each group) for diets of bird populations on the ALE Reserve, 1971-1974. N is the number of pairs compared. Juveniles defined as all birds less than 6 mo. old; AM birds defined as all specimens collected prior to 12:00 hrs. Calculations only performed for groups > 2 individuals.

Species	Date	Similarity Within Collection			Similarity Between Groups		
		$\bar{X}$	S. D.	N	ad./juv.	♂/♀	AM/PM
A. Horned Lark	Jan. 74	0.940	0.120	120	-	0.996	0.995
	Feb. 74	0.427	0.292	120	-	0.770	0.849
	Apr. 71	0.519	0.211	28	-	0.852	0.730
	May 71	0.672	0.244	66	0.919	0.932	0.608
	May 72	0.796	0.264	231	-	0.933	0.995
	June 74	0.410	0.326	253	0.830	0.780	0.829
	Aug. 74	0.692	0.246	231	0.878	0.940	0.970
	Oct. 73	0.601	0.244	120	-	0.891	0.925
	Nov. 72	0.548	0.338	171	-	0.821	0.612
	Nov. 73	0.576	0.389	36	-	0.802	0.521
	Dec. 73	0.575	0.338	120	-	-	0.951
B. Sage Sparrow	Apr. 71	0.272	0.235	6	-	-	-
	May 71	0.646	0.256	66	-	0.867	0.855
	May 72	0.794	0.294	190	0.926	0.986	0.933
	June 74	0.639	0.237	153	0.889	0.928	0.799
	Aug. 74	0.675	0.216	91	0.905	0.789	0.882

Table 8. Continued.

Species	Date	Similarity Within Collection			Similarity Between Groups		
		$\bar{X}$	S. D.	N	ad./juv.	♂/♀	AM/PM
C. Western Meadowlark	May 71	-	-	-	-	-	-
	May 72	-	-	-	-	-	-
	June 74	0.539	0.301	45	-	-	0.836
	Aug. 74	0.754	0.279	28	0.910	-	-
D. Vesper Sparrow	June 74	0.768	0.205	10	-	-	-
E. White-crowned Sparrow	Nov. 74	0.663	0.218	36	1	0.961	-

Table 9. Significant prey size  $\log_2(\text{mm})$  / character size correlations for bird populations on the ALE Reserve, 1971-1974. Correlations are for adults only; 216 individuals, 5 species. Weight in g, all others in mm.  
 \* and \*\* as before; - indicates non-significant correlation.

Character	$\bar{X}$ Plant Length	$\bar{X}$ Animal Length	$\bar{X}$ Total Length
Weight	-	0.38**	0.63**
Bill length	-	0.40**	0.69**
Bill height	-	0.48**	0.57**
Bill width	-0.15*	0.38**	0.59**
Tarsus length	-	0.42**	0.68**



Table 10. Bioenergetic model estimates of prey consumption of taxa ( $\text{g m}^{-2} \text{yr}^{-1}$ ) for each of the major species on the ALE Reserve, 1974.

Prey Taxon	Species			Total
	Horned Lark	Sage Sparrow	Western Meadowlark	
Graminae	0.0336	0.0099	0.0034	0.0469
Forbs	0.0179	0.0015	0.0009	0.0204
Arachnids	0.0017	0.0010	0.0007	0.0034
Coleoptera	0.0208	0.0142	0.0268	0.0618
Hymenoptera	0.0019	0.0013	0.0017	0.0049
Lepidoptera	0.0027	0.0017	0.0036	0.0080
Diptera	0.0025	0.0009	0.0009	0.0042
Neuroptera	0.0006	0.0009	0.0001	0.0016
Hemiptera	0.0011	0.0003	0.0006	0.0020
Orthoptera	0.0097	0.0130	0.0298	0.0525
Homoptera	0.0015	0.0007	0.0046	0.0068
Others	0.0004	0.0008	0.0005	0.0017
Total	0.0944	0.0462	0.0736	0.2142

Table 11. Comparison between bioenergetic model estimates of daily prey consumption of taxa ( $\text{g m}^{-2} \text{ day}^{-1}$ ; "BIRD") and drop-trap estimates of arthropod standing crop ( $\text{g m}^{-2}$ ; "INSECT"), for median dates of drop-trap sampling, 1974. See text for calculations of diversity and similarity.

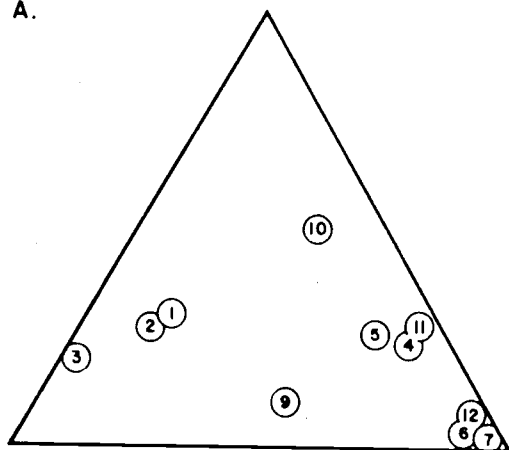
Prey Taxon		1 March	16 April	28 May	7 July	29 Aug.
Arachnids	BIRD	0.00002	0.00003	0.00003	0.00003	0.00003
	INSECT	0.0021	-	0.0409	0.0029	0.0089
Coleoptera	BIRD	0.00030	0.00083	0.00071	0.00033	0.00033
	INSECT	0.2131	0.0213	0.0734	0.2051	0.0932
Hymenoptera	BIRD	0.00002	0.00002	0.00003	0.00004	0.00007
	INSECT	0.0013	0.0908	0.0457	0.1455	0.0101
Lepidoptera	BIRD	0.00003	0.00010	0.00016	0.00006	-
	INSECT	0.0126	0.3041	0.0122	0.0112	0.0028
Diptera	BIRD	-	-	0.00003	0.00005	0.00005
	INSECT	0.0036	0.0085	0.0085	0.0059	0.0049
Neuroptera	BIRD	-	0.00002	0.00002	0.00001	0.00001
	INSECT	-	0.0004	0.0001	0.0002	-
Hemiptera	BIRD	0.00001	0.00001	0.00002	0.00001	0.00002
	INSECT	0.0015	0.0012	0.0080	0.00081	0.0121
Orthoptera	BIRD	0.00010	0.00016	0.00031	0.00089	0.00069
	INSECT	-	-	0.0040	0.0411	0.0173

Table 11. Continued.

Prey Taxon		1 March	16 April	28 May	7 July	29 Aug.
Homoptera	BIRD	-	0.00001	0.00009	0.00025	-
	INSECT	0.0015	0.0193	0.0223	0.0085	0.0183
All others	BIRD	-	0.00002	0.00001	0.00001	-
	INSECT	-	0.0021	0.0069	0.0014	0.0003
Total	BIRD	0.00048	0.00120	0.00141	0.00168	0.00120
	INSECT	0.2357	0.4477	0.2220	0.4299	0.1679
Diversity	BIRD	2.26	1.98	3.12	2.90	2.43
	INSECT	1.22	1.97	4.93	2.84	2.91
BIRD/INSECT Total		0.2%	0.3%	0.6%	0.4%	0.7%
BIRD/INSECT Similarity		0.95	0.19	0.76	0.45	0.58

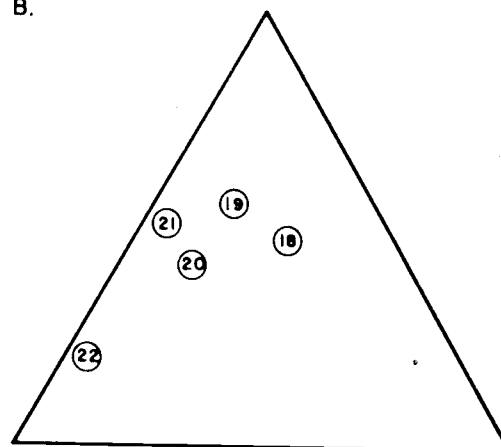
Figure 1. Proportions of seeds, beetles, and other arthropods in the diet of birds from the ALE Reserve, 1971-1974. The perpendicular distance from one side of the triangle is proportional to the percent contribution of that prey category to the diet. Numbers refer to specific collections. A. Horned Larks: 1 = Apr. 71; 2 = May 71; 3 = May 72; 4 = Nov. 72; 5 = Oct. 73; 6 = Dec. 73; 7 = Jan. 74; 9 = Feb. 74; 10 = June 74; 11 = Aug. 74; 12 = Nov. 73. B. Sage Sparrows: 18 = June 74; 19 = Aug. 74; 20 = Apr. 71; 21 = May 71; 22 = May 72. C. Western Meadowlarks: 13 = June 74; 14 = Aug. 74; 15 = May 71; 16 = May 72; Vesper Sparrows: 23 = June 74; White-crowned Sparrows: 25 = Nov. 74.

A.



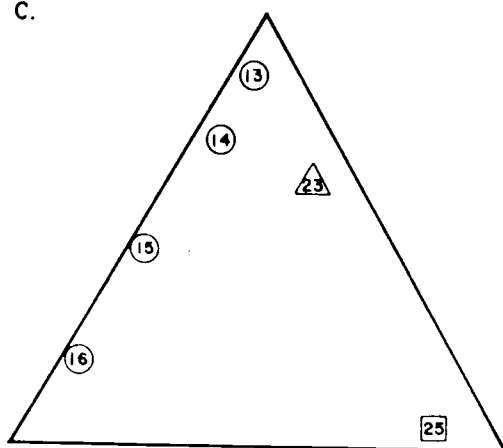
HORNED LARK

B.

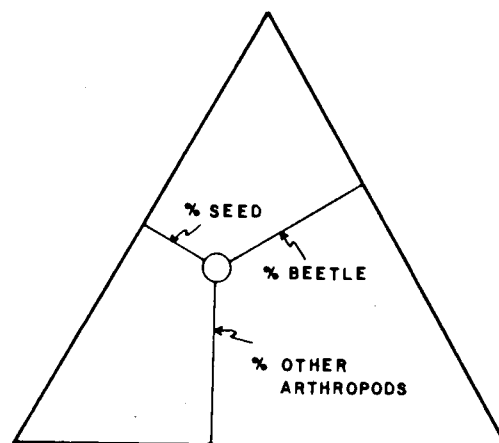


SAGE SPARROW

C.



- W. MEADOWLARK
- △ VESPER SPARROW
- WHITE-CROWNED SPARROW



KEY

Figure 2. Seasonal variation in Horned Lark diets.

- A. Arthropods and seeds as percent of total biomass.
- B. Grasses and forbs as percent of total plant biomass.
- C. Beetles and other arthropods as percent of total arthropod biomass.

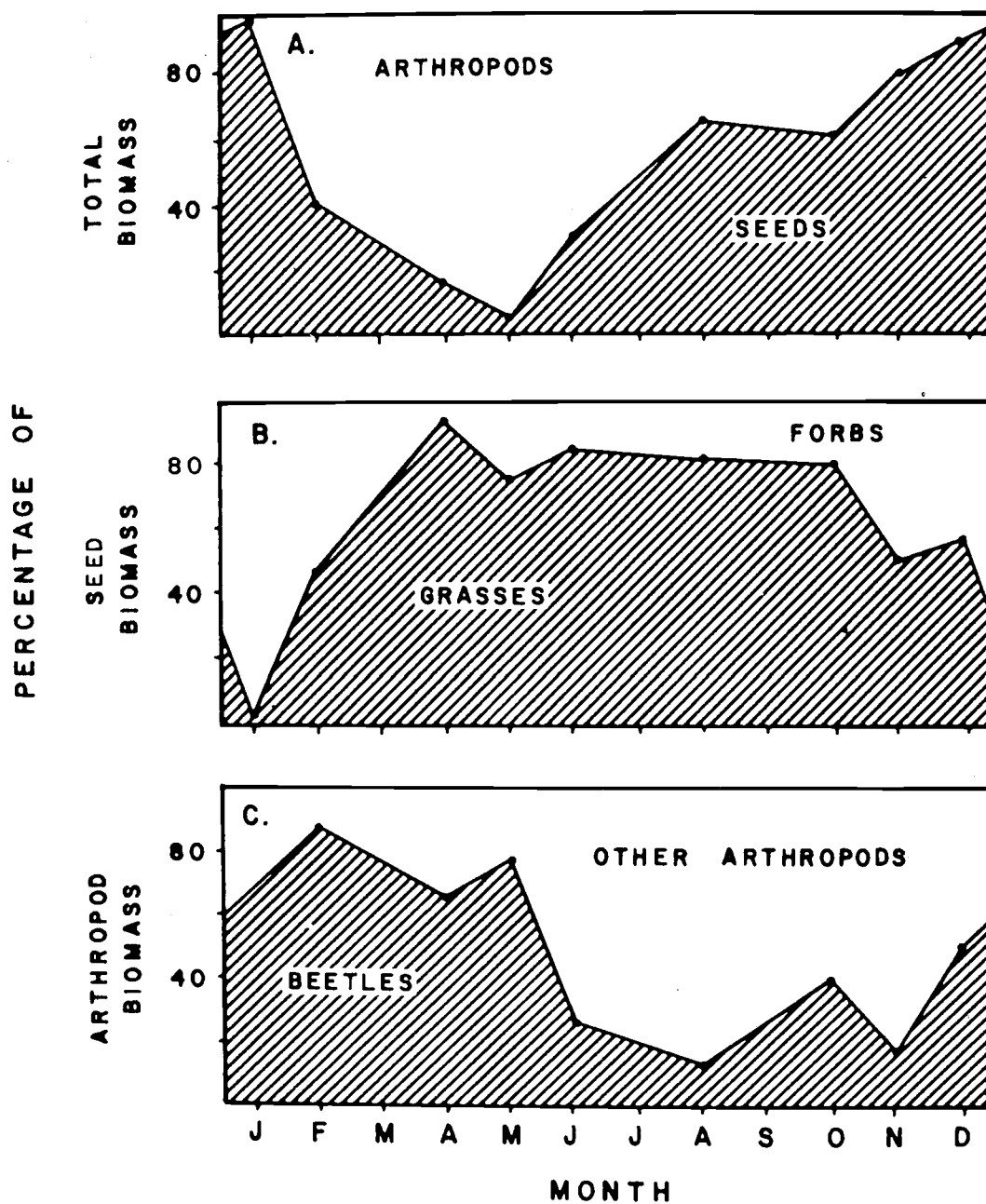
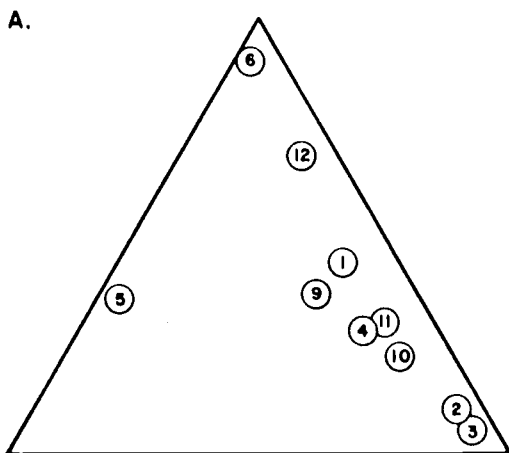


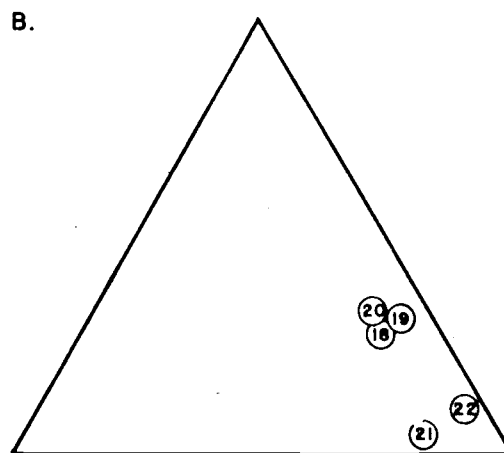
Figure 3. Proportions of ecological categories of arthropods in the diets of birds from the ALE Reserve, 1971-1974.

The perpendicular distance from one side of the triangle is proportional to the percent contribution of that prey category to total arthropod biomass in the diet. Taxa in each category defined in the Appendix. Numbers refer to specific collections as in Fig. 1.

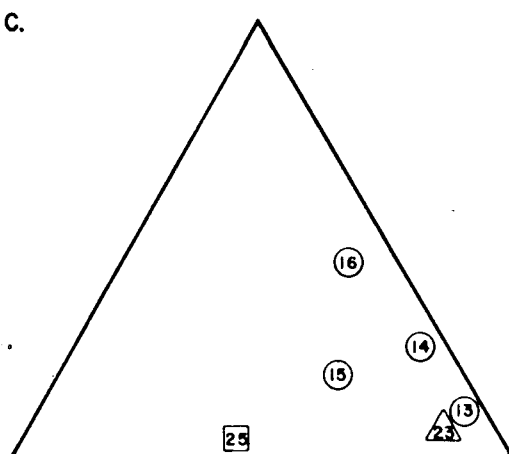




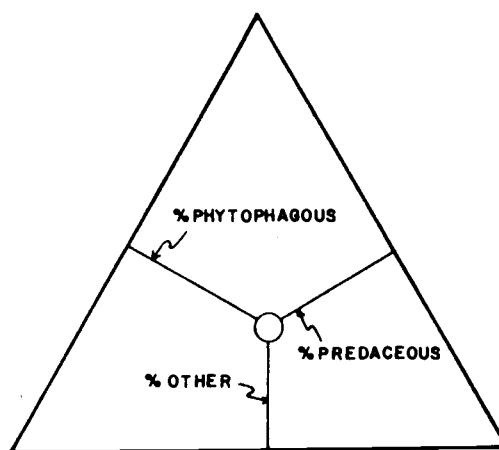
HORNED LARK



SAGE SPARROW



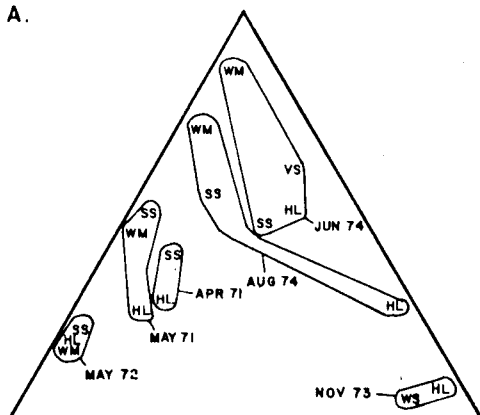
- W. MEADOWLARK
- VESPER SPARROW
- △ WHITE-CROWNED SPARROW



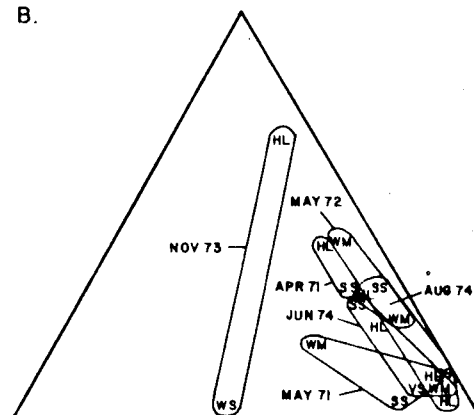
KEY

Figure 4. Proportions of various prey taxa in the diets of birds from the ALE Reserve, 1971-1974. Lines enclose contemporaneous samples of different species. The perpendicular distance from one side of the triangle is proportional to the percent contribution of that category to the diet. HL = Horned Lark, SS = Sage Sparrow, WM = Western Meadowlark, VS = Vesper Sparrow, WS = White-crowned Sparrow. A. Prey categories as in Fig. 1 (seeds, beetles, and other arthropods); all bird species combined. B. Prey categories as in Fig. 3 (phytophagous, predaceous, and other); all bird species combined. C. Relative contributions of curculionidae, orthoptera, and lepidopteran larvae to bird diets; all bird species combined.

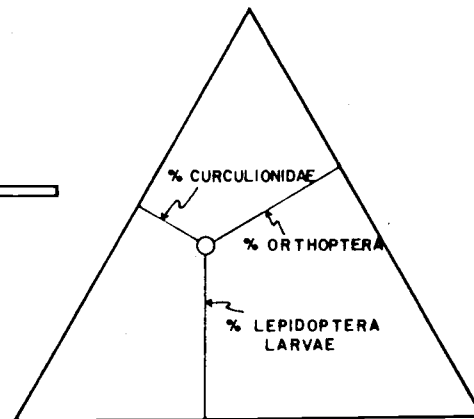
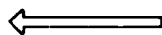
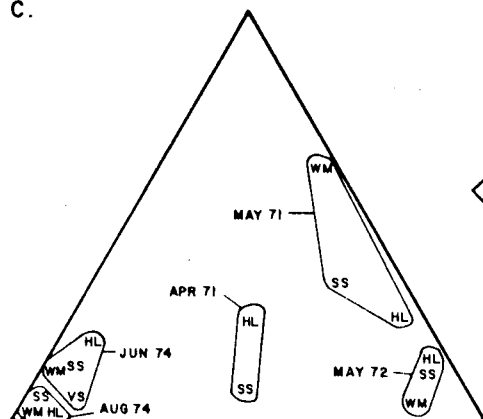
A.



B.



C.



KEY

Figure 5. Avian dietary relationships determined by cluster analysis of similarities (SIMI) based on relative biomass of all prey taxa in the diets. Species codes as in Fig. 4.

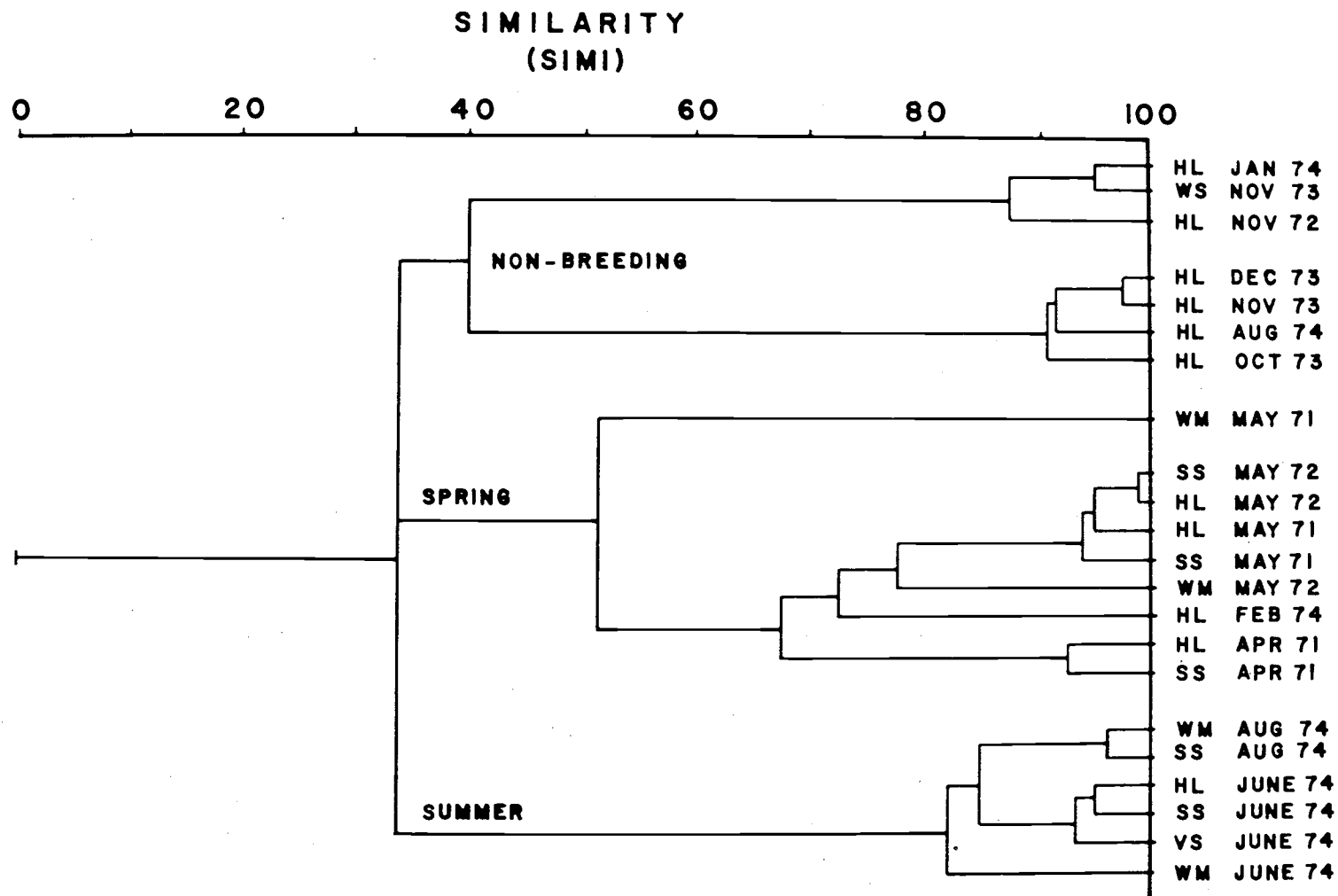


Figure 6. Size distributions of all prey items selected by birds on the ALE Reserve, 1971-1974. Prey size categories increase logarithmically ( $\log_2$ ). Bird species arranged by contemporaneous samples.

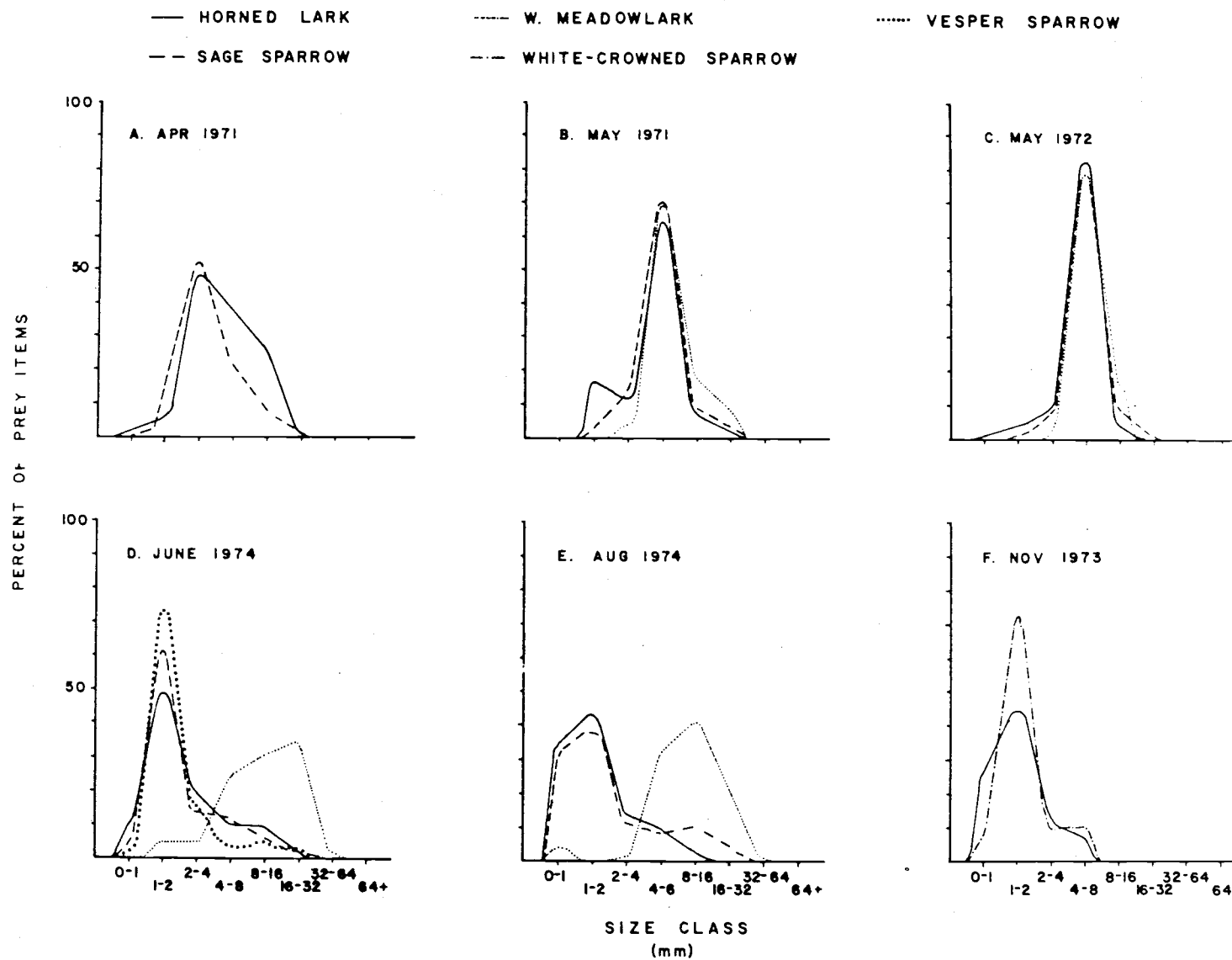


Figure 7. Size distribution of arthropod prey items selected by birds on the ALE Reserve, June 1974. Prey size categories increase logarithmically ( $\log_2$ ).



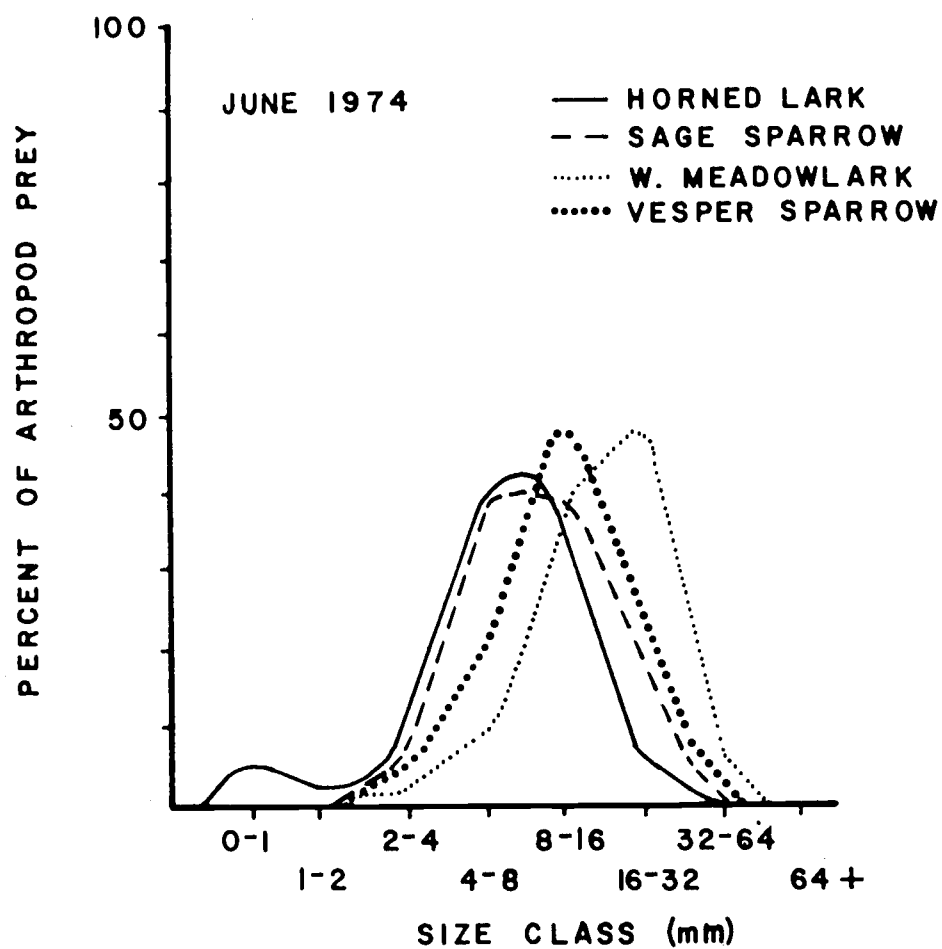


Figure 8. Intraspecific character ratios (ICR) for several morphological characters of birds collected on the ALE Reserve, 1971-1974.

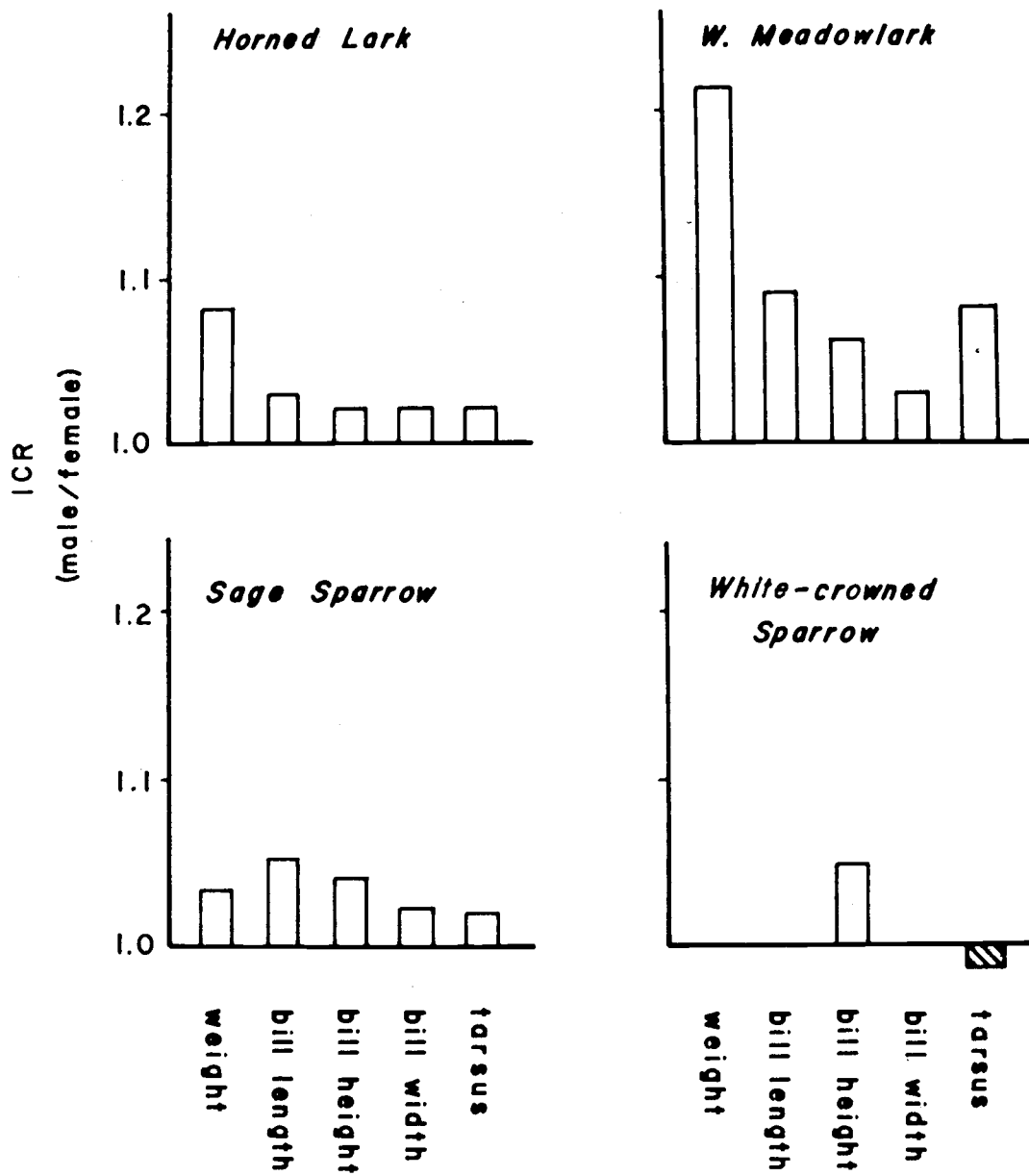
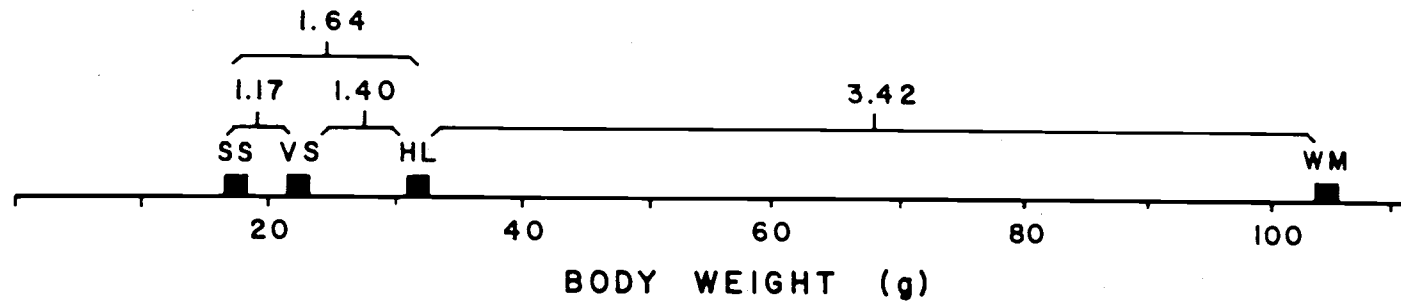


Figure 9. Distribution of (A) body weights and (B) mean bill lengths of birds collected on the ALE Reserve, 1971-1974. Numerical values are the ratios of larger to smaller between adjacent species pairs. Species codes as in Fig. 4. Upper ratio (1.64) in (A) generated by omission of irregularly occurring Vesper Sparrow.

A.



B.

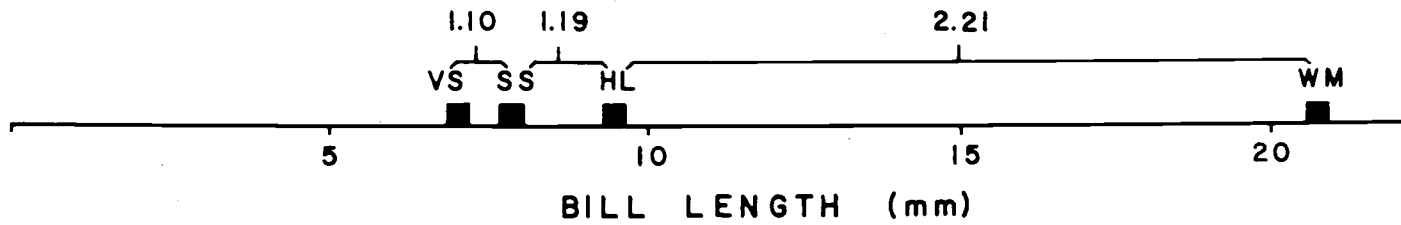
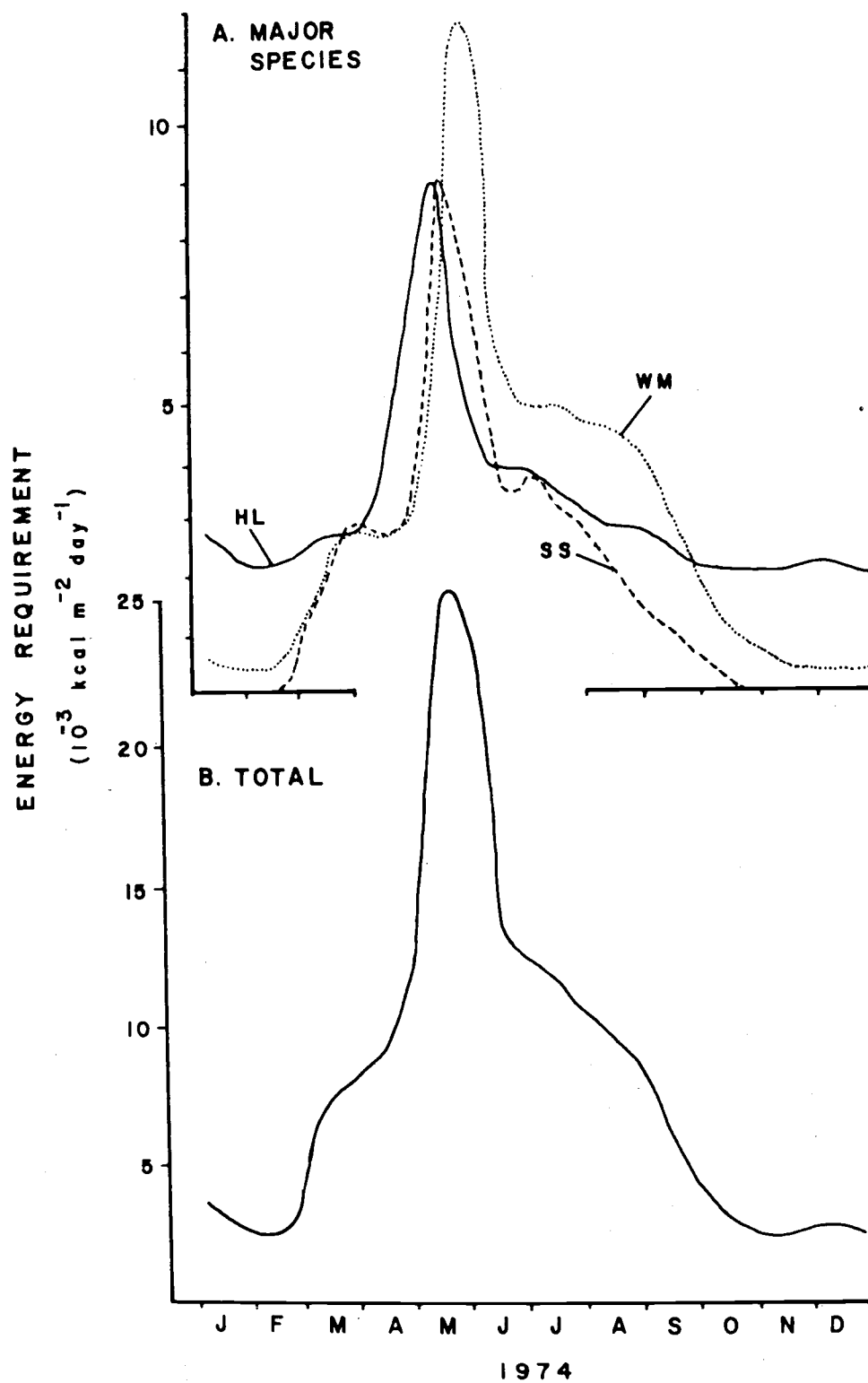


Figure 10. Estimated energy requirements of bird populations on the ALE Reserve, 1974. A. Estimates for individual species; species codes as in Fig. 4. B. Estimates for all species combined.



## APPENDIX



APPENDIX

Arthropod Trophic Categories

I. Phytophagous

Curculionidae  
Lepidoptera larvae  
Hemiptera  
Orthoptera  
Cicadidae  
misc. Homoptera

II. Predaceous

Araneida  
Solpugida  
Carabidae  
"wasps"  
Asilidae  
Neuroptera

III. Other

Tenebrionidae  
Scarabaeidae  
Coleoptera larvae  
misc. Coleoptera  
Formicidae  
misc. Diptera  
other Insecta