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AVAILABILITY AND USE OF ARTHROPOD FOOD RESOURCES BY WILSON'S WARBLERS AND LINCOLN'S SPARROWS IN SOUTHEASTERN WYOMING[1]

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Abstract. We examined availability and use of arthropods by Wilson's Warblers (*Wilsonia pusilla*) and Lincoln's Sparrows (*Melospiza lincolnii*) to determine whether all arthropods selected by these birds were equally preferred. Preferences were identified by comparing proportional availability of arthropods in willows to their proportional use by birds foraging in willows. Actively foraging birds were collected during the breeding seasons of 1984 and 1985 in montane riparian zones located on the Medicine Bow National Forest in southeastern Wyoming. Arthropods were sampled at bird foraging sites by applying a pyrethrin-based fogacide to the willows. We identified 115 families of arthropods in our spray samples from willows over the two breeding seasons. Of these families, 53 and 54 were identified in warbler and sparrow diets, respectively. Warblers were selective in the sizes of prey they consumed, with smaller prey (1 to 3 mm) being underrepresented in their diets for five of the eight arthropod groups considered. We employed a ranking procedure (PREFER) to investigate bird species' preferences among 10 arthropod food groups. The group ranked highest for both warblers and sparrows was Coleoptera, of which beetles with soft elytra were a major component. Of the remaining groups, arthropods that ranked high in preference for warblers were noncryptic and patchy in distribution, while those that ranked high for sparrows tended to be cryptic and more uniformly distributed. We suggest that the foraging strategies of Wilson's Warblers and Lincoln's Sparrows, and arthropod behavior, morphology, and distribution explain the differences we detected in proportional availability and use of arthropods by these birds.

Key words: Wilson's Warbler; Lincoln's Sparrow; arthropod food resources; prey selection; availability and use comparison.

INTRODUCTION

Central to the study of avian ecology is the relationship between birds and their food resources. Ecologists have examined the relationships among selection of food items by insectivorous birds, foraging strategies, and habitat structure in diverse ways (e.g., Rotenberry 1980; Robinson and Holmes 1982, 1984; Sherry 1984; Airola and Barrett 1985). Several studies have focused on the abundance of arthropods associated with various foraging substrates used by birds (Greenberg and Gradwohl 1980, Greenberg 1987). Holmes and Schultz (1988) investigated avian response to the distribution and abundance of lepidopteran larvae in a hardwood forest. Yet, studies comparing selection of arthropod food resources with available food resources have been relatively infrequent (Busby and Sealy 1979, Bibby 1981, Moeed and Fitzgerald 1982, Quinney and Ankney 1985), due primarily to the difficulty of sampling available arthropods, especially in structurally complex environments (Greenberg and Gradwohl 1980, Sherry 1984, Holmes and Schultz 1988). High elevation zones in the Rocky Mountain region, where the present study was conducted, are structurally simple relative to forest and lower elevation riparian environments (Finch 1989). The lack of an upper canopy in high elevation riparian zones alleviates many of the arthropod sampling problems that might otherwise be encountered.

The primary objective of this study was to examine availability and selection of arthropods by two species of passerine birds common to montane riparian zones in the Wyoming Rocky Mountains. Based on random encounters, the chance of an abundant food item being con-

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sumed by a bird is greater than it is for a less abundant item. If all items are equally preferred the proportion of a particular item in the diet should reflect its proportional availability. In this paper, we test the hypothesis that all arthropods selected by Wilson's Warblers (*Wilsonia pusilla*), and all arthropods selected by Lincoln's Sparrows (*Melospiza lincolnii*), were equally preferred. These species were selected because, in our study region, they were abundant and obligates of montane riparian zones during the breeding season (Krueger 1985).

We use two terms, abundance and availability, as defined by Johnson (1980). Abundance refers to the quantity of arthropods present in the environment (willow shrubs in this study) whereas availability refers to arthropods accessible to birds. We considered any taxonomic group (i.e., families except in the case of Araneae and Lepidoptera) identified in the diets, regardless of amount, as available to that bird species. The availability of these arthropods in willows was subsequently compared to their use by birds. The term "preference" indicates that proportional use by the bird was greater than proportional availability.

STUDY SITES AND METHODS

We studied food selection by Wilson's Warblers and Lincoln's Sparrows along Pelton and Illinois creeks in the southern portion of Medicine Bow National Forest, Carbon County, Wyoming. Pelton and Illinois creeks are perennial streams located at 2,532 m to 2,623 m elevation that support a continuous riparian zone varying in width from 20 m to over 100 m. Precipitation in this region is primarily in the form of snow and averages 50 cm to 60 cm annually. Spring thaw begins in early May with full leaf-out of willows occurring early in June. Temperatures can fall below freezing throughout June and the first regular freezing temperatures begin again in September.

The riparian zone is defined by willow shrubs averaging 2 m in height interspersed with meadows of sedges (*Carex* spp.), reedgrass (*Calamagrostis* spp.), and hairgrass (*Deschampsia caespitosa*). *Salix geyeriana* is the dominant willow species along with *S. boothii* and *S. wolfii*. The riparian zone is flooded at various times throughout the summer months as water levels fluctuate due to beaver activity. Big sagebrush (*Artemisia tridentata*), Idaho fescue (*Festuca idahoensis*), junegrass (*Koeleria cristata*), and bluebunch wheatgrass (*Agropyron spicatum*) are characteristic of the stream valley slopes. Lodgepole pine (*Pinus contorta*) comprises the dominant forest cover on the upper slopes and ridge tops, with some Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) also present.

Breeding birds arrived at Pelton and Illinois creeks in late May and began establishing territories. Generally nest building did not commence until full leaf-out in early June. Our general observations, and the physiological condition of birds that we collected during 1984 and 1985, indicated that Wilson's Warblers and Lincoln's Sparrows laid eggs in mid-June and hatched young in the first 2 weeks of July.

DATA COLLECTION

We established three avian sampling sites on Pelton Creek and one on Illinois Creek upstream from the confluence with Pelton Creek. Each site was marked with flagging at 50-m intervals for a total length of 1 km and included the entire width of the riparian zone. These sites were generally contiguous and we established them primarily to facilitate systematic searches for foraging birds and to locate randomly selected points for arthropod and vegetation sampling.

Our observations indicated that Wilson's Warblers gleaned insects from leaves and twigs of willows, and rarely foraged on the ground. We also observed that, while often described as ground foragers (Bent 1968), Lincoln's Sparrows regularly foraged in willows during the breeding season on our study sites. Based on these observations, we focused our sampling efforts on measuring availability and use of food resources by birds at willow foraging sites. It was not necessary to consider other shrub types since willows were virtually the only species present.

Birds were collected July through August in 1984 and June through August in 1985 using a shotgun or .22 caliber rifle with bird shot. We began systematic searches of the study sites shortly after dawn and collected birds that were observed to successfully capture and consume at least one prey item. Since we collected only actively foraging birds, collections could be made throughout the day, but most birds were collected during the morning hours when feeding rates were high.

The esophagus and gizzard were removed immediately after a bird was collected and preserved in 80% ethanol to prevent post-mortem digestion of food items. In the laboratory each sample was examined under a dissecting microscope and the arthropods were identified to family when possible. In addition, life stage (i.e., adult, larva), length (to the nearest 1 mm), and number of arthropods were recorded for each sample. The number of arthropods per sample was determined by counting whole individuals and paired parts (e.g., wings of wasps and flies, beetle elytra, spider claws, etc.).

Coincident with the bird collections we sampled willows in which the birds had been foraging for arthropods. Twenty-seven and 35 willows used as foraging sites by Wilson's Warblers were sampled for arthropods in 1984 and 1985, respectively. Twenty-six and 34 willows used as foraging sites by Lincoln's Sparrows were sampled for arthropods in 1984 and 1985, respectively. To examine whether arthropod composition differed among foraging sites and random sites we sampled an additional 37 willows (12 on each of two sites, 13 on one site) in 1984 and 30 willows (10 on each site) in 1985. Willows, for the random samples, were selected using a table of random digits to locate points along a flagged line running the length of the riparian zone. At each point, random digits were used to determine the direction of travel and distance to the random sample location.

Arthropods were collected by placing eight 25- × 25-cm sampling cards under a willow and applying a full-strength pyrethrin-based fogacide (manufactured by United Lab, Inc.) with a hand-held garden sprayer. Southwood et al. (1982), using a similar technique to collect arboreal arthropods in Britain and South Africa, indicated that results were comparable to faunal lists derived collectively from a variety of sampling methods. We conducted field tests that involved sweep netting shrubs following an application of pyrethrin to evaluate whether spraying was more effective on some arthropods than others. Sweep netting did not produce any arthropods that had not been collected by the spray technique. The quick knockdown capacity of pyrethrin allows arthropods to be collected with few losses due to escape behavior. Furthermore, the results are easily quantified by calculating the volume of shrub sprayed, and computational problems (i.e., trying to obtain comparable results) resulting from the use of several different sampling techniques are alleviated. However, there are some restrictions on this technique. In order to apply the pyrethrin effectively, the wind must be calm and the vegetation dry; thus there may be only a short period of time during each day when conditions are favorable.

Following the application of the pyrethrin, arthropods were allowed to drop onto the sampling cards for one-half to three-quarters of an hour. Shaking the shrub prior to retrieving the sampling cards helped to ensure that all possible individuals were collected. Arthropods were removed from the cards and preserved in 80% ethanol. In the laboratory we examined the spray samples using a dissecting microscope and identified arthropods to the family taxonomic level. Araneae (spiders) and Lepidoptera (moths and butterflies) proved difficult to identify to family consistently (except for family Geometridae within the Lepidoptera) and thus were not identified further than order. Terrestrial arthropods were identified following Borrer et al. (1981), while we used Merritt and Cummins (1978) to identify adult aquatic insects. Some identifications were verified by the U.S.D.A. Agricultural Research Service in Beltsville, Maryland. Other identifications were verified by comparing specimens collected to those in the museum collection at the University of Wyoming.

A subsample of individuals from each family, life stage, and size category were dried at 90° for 20 hr and then weighed to the nearest 10^{-4} g using a Mettler H31AR scale. We used mean dry weights to estimate biomass of available arthropods in willows sampled as well as biomass of arthropods consumed by birds.

ANALYSIS

Arthropod abundance. Arthropod abundance was measured as biomass per cubic meter of shrub. Mann-Whitney and Kruskal-Wallis nonparametric tests (BMDP Statistical Software Package, Berkeley, California, 1985) were used to compare abundance between and within years, and among foraging sites and randomly selected willows.

Prey-size selection. The distribution of arthropod sizes available in willows and the distribution of sizes selected by Wilson's Warblers were compared using a Kolmogorov-Smirnov two-sample test (SPSS/PC + V2.0, Base Manual for the IBM PC/XT/AT and PS/2, 1988). Only 1985 data were analyzed due to small sample sizes in 1984. Additionally, we felt that the size of arthropods consumed by Lincoln's Sparrows could

TABLE 1. Percent composition (based on frequency and biomass) of arthropods and seeds identified in Lincoln's Sparrow diets. Arthropods are categorized according to whether they were taken while the birds were foraging in willows or on the ground.

Food and substrate types	1984		1985	
	Frequency	Biomass	Frequency	Biomass
Arthropods				
Willows	54.2	67.6	70.5	61.6
Ground	24.3	26.9	25.7	38.0
Seeds	21.5	5.5	3.8	0.4

not be analyzed because ingestion of grit and subsequent grinding of food items precluded accurate measurements of lengths. Even though arthropod lengths could not be accurately determined, individuals could still be taxonomically identified from various body parts.

Comparison of arthropod availability with arthropod consumption. To determine if birds were selecting arthropods in proportion to their availability in willows we used the analysis program PREFER described by Johnson (1980). By comparing mean ranks of arthropods available with ranks of those consumed, food items were ranked from most to least preferred. Subsequently, PREFER performed pairwise comparisons to test for differences among food items. No inferences were made about avoidance if one food item was preferred over another, only that the second item was less preferred.

Data from both years were used to analyze preference of arthropods by birds. Differences in arthropod abundance between years did not present a problem because PREFER ranks data from paired samples and examines the relationship between availability and use for individual birds at one point in time.

Ten arthropod classifications were used in the analyses and all but two represented orders. The category that we designated "larvae" was comprised of immature Coleoptera, Hymenoptera, and Lepidoptera based on the criterion of similar form and behavior. Likewise, we combined adult Lepidoptera and Trichoptera based on similar daily activity patterns and habitat use.

All food items consumed by Wilson's Warblers were represented in the 10 arthropod categories. Lincoln's Sparrows presented a slightly different situation due to their more generalized foraging behavior, and because this study concentrated on willows as the sample unit. Consequently, we subdivided food items identified in sparrow diets into items consumed while foraging in willows and items consumed while foraging on the ground (Table 1). The distinction between these two categories was based on arthropod-habitat associations and arthropods we identified from spray samples. Thus, for the Lincoln's Sparrow, only food items determined to have been consumed while foraging in willows were included in these analyses.

RESULTS

ARTHROPOD ABUNDANCE

Using the Kruskall-Wallis test, there was no statistical difference in biomass of 12 arthropod groups between warbler foraging sites, sparrow foraging sites, and randomly selected willows within each year. Considering all willows sampled, nine of 12 arthropod groups were statistically more abundant (Mann-Whitney U-test, $P < 0.01$) in 1985 than 1984 (Table 2). Total arthropod biomass was much higher in 1985, 0.15 g/m^3, than in 1984, 0.04 g/m^3 of willow. Part of this difference can be attributed to an outbreak of geometrid larvae (family Geometridae, order Lepidoptera) in 1985, accounting for over one-third of the total biomass collected. Biomass of all lepidopteran larvae collected in 1985 was 11 times greater than that collected in 1984.

To test whether differences in sampling dates between 1984 and 1985 may have been responsible for the apparent differences in biomass, 1985 data were split into three sample periods representing early season (15 June–30 June), mid-season (1 July–17 July), and late season (18 July–21 August). Late season corresponds to the period during which the majority of samples was collected in 1984. There was no significant difference ($P = 0.417$) in total arthropod biomass collected among the three sampling periods in 1985. However, among the 12 arthropod groups four were significantly different in abundance ($P < 0.01$) among the three sample periods (Table 3). Hymenoptera and adult Lepidoptera were more abundant during mid-season and late season. Trichoptera biomass was low early in the season but peaked in mid-season and remained high throughout the summer. Plecoptera biomass was greatest early in the season. These seasonal patterns do not account for the large differences in biomass of arthropods sampled between 1984 and 1985.

TABLE 2. Comparison of mean ranks of invertebrate biomass per shrub volume (10^{-4} g/m^3) between 1984 and 1985 using the Mann-Whitney U-test.

Taxonomic group	Biomass $\bar{x} \pm$ SE 1984 (n = 90)	1985 (n = 99)	P
Araneae	10.6 ± 2.9	29.5 ± 4.5	0.0000
Coleoptera	44.3 ± 6.8	74.6 ± 9.6	0.0003
Diptera	51.9 ± 5.4	131.5 ± 9.93	0.0000
Ephemeroptera	0.7 ± 0.2	1.8 ± 0.4	0.0791
Hemiptera	29.8 ± 3.4	71.3 ± 6.3	0.0000
Homoptera	157.7 ± 12.5	479.5± 41.0	0.0000
Hymenoptera	24.7 ± 2.3	51.9 ± 5.0	0.0000
larvae	89.1 ± 17.2	96.5 ± 12.4	0.3130
Lepidoptera	4.8 ± 0.8	10.0 ± 2.1	0.2281
larvae	68.1 ± 18.9	732.3 ± 129.2	0.0000
Plecoptera	5.3 ± 1.3	18.5 ± 3.9	0.0003
Trichoptera	2.7 ± 1.2	16.5 ± 3.7	0.0000

PREY-SIZE SELECTION

Wilson's Warblers appeared to be selective in sizes of arthropods they consumed. Distribution of sizes of seven out of eight arthropod groups consumed by warblers were significantly different (Kolmogorov-Smirnov two-sample test, $P <$ 0.01) from the distribution of sizes available in willows. Small arthropods, 1 to 3 mm in length, were consistently underrepresented in warbler diets (Fig. 1). Sizes of Ephemeroptera captured by warblers were similar to sizes in the spray samples. Sample sizes for Araneae and adult Lepidoptera and Trichoptera consumed by warblers were not sufficient (<20 individuals) for this particular analysis.

COMPARISON OF ARTHROPOD AVAILABILITY WITH ARTHROPOD CONSUMPTION

Fifty-three and 54 families of arthropods (excluding the Araneae, most of the Lepidoptera, and miscellaneous orders such as Collembola and Psocoptera) were identified in Wilson's Warbler and Lincoln's Sparrow diets, respectively, over the 2-year study period. We identified a total of 115 families in the spray samples. All families of arthropods identified in warbler and sparrow diets (excluding ground-dwelling arthropods found in Lincoln's Sparrow diets) were found in the spray samples.

Using program PREFER, we rejected the hy-

TABLE 3. Comparison of mean ranks of invertebrate biomass per shrub volume (10^{-4} g/m^3) between three sampling periods during 1985 using the Kruskal-Wallis test. Sample sizes are in parentheses.

Taxonomic group	Biomass $\bar{x} \pm$ SE 15–30 June (30)	1–17 July (43)	18July–21 Aug (26)	P
Araneae	29.6 ± 7.3	30.0 ± 8.1	28.7 ± 6.4	0.9424
Coleoptera	55.9 ± 12.4	100.2 ± 17.7	53.8 ± 14.7	0.1056
Diptera	153.0 ± 21.3	138.3 ± 13.4	95.6 ± 10.8	0.0630
Ephemeroptera	2.2 ± 0.8	1.8 ± 0.6	1.5 ± 0.7	0.8315
Hemiptera	51.8 ± 7.7	69.2 ± 8.7	97.2 ± 15.9	0.1509
Homoptera	410.5 ± 59.0	527.5 ± 75.3	479.7 ± 66.2	0.6455
Hymenoptera	32.0 ± 5.9	60.8 ± 7.7	60.0 ± 11.9	0.0053
larvae	97.0 ± 25.5	100.8 ± 20.3	88.7 ± 16.2	0.6302
Lepidoptera	4.2 ± 1.4	11.8 ± 4.2	13.7 ± 3.0	0.0024
larvae	332.4 ± 45.3	697.1 ± 187.1	1,251.9 ± 362.0	0.7340
Plecoptera	34.0 ± 10.2	11.8 ± 3.7	11.7 ± 5.5	0.0015
Trichoptera	3.6 ± 2.4	26.1 ± 6.8	15.6 ± 7.6	0.0007
Total biomass	1,210.2 ± 94.6	1,785.9 ± 260.0	2,221.8 ± 408.8	0.4170

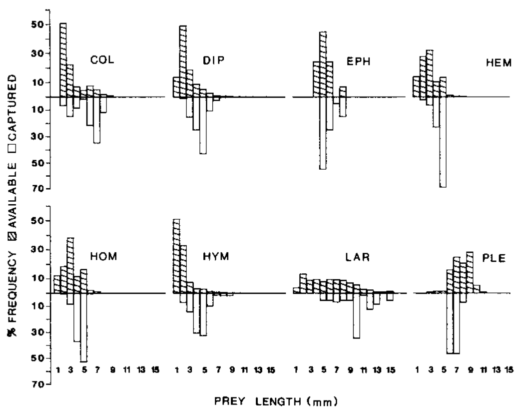

FIGURE 1. Distribution of prey lengths for eight arthropod groups identified in spray samples (available) compared with those captured by Wilson's Warblers. Arthropod group abbreviations are as follows: COL—Coleoptera, DIP—Diptera, EPH—Ephemeroptera, HEM—Hemiptera, HOM—Homoptera, HYM—Hymenoptera, LAR—all larvae, PLE—Plecoptera.

pothesis that all food items were equally preferred ($P < 0.0005$) for Wilson's Warblers (Table 4). Coleoptera were ranked most preferred whereas Homoptera were ranked least preferred. Based on the mean difference in ranks, proportional use of Coleoptera, Ephemeroptera, Plecoptera, Diptera, and Hymenoptera by Wilson's Warblers was greater than proportional availability. As a group these orders of insects were preferred over Araneae, larvae, and Homoptera (Fig. 2). Within these groups no clear distinctions could be made about preferences. The same pattern of preference resulted when we analyzed the 1985 data separately. Data from 1984 could not be analyzed alone due to the small sample size.

Likewise, we rejected the hypothesis that all food items were equally preferred for Lincoln's Sparrows (Table 5). Preference among the 10 arthropod groups was statistically different ($P < 0.0005$). Coleoptera were preferred over all other groups (Fig. 3). In contrast to the pattern for Wilson's Warblers, larvae were ranked high in preference while Ephemeroptera and Plecoptera were ranked low. The pattern of preference was the same for 1985 data alone.

TABLE 4. Ranking of arthropod food groups for Wilson's Warblers during the breeding seasons of 1984–1985 ($n = 40$). Groups are arranged from most to least preferred. Preference among groups was statistically different, $F(9, 30) = 16.881$, $P < 0.0005$.

Rank	Food group	Mean difference in ranks*
1	Coleoptera	−1.4615
2	Ephemeroptera	−1.3333
3	Plecoptera	−1.6667
4	Diptera	−0.9744
5	Hymenoptera	−0.4231
6	Hemiptera	0.2308
7	Trichoptera–Lepidoptera	0.4359
8	Araneae	0.6154
9	Larvae	1.5256
10	Homoptera	2.5513

* Difference in ranks between availability and use. A negative value indicates proportional use was greater than proportional availability, and vice versa for a positive value.

DISCUSSION

ARTHROPOD ABUNDANCE

Holmes and Schultz (1988) demonstrated that abundances of lepidopteran larvae, in a New Hampshire forest, differed among tree species, and birds directed foraging attacks differentially among tree species. We did not detect significant differences in arthropod composition and abundance between foraging sites and randomly selected willows. Shrub diversity within the riparian zone was low and all were species of *Salix.* Therefore, specific arthropod-shrub associations are likely to be similar for all shrubs, and gross cues that might exist for a bird (i.e., the choice between a willow and another shrub type) were not present. In addition, on a small (per shrub) scale, arthropod distributions were highly variable within the sampled habitat. This is supported by the large standard errors of the spray samples (Table 2). However, on a large scale (the riparian zone) arthropod biomass was relatively stable during the breeding season (i.e., overall there were no significant differences in abundance and composition of arthropods between early, mid-, and late season samples).

PREY-SIZE SELECTION

According to the optimal foraging theory, predators should select more profitable prey items, where profitability is a measure of net energy gain per unit handling time (Krebs 1978). Wilson's Warblers in our study area were selecting more profitable prey items by capturing disproportionate numbers of larger prey relative to availability, whereas few of the more abundant smaller (<3 mm) prey were captured. Warblers also exhibited an upper size limit of plecopteran prey

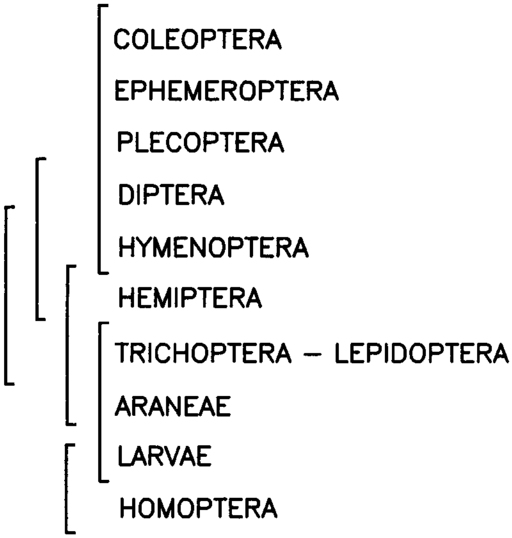

FIGURE 2. Food preferences for Wilson's Warblers during the breeding seasons of 1984 and 1985. Food groups within the same bracket were statistically similar ($P > 0.05$). Groups are arranged from most to least preferred.

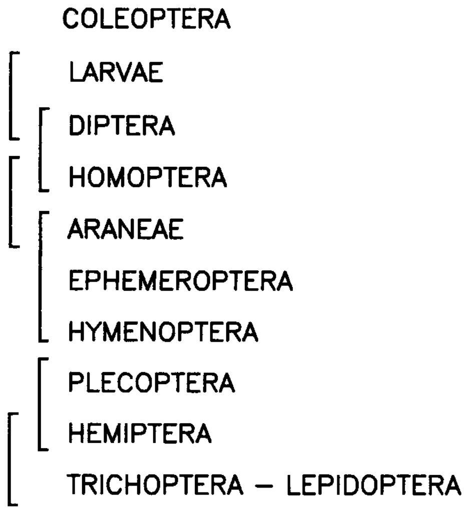

FIGURE 3. Food preferences for Lincoln's Sparrows during the breeding seasons of 1984 and 1985. Food groups within the same bracket were statistically similar ($P > 0.05$). Groups are arranged from most to least preferred.

captured. Plecoptera larger than 7 mm were noticeably underrepresented in warbler diets even though larger Plecoptera were more abundant than most of the smaller size classes. In contrast, there was no apparent upper size limit of larvae captured by warblers. Perhaps the handling time required for larger Plecoptera is disproportionate to the food value, whereas in comparison, the handling time required to subdue and consume a nonflying soft-bodied larva is much less. Davies (1977) observed that adult Spotted Flycatchers (*Muscicapa striata*) captured fewer very small and very large flies, and hypothesized that handling times were disproportionately long for the very large flies. Quinney and Ankney (1985) reported that Tree Swallows (*Tachycineta bicolor*), while not rejecting small insects, selected larger and thus more profitable prey.

AVAILABILITY VS. CONSUMPTION OF ARTHROPODS

By comparing arthropod availability with use, we rejected the hypothesis that all foods were equally preferred for the two bird species studied. However, even though certain arthropod groups were ranked low in preference, we do not imply that these groups were not important in bird diets. The order Homoptera was ranked least preferred for warblers but the family Cicadellidae (leafhoppers) comprised 16% of the diet. Similarly the "larvae" group ranked low in preference but comprised over 30% of warbler diets. What these data do indicate is that consumption was less than expected based on random encounters; likewise for arthropods that were ranked high in preference, consumption was greater than expected.

Cantharidae (soldier beetles) represented a large

TABLE 5. Ranking of arthropod food groups for Lincoln's Sparrows during the breeding seasons of 1984–1985 ($n = 49$). Groups are arranged from most to least preferred. Preference among groups was statistically different, $F(9, 40) = 29.321$, $P < 0.0005$.

Rank	Food group	Mean difference in ranks*
1	Coleoptera	−5.3673
2	Larvae	−2.6939
3	Diptera	−1.6224
4	Homoptera	−1.0816
5	Araneae	−0.1837
6	Ephemeroptera	−0.0204
7	Hymenoptera	0.0918
8	Plecoptera	2.8673
9	Hemiptera	3.6531
10	Trichoptera–Lepidoptera	4.3571

* Difference in ranks between availability and use. A negative value indicates that proportional use was greater than proportional availability, and vice versa for a positive value.

proportion of Coleoptera consumed by both warblers and sparrows. These are soft-elytra beetles, relatively large (7 mm) with noncryptic coloration. In addition, they are slow fliers and tend to crawl rather than fly from disturbances, thus are probably very susceptible to predation by birds.

Arthropods that were ranked high in preference for warblers were noncryptic and patchy in distribution, while sparrows selected more cryptic and more uniformly distributed prey. Adult Ephemeroptera (mayflies) and Plecoptera (stoneflies) emerged from streams in large numbers and swarmed around nearby vegetation. Their distribution was very unpredictable; in some cases a hatching occurred and disappeared in 1 or 2 days. Actively flying insects like Diptera (flies) and Hymenoptera (wasps) were abundant in willows and sluggish in the cool morning hours when foraging activity by birds was high. Wilson's Warblers are active searchers that primarily glean arthropods from foliage but will frequently take prey while hovering, or leave a perch to catch flying prey items, i.e., hawking (Bent 1963, Eckhardt 1979). From our observations, warblers spent much less time foraging in any one shrub than sparrows. Eckhardt (1979) described Wilson's Warblers as having high velocity and search intensities, meaning a large number of perches were visited per unit time and per foraging attack. Lizards that use wide ranging (active) foraging behavior capture more unpredictably distributed and patchy prey than lizards exhibiting sit-and-wait foraging behavior (Huey and Pianka 1981). Thus, it may be possible that warblers on our study area cover more territory (i.e., more perches and shrubs) than sparrows, and encounter patchy prey, such as Ephemeroptera and Plecoptera, more frequently. Actively flying prey, or prey that fly in response to disturbances, should be more accessible to warblers, which have the ability to hawk for prey, than to sparrows.

The two arthropod groups ranked as least preferred for warblers (larvae and Homoptera) exhibit antipredator traits. For instance, brown geometrid larvae are cryptic, those with a striped pattern are found on willow branches and twigs while green larvae and leafhoppers use green leaves as foraging and resting substrates. Additionally, leafhoppers respond to disturbances with very quick and erratic jumps. Crypsis in geometrid larvae has been demonstrated to affect their availability as prey to insectivorous birds (Mariath 1982). Holmes and Schultz (1988) observed that lepidopteran larvae that closely matched their resting substrates (specifically twigs and petioles) were underutilized by birds. Thus, it appears that while larvae and Homoptera were relatively abundant on our study area, and in terms of biomass were an important component in warbler diets, their availability as a food resource for warblers is reduced due to cryptic coloration in concert with substrate choice and escape behavior. In contrast, sparrows exhibit a much slower foraging mode than warblers, and it has been proposed that birds with slower foraging rates search substrates more thoroughly and capture more cryptic prey items (Robinson and Holmes 1982).

Of the dipterans consumed by sparrows approximately 53% were Tipulidae (crane flies). Crane flies are slow fliers, and tend to be in the interior and lower portions of the shrubs where sparrows frequently forage. Numerous crane flies were also present in the sedge-grass meadows, and an alternative scenario is that sparrows were picking up crane flies in the meadows in addition to those in willows. If this was the case then perhaps proportional use of Diptera by sparrows was overestimated. However, we do not believe that this would markedly affect the overall patterns of preference observed for sparrows in this study. Johnson (1980) demonstrated that PREFER provided comparable results between remaining items when doubtful items were included or excluded in the analysis. Furthermore, by employing ranks of use and availability, PREFER is robust when measurements are not exact.

While many studies of western riparian avian communities have concentrated on habitat use and structure (e.g., Carothers et al. 1974, Anderson and Ohmart 1977, Knopf 1985, Knopf et al. 1988, Finch 1989), this study provides an initial insight into availability and consumption of arthropod food resources by birds during the breeding season. Published information on the food habits of the Lincoln's Sparrow is scarce (Judd 1901), and though there have been detailed studies on the foraging behavior of the Wilson's Warbler (Stewart 1973; Hutto 1981a, 1981b; Morrison 1981) there has been little work on diet composition.

We have demonstrated that, on our study sites, Lincoln's Sparrows and Wilson's Warblers were selecting arthropod prey disproportionate to availability, and the two species preferred different prey items. Sherry (1984) explained the variation in bird diets based on the response of birds to such characteristics as arthropod conspicuousness, distribution, antipredator behavior, and substrate (e.g., air, vegetation, bark). The type and abundance of prey, bird morphology and behavior, and foliage structure are three factors proposed by Holmes and Schultz (1988) that determine the kinds of food resources that will be available to birds. All arthropods consumed by birds are available but different degrees of availability will exist depending on the foraging behavior of the bird and the behavior, morphology, and distribution of their arthropod prey. These characteristics of both the predator and prey explain the food preference patterns detected in our study.

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