

## DIET OF NESTLING WINTER WRENS IN RELATIONSHIP TO FOOD AVAILABILITY<sup>1</sup>

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**Abstract.** We identified major arthropod taxa in the feces of nestling Winter Wrens (*Troglodytes troglodytes*) and quantified their number, size, and biomass. These data were compared with samples of arthropods obtained from habitats and microhabitats that were typical of breeding territories. Larval Lepidoptera on shrubs in the clearcut were more numerous and had a higher biomass than those on shrubs in forested areas. Total arthropod biomass, the biomass of Coleoptera, and numbers of Araneae on *Vaccinium* shrubs were higher in the forest. On the ground, numbers and biomass of most taxa were higher in the clearcut than in the forest. Coleoptera and Araneae were fed to nestlings in high proportions relative to their proportionate numbers and biomass in the environmental samples.

**Key words:** *Fecal analysis; Troglodytes troglodytes; arthropod; food availability; nestlings; diet.*

### INTRODUCTION

Male Winter Wrens (*Troglodytes troglodytes*) in the spruce-hemlock (*Tsuga heterophylla*-*Picea sitchensis*) forests of coastal Oregon defend distinct breeding territories in both clearcut-logged areas containing large amounts of logging slash (not those that have been burned), and in mature forests. Territories are used for both nesting and feeding. Some individuals are polygynous and males usually help to feed nestlings on their territories. Frequencies of visits to the nest are similar for males and females. Adults forage on virtually any substrate within about 3 m of the ground, including shrubs, logs, and the ground itself. They do not hawk for flying insects. Young hatch simultaneously and remain in the nest for an average of 15.5 days ( $n = 12$ ) on our study area. In Great Britain polygyny is common (Armstrong 1955; Garson 1978, 1980), and males do not help to feed the young in the nest. Perhaps because food density is lower than in the areas studied in Great Britain, assistance of both parents in feeding young may be required for successful nesting in coastal Oregon. If food availability on the male territory influences nesting success, then knowledge of the relationship between nestling diets and food availability is crit-

ical to understanding among-male variations in habitat use, mating success, and nesting success.

In this study we address the following questions: (1) Are there differences in the size and composition of the prey base in different habitats and microhabitats on coastal Oregon Winter Wren territories? (2) Are certain arthropod types preferred as food for nestlings? If so, do these preferences change with the age of nestlings? (3) Is there evidence that changes in prey availability influence diet composition?

Workers have taken two approaches in the study of foraging in free-living insectivorous passerines. They either observed foraging behavior, recording microhabitats used for foraging, and/or food being brought to nestlings, or they looked more directly at items consumed by examining gut contents, esophageal samples, or fecal material and then used samples of the prey base to interpret their findings. The former approach provides larger sample sizes but may be biased against certain prey and microhabitat types (e.g., smaller prey, microhabitats in which birds are difficult to see). We took the latter approach.

### METHODS

Van Horne studied Winter Wrens during the breeding seasons (March-June) of 1983-1985 in the Cascade Head Experimental Forest at Otis, Oregon. Part of the study area had been clearcut-logged 2 years previously and the remainder was

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in mature, multistoried spruce-hemlock forest. Males were color-banded and courtship, nesting, and territorial activity were monitored daily. Territories were mapped as minimum polygons enclosing singing perches using a 50-m grid over the entire area in combination with topographic features. Males sang frequently from prominent perches on their territories during the several-week period prior to hatching, so there was little ambiguity regarding the location of territory boundaries.

Two methods were used to sample arthropods in the environment. Pitfall traps, consisting of two 8.5-cm diameter plastic cups filled with 50% ethanol, were sunk to their rims at the ends of a 1-m piece of 10-cm high metal flashing set into the ground. The traps were covered by small roofs made of flashing. Ten pitfall traps spaced at 10-m intervals were placed in transects approximately 100 m apart perpendicular to a stream that ran through the study area, as we suspected that the prey base might vary with distance from the stream. Three transects were placed in logged and three in forested habitat. Traps were set for two consecutive days at approximately 2-week intervals for 6 weeks during the 1984 and 1985 breeding seasons. Samples were stored in 70% alcohol.

The second method of arthropod sampling consisted of beating shrubs over a 1-m<sup>2</sup> stretched canvas tarp. Arthropods that fell onto the tarp were placed in 70% alcohol. Arthropods were collected from 10 shrubs for each sample, and three samples were collected from each of the two most common shrub species, *Rubus spectabilis* and *Vaccinium alaskensis*, as we wished to know whether one of the two dominant shrub species was associated with a larger prey base, so that the type of shrub coverage on a male territory could provide insights into the availability of nestling food on that territory. Samples were also collected at each of three distances (near, 0–5 m; medium, 6–30 m; and far, >31 m) from the nearest stream in both forested and clearcut habitats. Three collections were made about 2 weeks apart in May and June 1984 and two collections were made in May 1985.

Individuals in each type of sample were identified to order (to family for coleopterans and some other taxa) and their total body length was measured. We used a reference collection, developed from both the ground and shrub samples, to identify fecal fragments. We developed

significant regression models ( $P < 0.001$ ) of predicted body length from the size of various body parts for the common orders of arthropods.

Both male and female Winter Wren parents removed mucoid fecal sacs, each with one fecal pellet, from the anuses of nestlings after they were 6–7 days old. These sacs were then deposited on bare branches 10–20 m from the nest. We did not observe any sacs being dropped. Fecal sacs were collected from such branches daily and stored in 70% alcohol. Not all fecal sacs were found, nor did we attempt to analyze all possible fecal pellets. Nestling age, date, distance of the nest from the nearest stream, and habitat of the parental territory (logged, forest, or edge) were recorded. In the laboratory, each fecal pellet was teased apart and pieces of arthropods identified (usually to order and specified as adult or larvae; Calver and Wooller 1982, Ralph et al. 1985, Moreby 1988), and their maximum length measured with an ocular micrometer. Within a fecal pellet the minimum number of arthropods was estimated by assuming that potentially paired body parts differing by more than 1 mm in length were from different individuals. Measurements of fecal arthropod parts along with the body size regressions were used to predict total body length. Where two parts could be from the same arthropod (i.e., an Araneae fang and chelicera) we used the regression with the narrower 95% confidence interval to predict body size. In addition to the fecal samples, two samples representing the gut contents of five nestlings each were collected from nests that failed in the first 1–2 days of nesting. These samples were treated and analyzed in a manner consistent with the analysis of the fecal samples, and produced two samples from nestlings too young to produce fecal sacs deposited by parents. It is possible that there were soft-bodied arthropods that were not detected by these methods, although all the arthropod types we saw in parental bills during nest observations were also found in the fecal samples.

Analyses were conducted using both numbers of individuals and biomass of each taxon (biomass predicted from size information using general regressions developed by Rodgers et al. 1976) in environmental and fecal samples. The minimum number of arthropods in each taxon and their predicted sizes were combined for feces or guts collected from the same nest and date and expressed as numeric or biomass proportions of the total sample for the analyses of effects. Thus

TABLE 1. Classes of effects tested and significant effects on numbers and biomass of arthropods in shrub and ground samples. Where there were significant interactions between habitat and other effects, tests were run within habitat and other effect classes. Classes within which the effects were significant are listed in parentheses. Biomass of "other" category not listed (see Methods). \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

Classes	Habitat Clearcut (C) Forest (F)	Stream* Near (N) Middle (M) Far (Z)	Date Early May (EM) Late May (LM) Early June (EJ)	Shrub species <i>Vaccinium alaskensis</i> (V) <i>Rubus spectabilis</i> (R)
<b>ANOVA results</b>				
<b>Shrub samples</b>				
<b>Number</b>				
Araneae	*F > C(V)		*LM > EM, EJ	*V > R (C)
Coleoptera			**EM, EJ > LM	
Lepidoptera larvae	**C > F	*N > M, Z		
Diptera			**EJ > EM, LM	
Other <sup>b</sup>				***V > R
Total number				
<b>Biomass</b>				
Araneae				
Coleoptera	**F > C			
Lepidoptera larvae	**C > F	*N > M, Z		
Diptera				
Total biomass	*F > C			
<b>Pitfall samples</b>				
<b>Number</b>				
Araneae	***C > F			
Coleoptera	***C > F		***EM, LM > EJ (C)	
Lepidoptera larvae				
Diptera	***C > F			
Other	**C > F			
Total number	***C > F	*N > Z (F) ***Z > N (C)		
<b>Biomass</b>				
Araneae	***C > F			
Coleoptera	***C > F (EM, LM)		**EM > LM, EJ (C)	
Lepidoptera larvae				
Diptera				
Total biomass	***C > F (EM, LM) **C > F (EJ)			

\* Stream classes used for shrub samples only. Stream distance was a continuous variable in the ground sample models. For ground models, N > Z means decrease with distance from stream, Z > N means increase with distance from stream.  
<sup>b</sup> Includes Chilopoda, Ephemeroptera, Hemiptera, Homoptera, Hymenoptera, Orthoptera, Plecoptera, Coleoptera larvae, Diptera larvae, Mecoptera, Maltophagia, Microcoryphera, Psocoptera, Neuroptera.

the original 102 feces/gut samples were consolidated into 39 samples.

Information on sizes and taxa of arthropods consumed by nestlings was used to remove arthropods apparently not used by the birds from the environmental samples prior to analysis. The maximum prey size predicted by the regressions in the diets was 28 mm for Lepidoptera larvae and 20 mm for other prey; larger individuals and those from taxa not found in the diets were therefore removed from the environmental data sets.

Individuals removed were diplopods, carabids (Coleoptera), collembolans, and crustaceans. It is possible that Collembola were consumed, but because their bodies are entirely soft they did not leave recognizable fragments in the feces. Guinan and Sealy (1987) did not find Collembola in stomachs of House Wrens (*T. aedon*) despite their high abundance in the environment.

Taxa in the environmental samples were lumped into the 22 more general categories used in categorizing the fecal samples (Table 1 in-

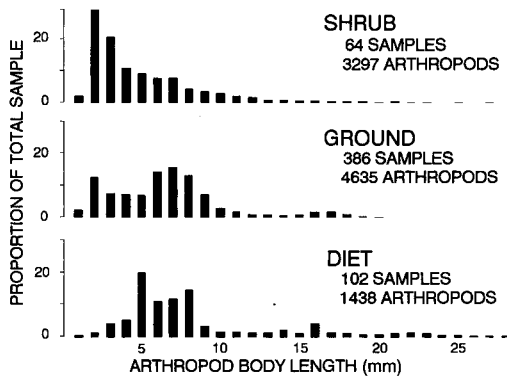


FIGURE 1. Size distributions of arthropods from shrub samples, ground samples, and diet (nestling feces).

cluding footnote "b"). Araneae, Coleoptera adults, Diptera adults, and Lepidoptera larvae were sufficiently common in the diet and environment so that the effects of habitat, distance from the nearest stream, Julian date, and shrub type (shrub samples only), and the interactions between habitat and each of the other effects could be tested with analysis of variance procedures (SAS). When interactions were significant ( $P < 0.05$ ), tests were repeated within classes of the effects involved in the interactions. Least squares means were used to interpret pairwise differences.

We used an approach that employs the difference between rank availability and rank usage to provide relative ranking of food preference among the categories considered (Johnson 1980). (The term "preference" is used in the operational sense to connote nonrandom use, and is not meant to imply active choice.) This approach is relatively insensitive to the inclusion or exclusion of seldom-used foods. Shrub and ground samples were used to calculate numeric- and biomass-based rank indices of availabilities of the four most common arthropod taxa, as well as the remaining taxa collapsed into the category "other." These categories were used so that interpretations could remain consistent with the results of the ANOVAs, and so that the number of samples would remain high relative to the number of taxon categories, producing a more robust analysis.

The environmental sample taken at the date closest to the date on which the fecal sample in the same habitat was taken was used to determine rank availability; in no cases were the environmental samples taken more than 10 days

before or after any of the comparison fecal samples. Diet samples for 1983 were omitted as there were no environmental samples taken that year. Only diet samples from nests in territories completely within the clearcut area or completely within the forested area were used for the analysis of preferences; edge nests were omitted. These restrictions greatly reduced sample size but produced a relatively stable result. We attempted general summary analyses averaging all environmental and diet samples using both rank and proportionate information, but these gave preferences very different than those we will present, probably because there was so much change in diet and availability among dates and years that the averaged information was unstable with regard to inclusion or exclusion of environmental samples, and irrelevant to what went on at any given time.

## RESULTS

### PREY SIZE

Do the size distributions of prey fed to nestlings differ from the size distributions in the environment, within the sizes of prey normally fed to nestlings? The overall size-frequency distributions of arthropods in the samples differed between the ground (pitfall) and diet samples [ $G$ -statistic for replicated goodness-of-fit tests (Sokal and Rohlf 1981),  $G_H = 1,158$ ,  $\chi^2_{0.005,28} = 51$ ] and between shrub (beating) and diet samples ( $G_H = 328$ ,  $\chi^2_{0.005,28} = 51$ ; Fig. 1). It appears that birds were selecting few prey less than 4 mm, more prey in the 4–5 mm size range, and more prey in the 13–28 mm size range in comparison to what was available in the ground and shrub samples. Prey in the 4–8 mm size range were the most common in the nestling diets.

### ENVIRONMENTAL SAMPLES

How much variation is there among the environmental samples, and how can this variation be explained? Understanding what drives the variation will be necessary to understanding differences in the availability of food for nestlings among male territories, and can be used to suggest further experimental work in this system.

The most obvious (to humans) difference in environment was that between the clearcut and logged habitat. The shrub samples indicated a higher biomass of Coleoptera and a higher total arthropod biomass on shrubs in the forest than

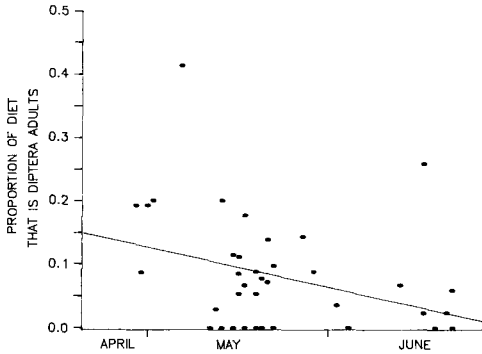


FIGURE 2. Proportion of Diptera adults (numbers) in the diet plotted against the Julian date of the sample.

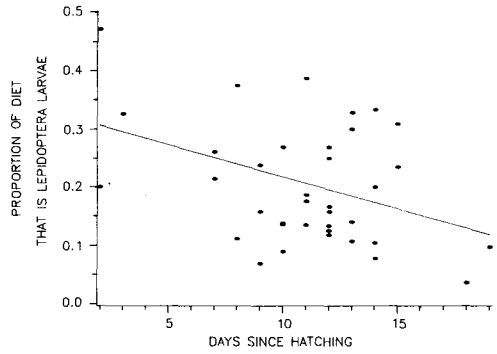


FIGURE 4. Proportion of Lepidoptera larvae (numbers) in the diet, plotted against days since hatching.

in the clearcut (Table 1). Numbers of Araneae were also higher in the forest than in the clearcut on *V. alaskensis* but not on *R. spectabilis*. The numbers and biomass of the Lepidoptera larvae on shrubs were higher in the clearcut habitat. Pitfall samples indicated higher numbers of Araneae, Coleoptera, Diptera, other arthropods, and total arthropods, and higher biomass of Araneae and all arthropods in the clearcut than in the forest (Table 1).

One might expect that the arthropod prey base would be increased near permanent streams because of an increase in emergent aquatics as well as larger foliage volume for foliage feeders. Indeed, numbers and biomass of Lepidoptera larvae on shrubs were higher near streams (Table 1). Total numbers of arthropods on the ground, however, increased with distance from the stream in the clearcut ( $R^2 = 0.06$ ,  $n = 181$ ) although they decreased with distance from the stream in the forest ( $R^2 = 0.03$ ,  $n = 181$ ).

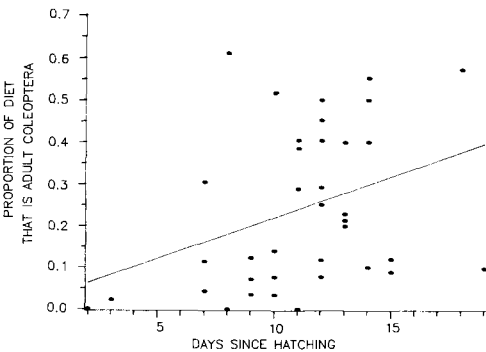


FIGURE 3. Proportion of Coleoptera larvae (numbers) in the diet plotted against days since hatching.

It would be of interest to know whether the prey base changed greatly over the 6-week period of sampling, as this would affect availability of prey for early as compared to later nests. Numbers of Araneae were highest in late May and numbers of Diptera on shrubs were highest in early June. Numbers of Coleoptera on shrubs were lowest in late May, while numbers and biomass of those sampled by pitfalls in the clearcut were higher in the early and middle (May) than in the late (June) samples ( $P < 0.001$ ).

Numbers of Araneae were higher on *V. alaskensis* than on *R. spectabilis* in the clearcut. Other arthropods (comprised primarily of Homoptera, Hymenoptera, and Plecoptera) were higher on *V. alaskensis* than on *R. spectabilis*.

DIET SAMPLES

What factors could be used to predict nestling diets? There were no significant effects of differences in habitat, age of nestlings, or Julian date on the biomass proportions of arthropods in the diet. Proportionate numbers of Coleoptera, however, were higher for nestlings whose parents foraged in the clearcut than for those whose parents foraged at the edge or within the forest. Proportionately fewer Lepidoptera larvae were fed to nestlings by adults that foraged in the clearcut compared with those that foraged at the edge or in the forest ( $P < 0.001$  for each pairwise comparison). Proportionate numbers of Diptera decreased with Julian date ( $R^2 = 0.11$ ,  $n = 38$ ,  $P < 0.05$ ; Fig. 2). Proportionate numbers of Coleoptera increased with nestling age ( $R^2 = 0.14$ ,  $P < 0.05$ ; Fig. 3), whereas proportionate numbers of Lepidoptera larvae decreased with age ( $R^2 = 0.15$ ,  $P < 0.05$ ; Fig. 4).

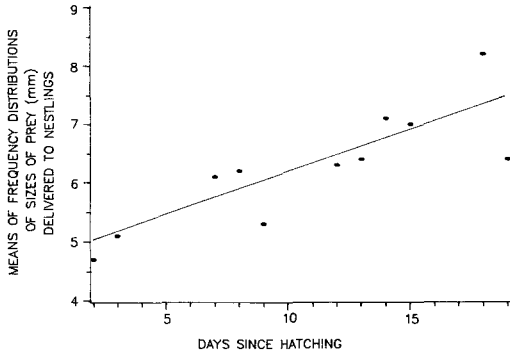


FIGURE 5. Mean length of arthropods fed to nestlings plotted against days since hatching.

The mean sizes of arthropods fed to nestlings increased with age of nestlings ( $R^2 = 0.61$ ,  $n = 11$ ,  $P < 0.01$ ; Fig. 5). The means were calculated from all arthropods fed to nestlings of a certain age, so that the  $n$ 's used to calculate the means averaged 120 and ranged from 24 to 240.

FOOD PREFERENCE

Despite the differences in diets and arthropod availability between the habitats, prey preferences were remarkably consistent among habitats (Table 2). In the shrub samples, Araneae were ranked highest except when diets were compared to ranked biomass availability in the clearcut. Coleoptera were consistently first- or second-ranked. "Other" taxa (mostly Homoptera, Hymenoptera, and Ephemeroptera) ranked in the middle, while Diptera and Lepidoptera larvae were consistently ranked as less preferred. This low ranking of the latter taxa was even true when the ground samples (in which they were likely to be underrepresented) were used to calculate preferences. Rankings based on ground samples were generally consistent with those based on shrub samples. It should be emphasized, however, that Coleoptera, Araneae, Diptera, and Lepidoptera were the most commonly consumed foods in terms of both numbers and biomass among the 22 taxa identified in the fecal samples; the preferences merely establish an ordering among these commonly used foods.

If preference rankings are consistent, the proportions of the major arthropod taxa in the diet and the environment in that time period should be positively correlated. No such correlation was found, indicating that the relationship between preference and abundance of arthropods in the

TABLE 2. Preferences for arthropod taxa. A = Araneae, C = adult Coleoptera, D = adult Diptera, L = Lepidoptera larvae, O = other taxa (see footnote Table 1). Taxa are ordered by decreasing preference from left to right. Those taxa not significantly ( $P < 0.05$ ) different from one another are underlined.  $n = 11$  and 7 for combined fecal samples for clearcut and forest samples, respectively.

Shrub	Ground
Number	
Clearcut	
<u>A C O L D</u>	<u>C A O L D</u>
Forest	
<u>A C O L D</u>	<u>O A C L D</u>
Biomass	
Clearcut	
<u>C O A D L</u>	<u>C A O L D</u>
Forest	
<u>A C O L D</u>	<u>A C O L D</u>

environment is complex, possibly involving maximum or minimum thresholds for certain prey.

DISCUSSION

Understanding the relationship between nestling diets and food availability may provide insights into the foraging behavior of birds and their choice of territory or habitat occupancy patterns. Sampling the prey base of insectivorous birds is difficult, however. It is unlikely that any single method is adequate (Norment 1987). Our sampling methods provide two relative indices of prey availability, and represent the microhabitats in which the birds were most commonly observed foraging.

Producing successful offspring depends in part on the parent's ability to provide nestlings with adequate food. Thus, strong selection should favor efficient foraging by parents during the nestling phase. The optimal foraging approach taken by Charnov (1976) is framed in terms of the ratio of energy to hunting time ( $E/T_{hn}$ ), and predicts that above a threshold density of large prey, animals should stop taking small prey and concentrate on the more profitable larger prey, as long as larger prey are at least equivalent nutritionally. Consistent with predictions of optimal foraging theory, Winter Wrens selected a higher frequency of larger prey than was randomly available (Fig. 1). In Great Tits (*Parus major*), adults bring in

larger prey as the young mature, possibly as a result of a greater ability of older nestlings to handle large prey (Royama 1970). We observed this pattern in the Winter Wren as well.

Samples obtained by beating shrubs in the forest contained a larger number of prey than those in the clearcut area. The reverse was true for the ground samples. Because the birds forage both on shrubs and in the slash and litter on the ground it is difficult to generalize about which habitat supports a larger prey base.

The pitfalls sampled more Coleoptera among the slash in the clearcut than on the mossy floor of the forest, and this difference was reflected in the diets of nestlings in these two habitats. Lepidoptera larvae on shrubs also showed a higher biomass in the clearcut than in the forest, and the larvae were more numerous near streams. Perhaps high foliage volumes of deciduous shrubs such as *R. spectabilis* and *V. alaskensis* in light and moist areas can explain this result.

Given the extent of significant differences between habitats in the numbers and biomass of taxa in the environment and in the diet, it is remarkable that prey preference values remained relatively constant between habitats. This indicates that major dietary shifts that do not show a simple correlation with changes in availability may lead to relatively constant patterns of ranked preference in the presence of considerable resource difference and fluctuation. One of us (Van Horne) spent many hours watching parents bring food to nests, and it is likely that if we had used direct observations of food being brought to nestlings we would have identified Lepidoptera larvae as the most preferred food, as this was consistently the most obvious food item carried by the adults.

Parents feeding young birds must increase their feeding rate as the young approach the age of fledging. The pressure to increase the feeding rate may have the same effect as a change in the hunger state (*sensu* Charnov 1976) of the foragers, leading them to be less selective. Royama (1970) found that spiders, a preferred food of Great Tits, formed a lower proportion of the diet of older nestlings, indicating that selectivity may decrease as the feeding rate increases. The increase in the proportion of Coleoptera with nestling age and concurrent decrease in the proportion of Lepidoptera could reflect either a higher selectivity early in the nestling period when trips to the nest are much less frequent (if Lepidoptera

larvae are indeed a highly preferred food) or differences in the digestive physiology of the nestlings that make it more difficult for them to consume the more heavily sclerotized Coleoptera early in the nestling period. Biermann and Sealy (1982) also found that the proportion of geometrid larvae in diets of very young Yellow Warblers (*Dendroica petechia*) was higher than that in older nestlings. In contrast, Meunier and Bédard (1984) determined that the proportion of Lepidoptera and Diptera increased with age in nestling Savannah Sparrows (*Passerculus sandwichensis*), while the proportion of Homoptera decreased.

## CONCLUSIONS

The microhabitat of Winter Wrens is an important determinant of the type and quantity of arthropod food available. There are differences in nestling consumption patterns associated with major habitat differences. Ranked preferences remain fairly constant across habitats, but the relationship between actual consumption and availability is complex. Among the four taxa most commonly fed to nestlings, Araneae and adult Coleoptera appear to be preferred over Lepidoptera larvae and adult Diptera. Size and taxa of prey fed to nestlings change with nestling age.

Identification of arthropod fragments in bird feces is a useful and nondestructive method for looking at relative differences in diet composition. In identifying preferences, it is important to use environmental samples temporally keyed to diet samples.

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