

VEGETATION, GROUND, AND FRUGIVOROUS FORAGING OF THE AMERICAN ROBIN

CYNTHIA A. PASZKOWSKI

Laboratory of Limnology, University of Wisconsin, Madison, Wisconsin 53706 USA

ABSTRACT.—American Robins (*Turdus migratorius*) were observed foraging for foliage invertebrates, terrestrial invertebrates, and *Amelanchier* fruits in a northern Wisconsin forest. Lengths of feeding and nonfeeding moves, move frequencies, and feeding frequencies were analyzed in order to categorize the robins' foraging mode on each of the three sites. Robins foraging for invertebrates in the vegetation displayed the low rates of movement and feeding and the long travel and capture moves characteristic of the "sit-and-wait" mode. High move and feeding rates and short move lengths suggested that ground foraging involved the "widely foraging" mode. Fruit foraging also involved this foraging mode, although rates and move lengths proved to be intermediate. The robins' behavior on a particular foraging site appeared to be influenced by the mobility, distribution, and abundance of food items and by environmental structure. Similarities between fruit and ground foraging occurred primarily because both sites involved immobile and aggregated food items. Fruit-foraging move-and-pause patterns, however, also resembled vegetation-foraging patterns, due to the shared complexities of the arboreal environment. Robin behavior preceding and following feedings was also examined for each site. Observed responses were not directly correlated with foraging mode but appeared to be due to food-item distribution and mobility. I postulate that the robin's versatility, with respect to foraging behavior, may play a role in this species' wide range and apparent success. Received 23 June 1981, accepted 11 February 1982.

A SPECIES' foraging mode can have profound effects on many aspects of its biology. Whether a species actively searches for prey, as is characteristic of the "widely foraging" mode, or depends on the ambush oriented "sit-and-wait" mode (Schoener 1971, Pianka 1978, Eckhardt 1979) not only affects its feeding behavior but is reflected in its morphology, interactions with predators, and reproductive rate (Huey and Pianka 1981). Yet many species seasonally or opportunistically switch from one food resource to another, a switch accompanied by behavioral adjustments and, in the extreme cases, complete shifts in foraging modes (Snow 1971, Davies 1977, Huey and Pianka 1981). What constrains a species' foraging behavior? What are the roles of the food source, the environment, and the species' own morphological or behavioral limitations in determining foraging mode?

Experiments have been used effectively in exploring flexibility in avian foraging behavior (Krebs et al. 1972, 1974, 1977; Smith 1974b, Zach and Falls 1976a, b). Simple parameters, such as prey density, size, and distribution, have been manipulated and avian responses successfully described. But such studies have concerned only a single foraging mode. Well-defined field

studies of foraging behavior have come closer to examining the variety of foraging options available to birds under natural conditions (Smith 1974a, Brownsmith 1977, Goss-Custard 1977, Davies 1977, Holmes et al. 1978, Emlen 1981).

I observed, during one breeding season at a single study area, the behavior of the American Robin (*Turdus migratorius*) utilizing three food resources associated with three foraging sites: (1) invertebrates among the foliage of trees and shrubs, (2) invertebrates on the ground, and (3) the fruit of *Amelanchier laevis* (the Juneberry). I focused my analyses on differences in foraging behavior among the three sites, their possible causes, and their relationship to foraging mode.

I analyzed behavioral patterns in two ways. First, in order to characterize the foraging mode for each site, I examined movement and feeding rates and the lengths of feeding and nonfeeding moves. In birds, the widely foraging mode is characterized by short moves and high move rates; conversely, the sit-and-wait mode involves long moves and low move rates (Williamson 1971, Eckhardt 1979, Landres and MacMahon 1980). My second analysis involved comparisons among foraging sites of the lengths

of movements and pauses preceding, during, and following feedings. These behavior patterns are indicators, on a finer scale than foraging mode, of a bird's response to the food resource it is exploiting (Smith 1974a, b, Pinkowski 1977, Zach and Falls 1977).

I used these two types of analyses to evaluate the effect on robin foraging patterns of (1) the mobility, distribution, and abundance of food items and (2) the structure of the environment.

METHODS AND DEFINITIONS

All behavioral data were collected between 1 June and 15 August 1976 in the area surrounding the University of Wisconsin Trout Lake Biological Station and the Mann Creek Wildlife Area in Vilas County, Wisconsin. Observations centered on the territories of four breeding pairs, visited regularly during the study period on a rotating basis. Territories were defined as areas patrolled regularly by singing males and/or containing an active nest.

Data were recorded using a stop watch and notebook. The record consisted of a chronology of all activities, including the location, type, direction, and length of all moves and the method of prey capture for feeding moves. My timings centered on pauses (termed intermove intervals), with movements serving as punctuation. An interval began when a bird moved, included the time in motion and the time spent, in whatever activity, on the subsequent fixed location, and ended with the beginning of the next move. As used here, movement implies a change of location. Travel moves were defined as those used simply to pass through the environment. Feeding moves involved attempted or realized prey captures. Feedings that occurred without changes in location were referred to as stationary feedings.

The study area supported a secondary growth forest of northern hardwoods, aspens, and conifers. Robins foraged in trees and shrubs from 0.5 m to 20 m in height. I collected vegetation-foraging data chiefly on six individuals, representing three of the breeding pairs. Prey captures typically involved large insects (>30 mm), such as adult lepidopterans and odonates, taken from the air or foliage.

I observed ground foraging in five adult birds and two fledglings, on two of the four territories. Ground foraging rarely occurred on the forest floor. Rather, it was used in habitat edges along the shoulders of roads and on the shores of Trout Lake and Mann Creek. Items frequently taken in shore foraging included insects washed in by the waves (e.g. adult ephemeropterans) or attracted to lake-side debris (e.g. dipteran swarms) and foliage insects fallen from the overhanging canopy (e.g. lepidopteran larvae). Annelid prey, like ground arthropods, tended to be small in size (<30 mm).

Although vegetation and ground foraging were observed throughout the study period, fruit-eating observations were limited to the period between 7 July and 19 July. Observations were concentrated on a group of large *Amelanchier laevis* bushes (3–4 m tall) located on the bank of Mann Creek outside of any known robin territory. Loose flocks of up to five adult and juvenile robins fed on the ripe fruits. Other species feeding on these bushes, in decreasing order of abundance, were Cedar Waxwings (*Bombycilla cedrorum*), Gray Catbirds (*Dumetella carolinensis*), Red-eyes Vireos (*Vireo olivaceus*), and Veeries (*Catharus fuscescens*).

Amelanchier clusters contained 3–15 fruits of which $\frac{1}{3}$ to $\frac{2}{3}$ were ripe simultaneously. Ripe fruits were 5–7 mm in diameter, purple-black in color, and pendant. Birds handled the fruits rapidly, picking them while perched or on the wing and swallowing them whole.

I collected data for approximately 400 sequences, totaling 452 min of observation. Most sequences were less than 3 min in length. For each site, I performed preliminary analyses, using χ^2 median tests to compare rates and move lengths between individual sequences, which represented different sexes, territories, and dates. No significant differences ($P > 0.05$) were revealed between these sample sequences. Therefore, data from all individuals and all sequences were pooled for each site, hereafter referred to as vegetation (351 min of observation), ground (67 min), and fruit (34 min). All behavioral analyses reported here involved two-way χ^2 tests, including χ^2 median tests (Siegel 1956). All test results with $P \leq 0.05$ are termed "significant" or "significantly different" in the text.

The robins' foraging behavior in the vegetation and on the ground suggested that the invertebrate distributions on these two sites differed substantially. Insect samples had been collected at the time of the study, but these proved inappropriate for distributional analyses. To obtain a simple measure of invertebrate distributions, I visually censused the invertebrates on the ground and in the vegetation in July 1980. The study sites had remained undisturbed between 1976 and 1980, and I assumed that, at the scale on which I sampled, the 1980 distributions reflected typical seasonal conditions.

Ground samples were made along the beach at Trout Lake, and vegetation samples were taken in the Mann Creek Wildlife Area. At randomly determined points along a 300-m transect, I placed a 1-m² circular hoop flush with the ground and counted any invertebrates I saw leaving the quadrat due to the disturbance caused by installation. I then stood about 5 m from the quadrat and waited 2 min for conditions to stabilize. At the end of this time, I searched the quadrat for 1 min, counting invertebrates ≥ 2 mm. On both sites, the count included the air or vegetation contained in an imaginary cylinder, 2 m in

TABLE 1. General use patterns for the three foraging sites. The numbers of travel moves and feedings observed in each site were compared, by means of χ^2 tests, to the numbers predicted by the fraction of the total observation time that the robins spent in each site.

Pattern	Vegetation	Fruit	Ground
Total amount of time spent in foraging site (min)	350.5	33.8	67.4
Number of travel moves observed (predicted by time investments)	320 (622)	33 (60)	448 (119)
Results of χ^2 test: observed vs. predicted number of travel moves. $\chi^2 = 1,068.37$, $df = 2$, $P < 0.001$			
Number of feedings observed (predicted by time investments)	75 (289)	88 (28)	209 (55)
Results of χ^2 test: observed vs. predicted number of feedings. $\chi^2 = 402.80$, $df = 2$, $P < 0.001$			

height, with the hoop as its base. I conducted 21 such censuses for the vegetation foraging site and 25 for the ground. I used χ^2 tests (based on variance to mean ratios) to compare the distribution of invertebrates/quadrat, for each site, with a Poisson series (Elliott 1977).

RESULTS

General patterns of foraging site use.—Site utilization can be viewed as a combination of time spent on a site and the number of moves and feedings occurring there. If robins behaved comparably on all three sites, the number of movements and feedings on each site should be proportional to the amount of time spent there. This was not the case. The robins' distribution of time among the three foraging sites proved significantly different from their distributions of travel moves and feedings (Table 1). More travel moves and feedings occurred on the ground than predicted by time investments. Fewer travel moves and feedings were made in the vegetation. Fruit foraging proved intermediate, with fewer travel moves but more feedings than predicted.

Movement rates.—I compared the distributions of time intervals elapsing between successive moves and between successive feedings among the three sites (Fig. 1). All three distributions of intermove intervals differed significantly from one another (Table 2). Robins used significantly shorter intermove intervals (and thus had a higher frequency of movement) in ground foraging than in both vegetation and fruit foraging. In turn, intermove intervals used in fruit foraging were significantly shorter than in the vegetation.

Pair-wise comparisons between sites showed that all three distributions of interfeeding-interval lengths differed significantly from one another (Table 2). As with intermove intervals, ground foraging involved the shortest interfeeding intervals, fruit intermediate intervals, and vegetation the longest.

Move lengths.—I compared the distributions of travel- and feeding-move lengths among the three sites (Fig. 1). All three differed significantly from one another with regard to the lengths of both travel and feeding moves (Table 2). For both move types, ground moves were the shortest, vegetation moves the longest, and fruit-foraging moves intermediate.

Pre- and postfeeding intervals and moves.—Pauses and moves connected with feeding can further define foraging patterns in the three sites, particularly events immediately preceding and following feeding as compared to non-feeding standards. I recognized three classes of intermove intervals: (1) intervals preceding feedings (pre-), (2) intervals following feedings (post-), and (3) intervals bounded by nonfeeding moves (nonfeeding). Because of my timing scheme, the postfeeding interval included the feeding move itself, prey handling, and whatever pause followed prey capture and preceded the next move. If feedings were consecutive, a single interval could be classed as both a pre- and postfeeding interval. This was true of 8%, 18%, and 57% of all intervals for vegetation, ground, and fruit foraging, respectively.

Similarly, I recognized four classes of moves (Fig. 2): (1) travel moves (previously defined), (2) feeding moves (previously defined), (3) moves preceding feeding moves (pre-), and (4)

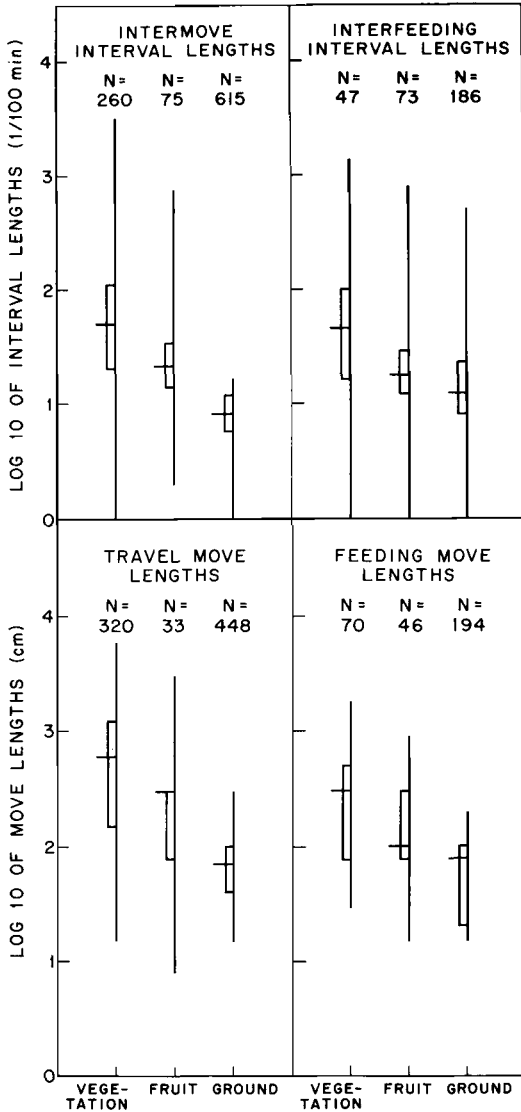


Fig. 1. The distributions of intermove- and interfeeding-interval lengths and of travel- and feeding-move lengths for vegetation, fruit, and ground foraging, based on \log_{10} scales. The upper and lower vertical lines represent the first and fourth quartiles, respectively. The vertical bars represent the second and third quartiles and are separated by the median, represented by a horizontal line. Note that for the fruit travel-move length distribution, the entire third quartile equalled the median value, so there is no upper vertical bar.

moves following feeding moves (post-). Pre- and postfeeding moves were not exclusive categories. They could be either travel or feeding moves. Likewise, due to consecutive feedings, a single move could be classed as both a pre- and postfeeding move. This was true of 2%, 10%, and 30% of all moves for vegetation, ground, and fruit foraging, respectively.

Robins altered their behavior both before and after prey capture (Fig. 2, Table 3). In vegetation, nonfeeding intervals were significantly longer than postfeeding intervals but did not differ significantly from prefeeding intervals. Travel moves were significantly longer than feeding, pre-, or postfeeding moves. In fruit foraging, nonfeeding intervals were significantly longer than both pre- and postfeeding intervals. Travel moves were significantly longer than feeding and prefeeding moves but did not differ significantly from postfeeding moves. In ground foraging, nonfeeding intervals were significantly shorter than postfeeding intervals but did not differ significantly from prefeeding intervals. Travel moves were significantly longer than feeding and postfeeding moves but did not differ significantly from prefeeding moves.

Invertebrate distributions.—Figure 3 presents abundance-frequency distributions for the invertebrate sampling quadrats on the ground and in the vegetation. The distribution in the vegetation did not differ significantly from a Poisson series ($\chi^2 = 19.60$, $df = 60$, $P > 0.05$). The distribution of ground invertebrates differed significantly, in the direction of aggregation ($\chi^2 = 61.65$, $df = 24$, $P < 0.05$). The two distributions also differed significantly from each other, with the ground quadrats containing higher densities of invertebrates ($\chi^2 = 9.54$, $df = 2$, $P < 0.01$).

DISCUSSION

Influence of the food resource: mobility, distribution and abundance.—The overall foraging patterns of the robin were very different among the three sites (Table 1, Fig. 2). Vegetation foraging was characterized by long moves and low movement and feeding rates, whereas ground foraging involved short moves and high rates (Fig. 1). These patterns suggest that robins employed the sit-and-wait mode in vegetation foraging and the widely foraging mode on the ground (Eckhardt 1979).

TABLE 2. The results of pair-wise χ^2 tests comparing interval-length and move-length distributions (Fig. 1) between foraging sites. Interval-length categories were based on 0.10-min intervals. Move-length categories were based on 1-m intervals. In both cases, length categories were combined for testing, so that the expected values of all cells were ≥ 5 .

Distribution	Pairwise comparison	χ^2	df	P
Intermove interval lengths	Vegetation vs. fruit	44.10	4	$P < 0.001$
	Vegetation vs. ground	431.41	4	$P < 0.001$
	Fruit vs. ground	109.18	4	$P < 0.001$
Interfeeding interval lengths	Vegetation vs. fruit	24.81	4	$P < 0.001$
	Vegetation vs. ground	35.91	4	$P < 0.001$
	Fruit vs. ground	15.47	4	$P < 0.001$
Travel move lengths	Vegetation vs. fruit	27.95	3	$P < 0.001$
	Vegetation vs. ground	453.56	2	$P < 0.001$
	Fruit vs. ground	231.53	2	$P < 0.001$
Feeding move lengths	Vegetation vs. fruit	12.55	3	$P < 0.01$
	Vegetation vs. ground	94.38	1	$P < 0.001$
	Fruit vs. ground	20.87	1	$P < 0.001$

Fruit-foraging behavior was intermediate in terms of both move lengths and rates (Fig. 1). Because *Amelanchier* fruit were absolutely immobile, robins could not sit-and-wait when fruit foraging but had to employ the widely foraging mode (Huey and Pianka 1981). Despite this inherent limitation, applying the mode concept to fruit foraging allows for useful intersite comparisons, because the fruit resource is so well known. For instance, the relatively sedentary nature of the food resource was certainly a factor that favored widely foraging behavior on the ground, as well as in fruiting shrubs (Smith 1974a). Compared to the flying insects, which robins captured in the vegetation (e.g. odonates and adult lepidopterans), terrestrial invertebrates were either active, but crawling (e.g. coleopterans), or inactive due to injury or death (e.g. lepidopteran larvae).

Robins could use short, uncomplicated capture maneuvers on the small, slow ground invertebrates (Fig. 1). Such simple gleans and picks are typical of widely foraging birds feeding on invertebrates (Eckhardt 1979, Morse 1979, Tye 1981), and robins employed similar actions in harvesting fruit. Conversely, capturing large, flying insects in the vegetation often required that robins make the long, complex flights characteristic of sit-and-wait species (Fig. 2) (Verbeek 1975, Eckhardt 1979, Landres and MacMahon 1980).

A second feature shared by fruit and ground foraging, which favored the widely foraging

mode, was the distribution of food items. *Amelanchier* fruit were clumped because of the plant's growth form. My census indicated that ground invertebrates were also aggregated (Fig. 3). In contrast, invertebrates were randomly distributed in the vegetation. Aggregated resources have been associated with the widely foraging mode. Conversely, use of the sit-and-wait mode has been correlated with nonaggregated food sources (Huey and Pianka 1981).

The degree of food-item aggregation in each foraging site was also reflected in the proportion of feedings that directly preceded or followed other feedings. Many such consecutive feedings are likely where food items are clumped. The discovery of one item means that others are probably close by and available for capture. For fruit and ground foraging, consecutive feeding composed 93% and 83% of all observed feedings. Only 52% of vegetation feeding was consecutive, however.

Prey abundance is the final food-related factor that may have influenced foraging mode, particularly in the two invertebrate sites. Compared to ground-foraging birds, robins had low feeding rates in the vegetation (Table 1, Fig. 1). In part, this was because the vegetation supported a variety of nonfeeding activities related to territorial defense, parental care, and self-maintenance. However, my census did show lower densities of visible invertebrates in the vegetation than on the ground (Fig. 3). The sit-and-wait mode, used by robins in the vegetation, is associated with food resources

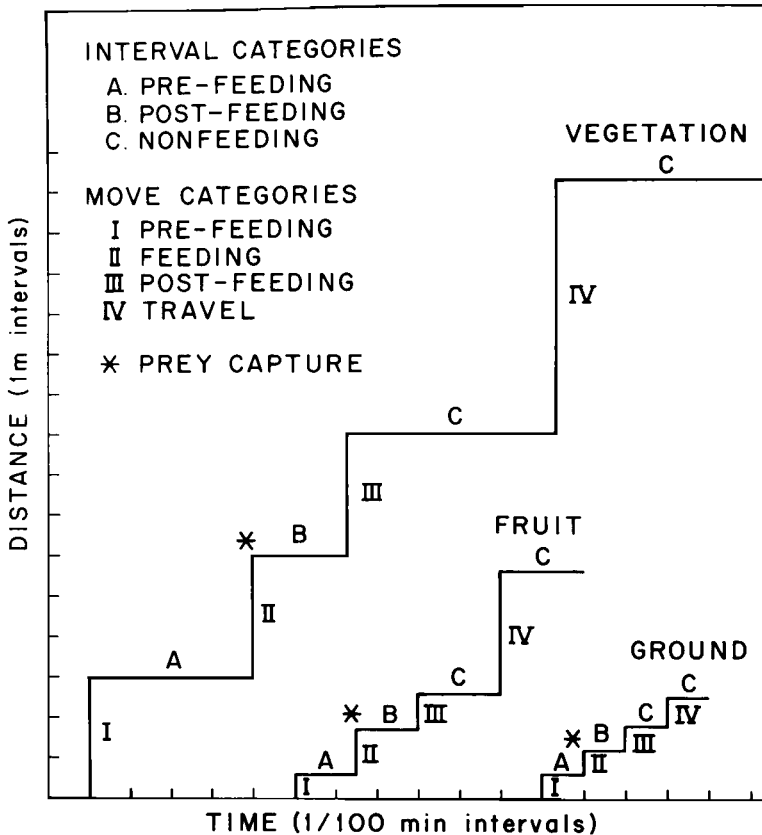


Fig. 2. Interval-length and move-length patterns preceding and following feedings for vegetation, fruit, and ground foraging. Based on diagrams used by Cody (1974), the steps' heights represent median move lengths for 4 move categories described in Results, and the steps' lengths represent median interval lengths for 3 interval categories. The three diagrams are scattered along the time axis to clarify presentation, not to indicate different temporal origins.

that are relatively rare (Huey and Pianka 1981). In this case, the low numbers of invertebrates in the vegetation may have been compounded by the fact that the robins seemed to select the less common, large insects.

Influence of environmental structure.—Although fruit and ground foraging both involved the widely foraging mode, the robins' movements and rate patterns were less extreme in fruit foraging and in some way resembled vegetation patterns (Fig. 1 and 2). Of all fruit-foraging moves, 82% were flights, as were 88% of all vegetation moves. In contrast, ground-foraging robins exclusively employed short, bipedal moves that occurred at significantly higher frequencies than the vegetation- and fruit-foraging flights (Table 1).

I propose that the robins' movement rates and lengths were influenced by the structure of the three foraging sites (Moermond 1979, Holmes and Robinson 1981). Birds foraging for fruit and vegetation invertebrates moved within complex three-dimensional arboreal environments. Ground-foraging birds encountered a simple, open, two-dimensional plane. Such marked differences in environmental complexity could easily affect maneuverability and food-item detectability, resulting in differences in movement rate, type, and length, even in birds employing the same overall foraging mode.

Pre- and postfeeding patterns.—The robins' behavior preceding and following feedings in the three foraging sites followed three different patterns, which were not directly related to for-

TABLE 3. A comparison of behavior preceding and following feedings to nonfeeding standards. χ^2 median tests ($df = 1$) were used to compare the duration of pre- and postfeeding pauses to nonfeeding pauses for each foraging site (A) and to compare the lengths of feeding moves and pre- and postfeeding moves to travel move lengths (B).

A. Interval length comparisons						
Nonfeeding	vs.	Prefeeding		Postfeeding		
Median (min) (n)		Median (min) (n)	χ^2 (P)	Median (min) (n)	χ^2 (P)	
Vegetation						
0.50 (202)		0.40 (34)	1.77 ($P > 0.10$)	0.23 (33)	10.97 ($P < 0.001$)	
Fruit						
0.20 (17)		0.15 (68)	6.61 ($P < 0.02$)	0.15 (80)	8.06 ($P < 0.01$)	
Ground						
0.10 (327)		0.10 (171)	0.03 ($P > 0.80$)	0.10 (164)	4.99 ($P < 0.05$)	
B. Move length comparisons						
Travel	vs.	Prefeeding		Feeding		Postfeeding
Median (m) (n)	Median (m) (n)	χ^2 (P)	Median (m) (n)	χ^2 (P)	Median (m) (n)	χ^2 (P)
Vegetation						
6.0 (320)	3.0 (45)	16.11 ($P < 0.001$)	3.0 (70)	20.95 ($P < 0.001$)	3.0 (39)	9.72 ($P < 0.01$)
Fruit						
3.0 (33)	0.6 (35)	11.54 ($P < 0.001$)	1.0 (46)	7.56 ($P < 0.01$)	1.0 (37)	0.15 ($P > 0.70$)
Ground						
0.7 (448)	0.6 (177)	0.55 ($P > 0.25$)	0.6 (194)	6.42 ($P < 0.02$)	0.6 (213)	5.28 ($P < 0.05$)

aging mode but were influenced by the same factors, especially the mobility and distribution of food items. Fruit-foraging patterns were the most distinctive. Short pre- and postfeeding pauses and short prefeeding moves reflected the intensity of fruit-foraging bouts and their focus on cluster exploitation (Fig. 2, Table 3). Stationary feedings, in which a bird gathered up to seven fruits without shifting location, composed 38% of all fruit feedings but less than 10% of ground and vegetation feedings. Unlike fruits, which are conspicuous, immobile, and "designed" for avian consumption (c.f. Snow 1971), invertebrates have adaptations for escaping detection, and even sedentary terrestrial forms require some pursuit and capture maneuvers.

The relatively long pauses and short moves observed in robins after ground feedings (Fig. 2, Table 3) were another set of responses that promoted the effective use of an aggregated food source, but a more evasive one than fruit. These and similar responses have been repeatedly reported for ground-foraging passerines (Smith 1974a, Tinbergen 1976, Zach and Falls 1977). They effectively produce extended periods of search near the capture site and, thus, within a prey patch. Unlike ground foraging, postfeeding pauses in the vegetation were exceptionally short (Fig. 2, Table 3). For a foraging bird, there would be no predictable advantage in remaining at a capture site if foliage invertebrates were randomly dispersed. Rather, vegetation patterns seemed designed for

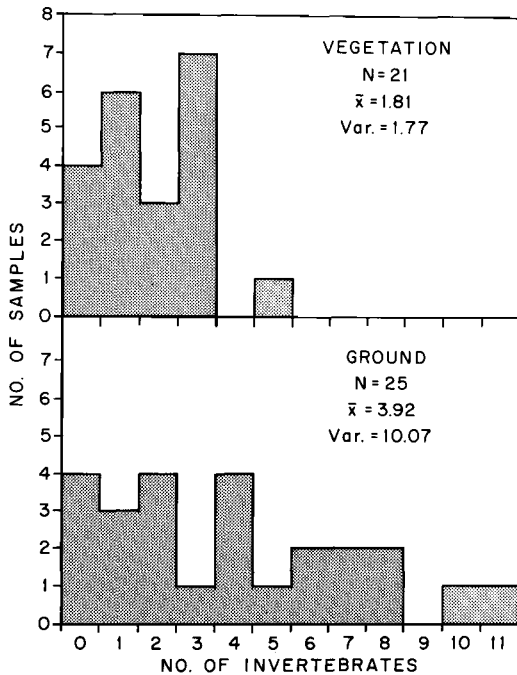


Fig. 3. Abundance-frequency distributions of visually censused invertebrates, based on randomly located 1-m² quadrats in the vegetation (extending 0.1–2.0 m) and on the ground. The vegetation distribution did not differ significantly from a Poisson distribution; the ground distribution did ($P < 0.05$).

stalking (short prefeeding pauses), then flushing and pursuing (short postfeeding pauses and moves) mobile prey in a complex environment where visibility and maneuverability were limited (Pinkowski 1977, Rasmussen 1977).

CONCLUSIONS

In this study, the American Robin employed both the widely foraging and the sit-and-wait modes while feeding in the vegetation, on fruit, and on the ground. The choice of mode was related most clearly to food-item attributes, particularly distribution and mobility, rather than to the structure of the three foraging sites. The robin appears to be basically a widely foraging species, with occasional, opportunistic uses of the sit-and-wait mode. Of the three foraging sites examined here, the robin's behavior on the ground has previously received the most attention (Bent 1949, Heppner 1965, Eiserer 1980), but the importance of this foraging site may vary seasonally and geographically

(Brown 1976). The robin's ability to shift foraging modes allows it to exploit a wide variety of habitats and food resources. This foraging versatility may explain, in part, the species' wide range in North America and its success in the man-altered landscape (Bent 1949).

ACKNOWLEDGMENTS

I wish to thank T. C. Moermond and W. M. Tonn for their suggestions, their intellectual stimulation, and their support. The comments of T. M. Frost, J. M. N. Smith, and two anonymous reviewers were also very helpful in preparing this manuscript. Finally, I thank J. J. Magnuson and W. R. Schmitz for allowing me to use the facilities at Trout Lake.

LITERATURE CITED

- BENT, A. C. 1949. Life histories of North American thrushes, kinglets, and their allies. U.S. Natl. Mus. Bull. No. 196.
- BROWN, R. G. R. 1976. Bird damage to fruit crops in the Niagara Peninsula. Can. Wildl. Serv. Rept. Ser. No. 27: 1–57.
- BROWNSMITH, C. B. 1977. Foraging rates of Starlings in two habitats. *Condor* 79: 386–387.
- CODY, M. L. 1974. Competition and the structure of bird communities. Princeton, New Jersey, Princeton Univ. Press.
- DAVIES, N. B. 1977. Prey selection and the search strategy of the spotted flycatcher (*Muscicapa striata*): a field study on optimal foraging. *Anim. Behav.* 25: 1016–1033.
- EISERER, L. A. 1980. Effects of grass length and mowing on foraging behavior of the American Robin (*Turdus migratorius*). *Auk* 97: 576–580.
- ECKHARDT, R. C. 1979. The adaptive syndromes of two guilds of insectivorous birds in the Colorado Rocky Mountains. *Ecol. Monogr.* 49: 129–149.
- ELLIOTT, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Ferry House, United Kingdom, Freshwater Biological Assoc., Sci. Publ. No. 25.
- EMLEN, J. T. 1981. Divergence in the foraging responses of birds of two Bahama Islands. *Ecology* 62: 289–295.
- Goss-CUSTARD, J. D. 1977. Predator responses and prey mortality in the redshank *Tringa totanus* (L.) and a preferred prey *Corophium volutator* (Pallas). *J. Anim. Ecol.* 46: 21–36.
- HEPPNER, F. 1965. Sensory mechanisms and environmental clues used by the American Robin in locating earthworms. *Condor* 67: 247–256.
- HOLMES, R. T., & S. K. ROBINSON. 1981. Tree species preference of foraging insectivorous birds in a northern hardwoods forest. *Oecologia* 48: 31–35.
- , T. W. SHERRY, & S. E. BENNETT. 1978.

- Diurnal and individual variability in the foraging behavior of American Redstarts (*Setophaga ruticilla*). *Oecologia* 36: 141-149.
- HUEY, R. B., & E. R. PIANKA. 1981. Ecological consequences of foraging mode. *Ecology* 62: 991-999.
- KREBS, J. R., M. H. MACROBERTS, & J. M. CULLEN. 1972. Flocking and feeding in the great tit (*Parus major*): an experimental study. *Ibis* 114: 507-530.
- , J. RYAN, & E. L. CHARNOV. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Anim. Behav.* 22: 953-964.
- , T. ERICKSEN, M. I. WEBER, & E. L. CHARNOV. 1977. Optimal prey selection in the great tit (*Parus major*). *Anim. Behav.* 25: 30-38.
- LANDRES, P. B., & J. A. MACMAHON. 1980. Guilds and community organization: analysis of an oak woodland avifauna in Sonora, Mexico. *Auk* 97: 351-365.
- MOERMOND, T. C. 1979. The influence of habitat structure on *Anolis* foraging behavior. *Behaviour* 70: 147-167.
- MORSE, D. H. 1979. Habitat use by the Blackpoll Warbler. *Wilson Bull.* 91: 234-243.
- PIANKA, E. R. 1978. *Evolutionary ecology*. New York, Harper & Row.
- PINKOWSKI, B. C. 1977. Foraging behavior of the Eastern Bluebird. *Wilson Bull.* 88: 404-414.
- RASMUSSEN, P. W. 1977. Foraging patterns in two species of wood warblers. Unpublished M.S. thesis, Madison, Wisconsin, Univ. Wisconsin.
- SCHOENER, T. W. 1971. Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* 2: 369-404.
- SIEGEL, S. 1956. *Nonparametric statistics for the behavioral sciences*. New York, McGraw-Hill.
- SMITH, J. N. M. 1974a. The food searching behavior of two European thrushes. I: Description and analysis of search paths. *Behaviour* 48: 276-302.
- . 1974b. The food searching behavior of two European thrushes. II: The adaptiveness of the search patterns. *Behaviour* 49: 1-61.
- SNOW, D. W. 1971. Evolutionary aspects of fruit-eating by birds. *Ibis* 113: 194-202.
- TINBERGEN, J. M. 1976. How starlings (*Sturnus vulgaris* L.) apportion their foraging time in a virtual single-prey situation on a meadow. *Ardea* 64: 155-170.
- TYE, A. 1981. Ground-feeding methods and niche separation in thrushes. *Wilson Bull.* 93: 112-114.
- VERBEEK, N. A. M. 1975. Comparative feeding behavior of three co-existing tyrannid flycatchers. *Wilson Bull.* 87: 231-240.
- WILLIAMSON, P. 1971. Feeding ecology of the Red-eyed Vireo and associated foliage gleaning birds. *Ecol. Monogr.* 41: 129-152.
- ZACH, R., & J. B. FALLS. 1976a. Ovenbirds (Aves: Parulidae) hunting behavior in a patchy environment: an experimental study. *Can. J. Zool.* 54: 1863-1879.
- , & ———. 1976b. Foraging behavior, learning, and exploration by captive Ovenbirds (Aves: Parulidae). *Can. J. Zool.* 54: 1880-1893.
- , & ———. 1977. Influence of capturing a prey on subsequent search in the Ovenbird (Aves: Parulidae). *Can. J. Zool.* 55: 1958-1969.