THE DIET OF AMERICAN ROBINS: AN ANALYSIS OF U.S. BIOLOGICAL SURVEY RECORDS

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ABSTRACT.—I present a quantitative description of the diet of American Robins (*Turdus migratorius*) and consider how food habits (particularly the proportion of fruit eaten and the diversity of individual meals) are influenced by season, habitat, sex, and time of day. The study is based on an analysis of records of stomach contents compiled by the U.S. Biological Survey and the U.S. Fish and Wildlife Service. Across their entire range, robins ate fruits representing over 50 genera and invertebrates representing over 100 families. Diets were diverse even within local regions, and there was no obvious single feeding niche. The major food classes, consumed in every combination, were soft-bodied invertebrates, hard-bodied invertebrates, and fruits. The same taxa (especially fruits of the family Rosaceae and invertebrates of the orders Coleoptera and Lepidoptera) predominated in robins' diets, irrespective of habitat or geographical location, which presumably reflects both selective foraging and the availability of these widespread taxa.

The proportion of fruit (by volume) in the diet was much higher in the fall and winter (median values >90%) than in the spring (<10%); summer values were intermediate. The transition from a diet dominated by invertebrates to a diet dominated by fruits occurred over a 1-2-month period. The number of distinct food items in stomachs, a measure of the species diversity of individual meals, was positively correlated with the fraction of invertebrates in the diet. Thus, at the time of year when robins were dependent on fruits for food, the diversity of their meals was also lowest. The degree of fullness of the stomach showed few consistent trends with season or habitat.

Despite different sex roles and nutritional requirements, male and female robins did not differ in the proportion of fruit in the diet in any month or in any region. Nor did their stomachs contain different numbers of distinct food items, different amounts of food, or a different range or distribution of prey taxa. Habitat was an important variable explaining dietary differences.

The Biological Survey records have unavoidable shortcomings, most notably problems of sampling biases and the inability to correct for differential digestion of food items. Nonetheless, they are a valuable and underused data base for testing hypotheses, generating new questions of ecological interest, and describing in detail the diets of North American bird species. *Received 30 September 1985, accepted 5 March 1986.*

UNDER simple conditions, foraging models have successfully predicted birds' instantaneous food preferences on the basis of the energetic value, handling time, or other characteristics of potential prey (Krebs et al. 1983). Predicting total diets is much more difficult. The food that birds eat over their lifetimes or even a single day is a complex result of numerous foraging decisions. The foraging behavior of individuals may change diurnally (Holmes et al. 1978), seasonally (Baker and Baker 1973, Hutto 1981), or annually (Fogden 1972). Diet may depend on age (Greenberg 1983) or morphology (Herrera 1978), and it may differ in different parts of a species' range due to intrinsic preferences (Emlen and DeJong 1981) or geographical variation in prey availability (Fox and Morrow 1981). Such variation is also found in birds that eat both fruits and invertebrates (Colling 1941, Leck 1972, Crome 1975, Herrera 1978), two food types that differ strikingly in accessibility, edibility, and nutrients (Snow 1971, Morton 1973). Fruits and animal prey present different challenges for the digestive system (Walsberg 1975, Foster 1978, Milton 1981) and satisfy birds' nutritional needs to different degrees (Robbins 1983). When fruits and insects are similarly colored, their appearance may signal quite different palatability (Herrera 1985, Wheelwright and Janson 1985). Variation in the diet of fruit-eating birds has direct consequences for interactions between

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birds and the plants whose seeds they disperse (Howe and Smallwood 1982, Wheelwright and Orians 1982).

I examined in detail the diet of one species of fruit-eating bird, the American Robin (*Turdus migratorius*), to evaluate the effects of time (hour of day, season, age, year) and space (habitat, geographical region) on consumption of different food types. Knowledge of the diet of American Robins may yield insights applicable to many other passerine species besides fruit-eaters; robins belong to a diverse genus (including over 60 species) and one of the largest avian families (Muscicapidae). An analysis of stomach-content records for over 1,900 individual robins collected by the U.S. Biological Survey formed the basis of the study.

The stomach samples compiled by the Biological Survey possibly represent the most detailed data base on avian food habits in the world. Over 250,000 records exist for more than 400 native North American bird species (Martin et al. 1951). In the case of robins, birds were collected over most of their North American range, in all months of the year, at all hours of the day, and in a variety of habitats. Large samples of males, females, juveniles, and nestlings are represented. United States Department of Agriculture entomologists and botanists used extensive reference collections to identify food items to species or genus in most cases. To assemble such a data base today would be exceedingly difficult, prohibitively expensive, and ethically unjustifiable. Given the present interest in foraging behavior (Pyke et al. 1977, Krebs et al. 1983), seed dispersal by birds (Howe and Smallwood 1982, Wheelwright and Orians 1982), and plant-animal interactions (Thompson 1982), the Biological Survey stomach samples ought to be widely exploited by ecologists. Yet the data base has scarcely been used except for the general survey of Martin et al. (1951). One of my goals is to draw attention to its value in addressing ecological questions and suggesting new hypotheses to test.

METHODS

The study is based on records of food items in the stomachs of American Robins collected from 1885 to 1950. Half of the samples date from before 1908, and three-quarters had been collected (although not fully analyzed) by the time Beal (1915a, b) presented a general summary of the data in his evaluation of the economic impact of thrushes on agriculture. The original records of the U.S. Biological Survey and the U.S. Fish and Wildlife Service are currently filed on index cards at the Patuxent Wildlife Research Center in Laurel, Maryland. Each card corresponds to an individual bird and contains information on the sex of the bird, location, habitat, time of day, date, relative amount (by volume) of vegetable and animal matter in the stomach, fullness of the stomach (volume of stomach contents), and a list of food items. The relative amount (by volume) of each item in the stomach also is recorded.

This study focuses on three variables: (1) relative amount of fruit in the stomach, (2) number of distinct food types (taxa) in the stomach, and (3) volume of stomach contents. The original records summarize the proportion of fruit in the stomach under "vegetable matter." In robins, which only rarely eat leaves or seeds, the relative amount of fruit is virtually equivalent to vegetable matter, so I used the latter to estimate the degree of fruit eating. When I excluded individual robins whose stomachs contained vegetable matter other than fruits, the results of the analyses were the same. The relative amount of fruit ranged from 0 to 100% by volume; the number of food types ranged from 0 to 14; and the volume of stomach contents was scored as 0% ("empty"), 25% ("nearly empty," "quarter-filled"), 50%, 75%, or 100% ("well-filled"). I use the terms "food type" and "taxon" interchangeably to designate distinct classes of stomach contents, regardless of their taxonomic level. Thus, a record listing "2 *Rhus typhina* seeds, elytra of unidentified Scarabaeidae, 4 spiders" was considered to contain 3 food types. This information was entered into the computer at Cornell University for analysis. The untransformed data were analyzed using nonparametric statistical tests and analyses of variance (ANOVAs) for unbalanced data sets (General Linear Models, SAS 1985).

Because robins were collected from a wide geographical area (46 states, 5 Canadian provinces) and because an ANOVA of the entire data set indicated regional differences in diet, I divided the sample into three broad regions: eastern (Atlantic Coast states and provinces westward to Ontario, Minnesota, Iowa, Missouri, Arkansas, and Louisiana); central (states and provinces between the eastern and western regions); and western (Pacific Coast states and provinces eastward to Idaho, Nevada, and Arizona). These regions correspond, respectively, to the northeastern coniferous and eastern deciduous forests and southeastern coastal plain; the central prairies and eastern Rocky Mountain foothills; and the west coast and mountains. Each of these large geographical regions, which contain large sample sizes necessary for multivariate statistical tests, inevitably combines quite dissimilar habitats. Nonetheless, the regions were chosen because they roughly delimit distinct robin migratory routes and subspecies' ranges (eastern: *T. m. migratorius, T. m. nigrideus, T. m. achrustus;* central: *T. m. migratorius, T. m. propinquus;* western: *T. m. caurinus, T. m. propinquus;* Bent 1949). Even if the regions were totally arbitrary groupings of states, however, they allow a division of the sample into independent subsamples that can be compared to determine the generality of patterns in robin diet and to provide a check for sampling biases within any one region. Further subdivision into northeastern deciduous forest, mountain regions, southwestern arid areas, etc. did not qualitatively change the results presented here. I chose a smaller, more homogeneous region, the northeastern United States [New York and the states that border it (plus the ecologically similar state of Maine, included because it increased the sample size to improve statistical tests; its inclusion did not otherwise affect the analyses)] to examine robin diets in more detail and to look for interactions between factors that influence diet. Although males outnumber females in the sample (709 males vs. 460 females) and in each region, sex ratios do not differ between months or habitats in any of the different regions (Chi-square test, $P > 0.17$).

The data base has several major shortcomings. The original goal of the Biological Survey was to assess the economic impact of American wildlife on agricultural crops (McAtee 1933). As a result, many robins were shot in cultivated fruit trees (19.8%), grain fields (14.7%), and suburban areas (3.8%) at hours or on days convenient to collectors (or angry orchardists). Hence, the data base is not a random sample, which limits its usefulness for making inferences about diet in the population as a whole. Second, stomach contents may not reflect the relative importance of food types because of different rates of digestion of different foods. For example, earthworms are conspicuous elements of robins' diets (Bent 1949, Gochfeld and Burger 1984), yet they contribute to only 1.5% of all recorded invertebrate prey items in the sample ($n = 6{,}378$), presumably because of the difficulty of detecting earthworms soon after they are ingested. Beetle elytra, in contrast, remain undigested in the gut for relatively long periods (Wroot 1985; see Hamilton 1940, 1943; Johnson 1969). Third, the data base does not lend itself to answering questions about selectivity in feeding because no data were gathered on food availability in the habitats where birds were collected. Finally, because birds were killed, the records give only point samples of birds' diets, from which long-term patterns in diet can only be inferred. Despite these shortcomings, these records point to trends in feeding behavior that can be explored with a more appropriate experimental design.

American Robins occur throughout continental North America, where they are the largest species of thrush (Muscicapidae, Turdinae). In New York State during the nonbreeding season, male mass averages 86.2 ± 6.1 g ($n = 26$), and female mass averages 83.6 ± 6.4 g ($n = 18$). During the breeding season, masses average somewhat less (77.4 g for males and 80.6 g for females, $n = 21$ and 6, respectively). Although observed most commonly on suburban lawns (Eiserer 1980), robins frequent most North American habitats, from grasslands to coniferous forests (Bent 1949). Foraging mode is nearly as varied as geographical distribution and habitat use (Paszkowski 1982).

Robins begin breeding in April or May (depending on latitude and elevation), soon after returning from migration. Initial breeding dates are delayed about 3 days for each additional degree of latitude in the east, and nesting occurs later in the west (James and Shugart 1974). As in most passerines, females are responsible for nest construction and incubation; males assist in feeding nestlings. Pairs typically produce two clutches over a 2-month period (Howell 1942). Occasionally, a third clutch may be raised (Howell 1942). A complete molt occurs in July and August, at which time the fall migration begins.

RESULTS

Frequencies of different food types.—American Robins eat fruits of at least 51 genera and 28 families across their entire range (Appendix 1). For the entire sample, the most important taxa of fruiting plants were Rosaceae (34% of all fruit records), particularly the genera *Prunus* (20%; an undetermined but probably substantial proportion of these represent commercial cherries) and *Rubus* (5%, some of which may have been cultivated); Anacardiaceae (10%), particularly *Rhus* (5%) and *Schinus* (4%); Vitaceae (6%); and Cornaceae (5%) ($n = 1{,}308$ fruit records).

Robins also eat invertebrates representing at least 107 families and 14 insect orders (Appendix 1). Coleoptera comprised about 40% of robins' invertebrate diets (by frequency in stomachs) in the sample as a whole ($n = 6{,}378$ invertebrate records) as well as in most regions and habitats. These results should be interpreted cautiously because different digestive rates may introduce sampling biases and because prey frequencies are not weighted by prey mass or energetic content. Three beetle families were especially important: Carabidae (10%, particularly the genus *Amara*), Curculionidae (8%, particularly *Phytonomus*), and Scarabaeidae (7%, particularly *Lachnosterna*). Coleoptera were followed in frequency by Lepidoptera (13%) and Hymenoptera (9%). These three orders accounted for over half of all food items (inver-

TABLE 1. The 10 most common fruit and invertebrate taxa recorded in American Robin stomachs in the eastern region, compared with their frequencies in the central and western regions. Frequencies are expressed as a percentage of the total number of occurrences of each food type (fruits or invertebrates).

	East	Central	West
Fruit genera			
Prunus	0.23	0.05	0.08
Cornus	0.07	0.01	0.0
Rhus	0.07	0.01	0.0
Rubus	0.06	0.01	0.01
Smilax	0.06	0.04	0.005
Vaccinium	0.04	0.01	0.005
Ilex	0.04	0.03	0.0
Morus	0.04	0.04	0.0
Celtis	0.03	0.13	0.0
Juniperus	0.03	0.02	0.0
Invertebrate taxa			
Lepidoptera (unidentified)	0.12	0.12	0.07
Carabidae	0.10	0.13	0.11
Curculionidae	0.08	0.10	0.09
Scarabaeidae	0.08	0.07	0.05
Formicidae	0.07	0.05	0.04
Elateridae	0.05	0.05	0.05
Acrididae	0.05	0.04	0.02
Coleoptera (unidentified)	0.04	0.05	0.11
Arachnida	0.04	0.04	0.02
Pentatomidae	0.03	0.01	0.01
No. of individual birds	1,260	240	436
No. of individual prey items	5,141	1,595	1,104
Total no. of fruit genera	50	27	23
Total no. of invertebrate families	91	66	48

TABLE 2. ANOVA of relative amount of fruit eaten by American Robins.

	Source of variation[a]					
Region	Month	Habitat	Sex	Time	Decade	*n*
Entire United States	***	***	NS	*	*	568
East	***	***	NS	NS	*	350
Central	***	NS	NS	**	NS	144
West	*	NS	NS	NS	NS	74

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant.

tebrates plus vertebrates, fruits, seeds, and vegetable matter; $n = 7{,}840$). Lepidopteran prey were almost exclusively caterpillars. Prey of other invertebrate orders were chiefly adults, although larval Scarabaeidae commonly were eaten. Caterpillars and other soft-bodied insect larvae, like earthworms, may be underrepresented in stomach-sample records, although unlike earthworms they have head capsules and mouthparts resistant to digestion.

Even within a restricted geographical area, such as the northeast, robins consumed fruits from at least 37 plant genera and 12 plant families. They preyed on invertebrates of 72 families and insects of 12 orders. In New York State alone, robins were recorded eating fruits from 31 genera and insects from 59 families; in the vicinity of Ithaca, New York, robins ate fruits from at least 17 genera and insects from at least 43 families. The most common fruit families in the northeast were Rosaceae (43% of fruit records), Cornaceae (12%), Ericaceae (9%), and Anacardiaceae (7%) ($n = 481$ fruit records). The commonest insect families in the northeast were Carabidae (9% of invertebrate records), Formicidae (8%), Curculionidae (7%), Scarabaeidae (6%), and Elateridae (6%) ($n = 1{,}943$ invertebrate records).

The same invertebrate taxa proved to be important in diets within each geographical region. For example, of the 10 most frequent taxa of invertebrate prey eaten in each region, 7 taxa were common to all three regions (Table 1). Their relative and absolute frequencies were almost the same. These same invertebrate taxa appeared in robins' diets in approximately the same order of frequency in a comparison of records from natural, agricultural, and suburban habitats. In all three regions and in most habitat types Rosaceae was the first or second (central region) most common family of fruits eaten by robins, followed in frequency by Anacardiaceae. Fruit diets were more variable between regions than invertebrate diets, however. Of the 10 fruit genera most frequently represented in the eastern subsample, only *Prunus* was commonly eaten elsewhere (Table 1).

The effect of season, habitat, time, and sex on diet.—The proportion of fruit in robins' diets

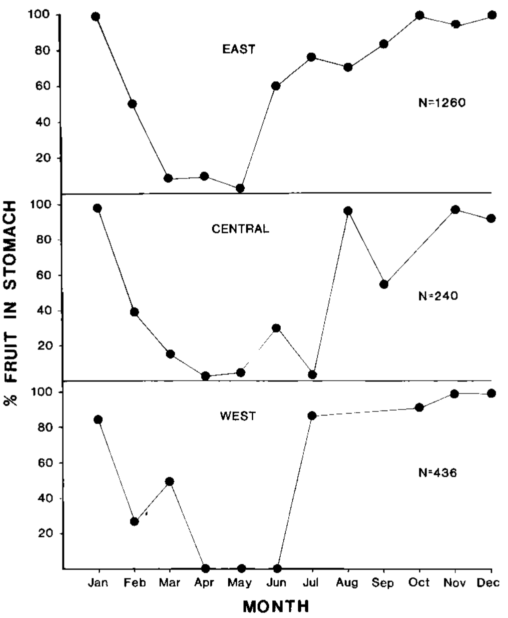

Fig. 1. Proportion of fruit (by volume, vs. animal prey) in the stomachs of robins collected in different months in three geographical regions of North America. Each point represents the median value for percentage of fruit for at least 5 individuals. Sample sizes (N) represent the number of individuals collected within each region over all months of the year.

was influenced by several factors. Most important was time of year (month when robins were collected), according to an ANOVA of the entire sample (Table 2). The same main effect was important in each of the regional samples (Table 2). For the entire sample and for certain regional samples, habitat and, to a lesser degree, time of day also affected the extent of fruit eating. Decade of collection had a minor effect, which could reflect long-term sampling biases, differences in methods of describing stomach contents used by different Biological Survey personnel, or actual long-term changes in the diets of robins (Table 2). Sex was an insignificant factor. In an ANOVA of records from the northeast, only month accounted for significant variation in the degree of fruit eating; interactive effects (habitat by month, sex by month, and sex by habitat) were not significant ($P > 0.05$).

TABLE 3. ANOVA of number of different food items in American Robin stomachs.

	Source of variation[a]					
Region	Month	Habitat	Sex	Time	Decade	*n*
Entire United States	***	**	NS	**	***	572
East	***	*	NS	**	***	350
Central	**	NS	NS	NS	NS	148
West	*	*	NS	NS	*	74

[a] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant.

The number of different food types in robin stomachs was also strongly affected by time of year in an ANOVA of all regions (Table 3). Habitat, time of day, and decade had significant effects in certain regions, but nowhere were they of major importance. Once again, there were no differences due to sex. In the northeast sample, time of year was apparently less important ($P = 0.09$) than time of day ($P < 0.01$) in explaining variation in number of food types. This inconsistent result probably is due to the fact that robins are scarce in the northeast during the late fall and winter (when fruits dominate their diets; Fig. 1), thereby affecting the ANOVA. All other factors, including interactive effects, were insignificant sources of variation in number of food types eaten at one time in the northeast.

The volume of stomach contents (fullness of the stomach) depended to some degree on time of year and time of day (Table 4). Habitat, sex, and decade were unimportant factors. In the northeast, only time of day approached statistical significance as a factor that accounted for variation in stomach fullness ($P = 0.06$). The results of the ANOVAs suggested that further analysis of individual factors was warranted.

TABLE 4. ANOVA of fullness of stomach in American Robins.

	Source of variation[a]					
Region	Month	Habitat	Sex	Time	Decade	*n*
Entire United States	*	NS	NS	**	NS	571
East	**	NS	NS	*	NS	349
Central	*	NS	NS	NS	NS	148
West	NS	NS	NS	NS	NS	74

[a] * = $P < 0.05$, ** = $P < 0.01$, NS = not significant.

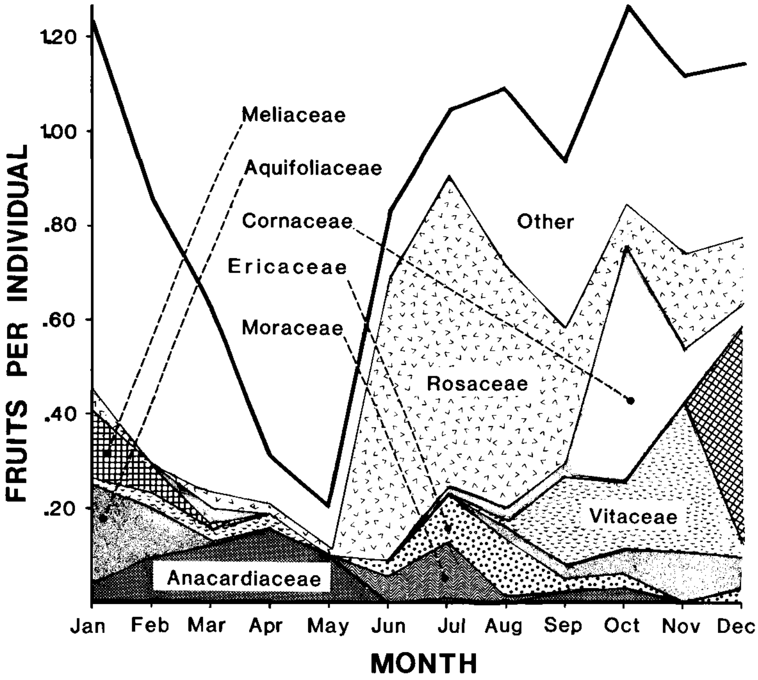

Fig. 2. Average occurrence of fruits of various plant families in the stomachs of robins in eastern North America in different months.

Each of these factors and their effects on the proportion of fruit, number of food types, fullness, and prey frequencies are considered in greater detail below.

Seasonal trends.—Robins ate fruits in every month of the year (Fig. 1). Most fruits eaten by birds that remained at high latitudes during the winter or returned in the spring were fall-ripening species that persist over the winter on plants. Perhaps the best examples are *Rhus* spp., whose fruits are eaten by robins in New York in every month of the year except August (pers. obs.); *Rhus* seeds were recorded in stomach samples in most months (Fig. 2). Different families of fruiting plants were prominent in robins' fruit diets at different times of year (Fig. 2). Species of Rosaceae dominated the fruit diet in mid- to late summer and were replaced in fall by species of Cornaceae and Vitaceae. The family Anacardiaceae was most conspicuous as a spring food. Genera within families also varied in importance over time. For example, within the Rosaceae, fruits in the genera *Prunus* and *Rubus* were eaten commonly in June, July, and August, whereas hawthorn fruits (*Crataegus* spp.) were eaten in late fall and again in spring (Fig. 3).

Although robins fed on fruits year-round, there was a clear seasonal pattern in fruit eating (cf. Jordano and Herrera 1981). The median percentage of fruit (by volume) in robins' stomachs was relatively low in the months immediately preceding breeding and during the breeding season; it declined to less than 10% in April and May in all three regions of North America (Fig. 1). (I use medians rather than means because values for the proportion of fruits eaten were bimodally distributed; means, however, showed similar seasonal trends despite being less extreme than medians.) During the fall and early winter (August through January), in contrast, over 80–99% of the diet (by volume) comprised fruits (Fig. 1). The change in diet occurred abruptly, with the proportion of fruit climbing from less than 10% to over 80% within 1–2 months (Fig. 1). The frequency of fruits in robins' stomachs was significantly lower in the breeding season (April through July) than in the nonbreeding season (Wilcoxon two-sample test, $P < 0.001$ in each region).

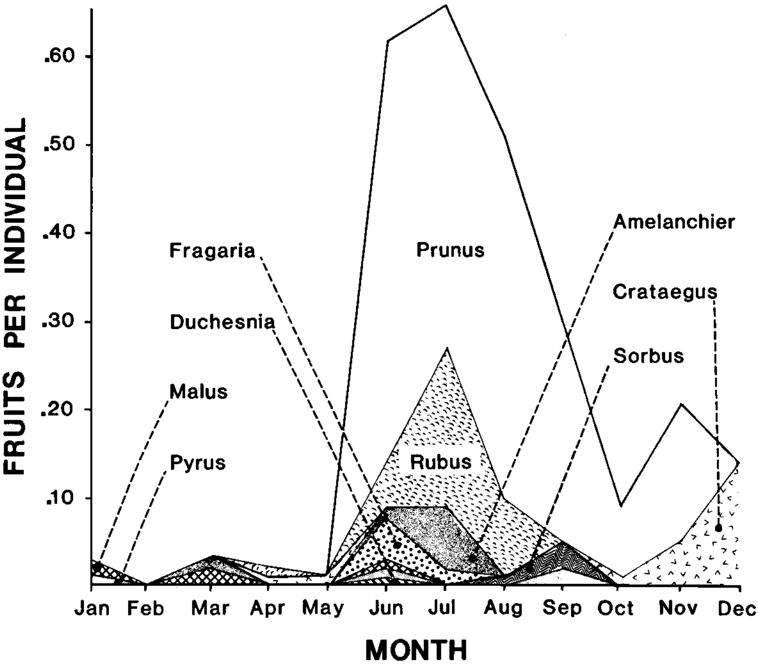

Fig. 3. Average occurrence of fruits of various genera in the Rosaceae (the plant family whose fruits were eaten most commonly by robins) in the stomachs of robins in eastern North America in different months.

In all regions, fruits were eaten most commonly in fall (median proportion eaten = 96%, mean = 77.2%, both sexes combined), with decreasing amounts eaten in winter (median = 93%, mean = 67.2%), summer (median = 66%, mean = 38.6%), and spring (median = 6%, mean = 37.7%) (Kruskal-Wallis test, $P < 0.001$; seasons defined as in Martin et al. 1951).

The number of distinct food types also varied seasonally. During the breeding season 4-6 taxa occurred on average in stomach contents. During winter months the mean number of distinct food types dropped by half (Fig. 4). The number of food items per stomach was significantly higher in the breeding season than in the nonbreeding season (Wilcoxon two-sample test, $P < 0.001$ in all regions). Consequently, the number of distinct food types and the degree of fruit eating were negatively correlated [Spearman rank test, $r_s = -0.49$, $P < 0.001$; linear regression: (percentage of fruit) = -6.5(number of distinct food types) + 78.0, $r^2 = 0.19$, $P < 0.001$, $n = 1{,}919$].

The fullness of stomachs varied with region. In the eastern sample, stomachs tended to be less full in the breeding season than in the nonbreeding season (Fig. 5; Wilcoxon two-sample test, $P < 0.001$). The opposite was true of the sample from the central region ($P < 0.001$), whereas there were no significant differences in fullness between seasons in the western region ($P = 0.12$). Within the sample as a whole, fullness of the stomach correlated positively with number of food types (Spearman rank test, $r_s = 0.19$, $P < 0.001$, $n = 1{,}919$) but not with proportion of fruit in the stomach ($r_s = 0$, $P = 0.92$).

Differences between sexes.—Male and female robins did not differ significantly in the proportion of fruit eaten in any month in any region, including New York State (Wilcoxon two-sample test, $P > 0.05$; Fig. 6). Both sexes showed similar seasonal trends in frugivory.

The sexes differed in the number of distinct food types (Wilcoxon two-sample test, $P > 0.15$) only in October in the eastern sample, July in the central sample, and November in the western sample. In these three months, the stomachs of females held more food types than the stomachs of males ($P < 0.05$). In 31 monthly comparisons from the three regions (12 months in the east, 9 months in the central region, 10

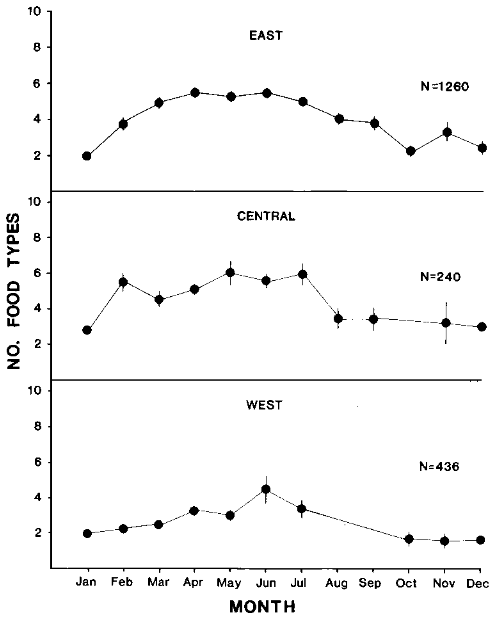

Fig. 4. Number of distinct food taxa in the stomachs of robins collected in different months in three geographical regions of North America. Each point represents the mean value of number of food types for at least 5 individuals; bars represent 1 SE of the mean.

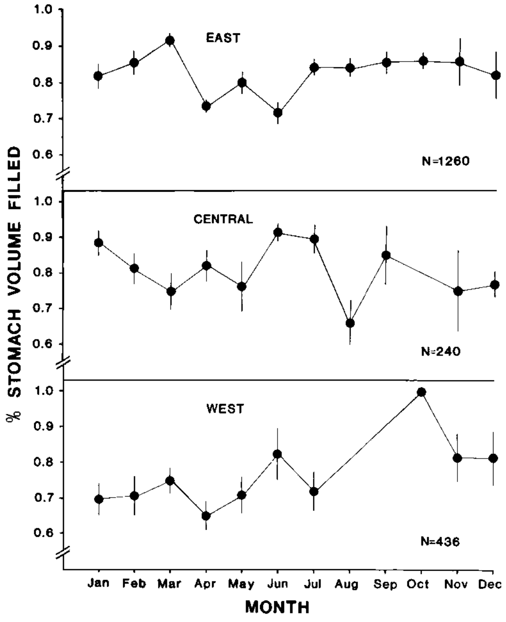

Fig. 5. Fullness of the stomachs of robins collected in different months in three geographical regions of North America. Each point represents the mean value of percentage of stomach volume filled for at least 5 individuals; bars represent 1 SE of the mean.

months in the west; not all months had sample sizes adequate for statistical comparisons), the number of food types per stomach in females exceeded that of males in 18 cases. The reverse was true in the remaining 13 cases, although, as noted above, differences were statistically significant in only 3 of these comparisons.

In 21 of 30 monthly comparisons, females had slightly fuller stomachs on average than males, although these differences were not significant in any month in any region (Wilcoxon two-sample test, $P > 0.05$).

The diet of the sexes was indistinguishable with regard to specific taxa of food items (vs. proportion of fruits, meal diversity, or volume of stomach contents). In most cases, sample sizes for particular taxa were too small to permit statistical tests of differences between sexes while controlling for time of year. However, the sexes did not differ in prey consumption in any month (Chi-square test, $P > 0.64$) in the four most commonly eaten insect orders (Coleoptera, Lepidoptera, Hymenoptera, Hemiptera) in the eastern region (which had the largest sample sizes). In the whole sample, without regard to time of year, the sexes did not differ in their consumption of these four insect taxa ($P = 0.66$, $n = 1{,}703$ prey items). Males and females ate similar numbers of taxa of invertebrates, fruits, and other vegetative matter (Table 5). Differences between the sexes in prey consumption of the most commonly eaten invertebrate orders and beetle families in the homogeneous New York sample during the four breeding-season months were slight or nonexistent (Fig. 7). At the prey-species level, sample sizes in homogeneous regions were too small to test for significant differences between males and females, but no such differences were suggested by the data.

Differences between age classes.—Stomachs of juvenile robins generally contained a higher proportion of fruit than stomachs of adults, at least in the eastern region where sample sizes were sufficiently large for statistical tests. In monthly comparisons from June through September (the period when juveniles can be easily distinguished by plumage), eastern juveniles consistently ate a higher proportion of

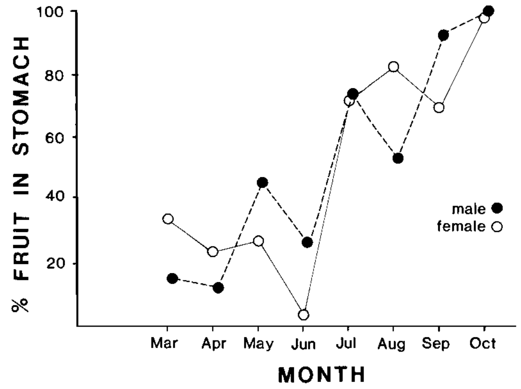

Fig. 6. Proportion of fruit (by volume, vs. animal prey) in the stomachs of male and female robins collected in different months in New York. Each point represents the median value for percentage of fruit for at least 5 individuals.

TABLE 5. Number of taxa of fruits, invertebrates, and grasses/seeds/leaves recorded eaten by adult male and female American Robins, and by juveniles in each geographical region.

	Region		
Food type	East	Central	West
Fruits			
Males	49	30	23
Females	46	28	23
Juveniles	21	9	2
Invertebrates			
Males	77	41	43
Females	60	45	43
Juveniles	54	36	9
Grasses/seeds/leaves			
Males	16	8	5
Females	12	8	5
Juveniles	11	3	0

fruits than did adults. The differences were significant in three of the four months (Wilcoxon two-sample test, $P < 0.01$, $n = 142$ juveniles and 405 adults).

The stomachs of juveniles in the eastern region contained significantly more food types on average than those of adults in June and August. This was reversed in July and September (Wilcoxon two-sample test, $P < 0.01$). In the central and western regions, juveniles' stomachs contained more food types than adults' in half of the monthly comparisons and fewer food types than adults' in the other half of the monthly comparisons, but none of these differences was significant ($P > 0.05$).

Eastern juveniles had fuller stomachs than adults in comparisons in June, July, and August, significantly so in June and August ($P < 0.01$). Adults, in contrast, had fuller stomachs in September ($P < 0.05$). There were no significant differences in the volume of stomach contents in monthly comparisons of juveniles and adults in the central and western regions, possibly due to smaller sample sizes. In terms of total numbers of taxa of fruits, invertebrates, and vegetation, fewer taxa were recorded for juveniles than for adults (Table 5). This pattern probably emerged because far fewer juveniles were sampled than adults. Furthermore, juveniles were collected chiefly in fall, when diets tend to be less diverse than in spring or summer.

Habitat effects.—Robin stomachs contained different proportions of fruit depending on the habitats in which birds were collected (Table 6). In the sample as a whole, the proportion of fruit per stomach was higher among birds collected in orchards (median percentage of fruit = 96.0%), native fruiting trees (90.0%), and forests (80.0%) than in agricultural fields collectively (10.5%). Birds found in meadows and edge habitats ate intermediate amounts of fruit (60.0% and 31.0%, respectively). Note that these figures are not adjusted for monthly biases. Habitat differences in fruit eating were greatest in the spring and early summer. In August, the extent of fruit eating began to converge in distinct habitats, and by October stomachs of birds collected in all habitats contained similar proportions of fruit (80–99%). Although the major habitat types were not represented in the same proportions in the three geographical regions (Chi-square test, $P < 0.02$), the same associations between fruit eating and habitat were found everywhere.

The number of distinct food types and the volume of stomach contents showed few consistent trends among habitats (Table 6). The consumption of insects from the four most commonly eaten orders depended on habitat (Chi-square test, $P < 0.001$). Coleoptera were eaten with disproportionate frequency in open habitats (fields, lawns) and relatively infrequently in edge habitats. The reverse was true for Hymenoptera and Lepidoptera. Hemiptera were preyed on more commonly than expected

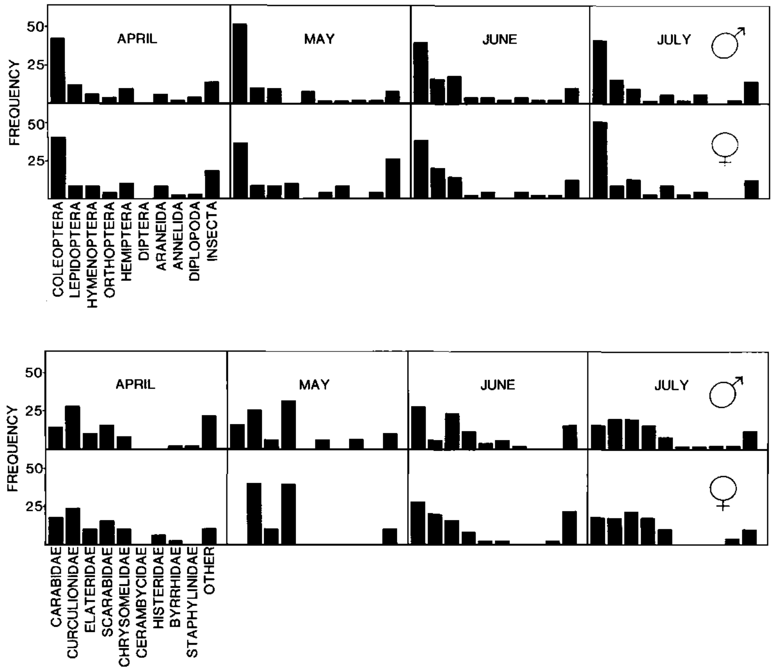

Fig. 7. Frequency (as a function of the number of all records of invertebrates eaten) of different invertebrate taxa (top) and beetle families (bottom) in the stomachs of male and female robins during the 4-month breeding season in New York.

by chance in forested habitats and less commonly than expected in open habitats ($P < 0.05$).

The influence of time of day.—Robin stomachs contained a smaller proportion of fruits in the morning ($n = 1{,}499$) than in the afternoon ($n = 423$) for the whole sample (Wilcoxon two-sample test, $P < 0.001$). In monthly comparisons, however, diurnal differences disappeared. Robins ate a greater percentage of fruits in the afternoon in 19 of 33 monthly comparisons, considering the three regions separately (sample sizes were too small in certain regions in certain months to permit statistical tests).

Neither the number of food types nor fullness of the stomach differed between morning and afternoon. Thus, in 18 of 33 monthly comparisons, robin stomachs contained more distinct food items in the afternoon than in the morning. Stomachs were fuller, on average, in the afternoon in 15 of 32 monthly comparisons. When considering only monthly comparisons that showed a significant difference between morning and afternoon ($P < 0.05$), there was somewhat better support for diurnal differences in diet. Relative to the morning, in the afternoon robins ate a significantly higher proportion of fruit in 5 of 7 monthly comparisons, their stomachs contained significantly more different food items in 4 of 5 comparisons, and their stomachs were significantly fuller in 4 of 5 comparisons.

Associations of food types within meals.—When two or more different prey types were found in stomachs, invertebrates were more likely to be associated with invertebrates, and fruits with fruits, than expected by chance (Chi-square test, $P < 0.001$, $n = 19{,}409$ associations of food items). Certain insect taxa co-occurred with greater frequency than expected by chance; others co-occurred relatively infrequently. A more detailed summary of prey associations within stomachs is given in Appendix 2. No general properties or associations emerged that could define a single feeding niche (Root 1967) for American Robins.

DISCUSSION

This study documents three distinct features of the diet of American Robins. First, robins eat

TABLE 6. Median proportion of fruit, mean number of distinct food types, and mean fullness of the stomach in American Robins collected in different habitats with $n > 30$ individual birds. These figures are not corrected for time of year.

Habitat	Percentage of fruit	No. of items	Fullness	n
Wheat fields	0.0	2.48	0.64	46
Alfalfa fields	3.5	5.67	0.87	72
Fields (general)	16.0	5.34	0.82	39
Pastures	52.0	4.35	0.82	97
Grain fields (miscellaneous)	72.0	2.16	0.65	73
Lake edges	0.0	4.64	0.47	47
Swamps	81.0	3.69	0.78	54
River edges	99.0	3.21	0.79	39
Lawns	81.0	3.50	0.79	34
Orchards (large fruits)	72.0	3.33	0.78	165
Vineyards	83.5	3.12	0.73	42
Cherry trees	90.0	5.29	0.83	127
Coniferous forests	51.0	5.18	0.78	34
Deciduous forests	77.0	3.79	0.85	182

a wide range of invertebrates and fruits throughout their range. Second, the nature of the diet changes dramatically and rapidly over time (Fig. 1). Robins rely on fruit during the fall and winter throughout their range. At the beginning of the breeding season, fruits comprise less than 10% of their diet. Third, the sexes do not differ in diet in any season. The first two results were recognized previously (Forbes 1879, Beal 1915a, Bent 1949, Brown 1976), although the abruptness and magnitude of the shift in diet were unanticipated. My study, however, provides a quantitative assessment of the breadth and seasonal variation in taxonomic composition of the diet in robins. The third result, the lack of differences between sexes, was unexpected because of sexual differences in reproductive roles and projected nutritional requirements (see below). These results raise several questions about seasonal changes in the diet of robins and other fruit-eating birds.

Both opportunity and choice probably determine diet depending on the time scale considered. On a daily basis diets do not appear to change with respect to amount of fruit eaten, diversity of meals, or fullness of the stomach, which could reflect relatively constant nutritional needs, nonselective foraging, and no differential depletion of distinct food types over short time periods. In contrast, during the year diets change markedly. Fruits in all habitats sampled varied seasonally in availability (Snow 1971, Morton 1973, Wheelwright 1985). In the Temperate Zone fruits tend to increase in abundance in the fall (Thompson and Willson 1979), which is when they dominate in robins' diets. The change in diets is far more sudden, however, than the change in relative availability of fruits. Insects are certainly common in most habitats in June, July, and August when robins begin to feed heavily on fruits. Furthermore, juveniles and adults differed in the amount of fruits consumed at the same times of year, suggesting that seasonal differences in diet reflect preferences (Brown 1976), age-related foraging skills (Gochfeld and Burger 1984), or nutritional needs as well as feeding opportunities.

Shifts from a cryptic, indigestible, nutritious insect diet to an accessible, easily digested, low-nutrition fruit diet presumably require major shifts in morphology and are constrained even over evolutionary time (Milton 1981, Demment and Van Soest 1985). Some species solve the problem by handling fruits and invertebrates in the stomach in distinct ways (Walsberg 1975). Other species may exhibit seasonal changes in gizzard thickness (Spitzer 1972), intestine length (Al-Jaborae 1980), cecum length (Pendergast and Boag 1973), or gut microflora (Jayne-Williams and Coates 1969). Conceivably, digestive enzymes could be adjusted to seasonal changes in diet, although this has not been documented. In any event, robins and other Temperate Zone fruit-eating birds must process fruits effectively, for molt and migration occur during periods when their diet is dominated by fruits. These events are presumably energetically and nutritionally expensive (Robbins 1983).

Another potential problem raised by these results is to account for the lack of detectable differences in diet between the sexes. Females of all bird species generally require elevated levels of protein, minerals, and energy during egg laying (Robbins 1983). Caloric intake and nitrogen requirements, for example, may quadruple during reproduction (Robbins 1981, Walsberg 1983). In contrast, males of most species invest relatively little in the early stages of reproduction, including egg laying, nest building, and incubation (Howell 1942). Such ecological differences would be expected to demand different diets for male and female robins. Yet I found no evidence that female robins eat a wider range or distinct taxonomic distribution of food items, that their stomachs contain a greater volume of food or more food types, or that they consume less fruit than males at any season or in any region. Female robins seem to eat the same things as males. If this is true, it is possible that female robins meet their nutritional requirements by eating more earthworms or other soft-bodied prey that are underrepresented in the sample, process foods at a faster rate, are more efficient at nutrient uptake, or forage for more hours per day than males. There is no published evidence for any of these possibilities, however. Conceivably, females select more nutritious individual prey items than males, or feed on distinct species (vs. genera or families) than males, differences that would not have been detected in this study (see Green and Jaksic 1983). Males may supplement females' diets through courtship feeding (E. Jones pers. comm.).

Differences in the amount of fruit eaten by adult and juvenile robins may be explained by age-specific differences in foraging ability. Because of their inexperience, juveniles have inferior foraging success when hunting invertebrates (Gochfeld and Burger 1984) and must turn to fruits to meet their caloric needs. Fruits, despite their nutritional limitations, are acquired more easily than invertebrates (Snow 1971, Wheelwright 1983). Thus, even though developing juveniles presumably have greater protein requirements than adults (Robbins 1983), they may have to sustain their growth on a nutritionally inferior diet high in fruits until they have learned to forage efficiently.

Diet breadth and the distribution of American Robins.—American Robins have an extremely broad diet, and it is tempting to relate this to their broad geographic range and population size. It is important to distinguish diet breadth from diet plasticity, however. Even though robins eat invertebrates from over 100 families, the same taxa predominate in stomach samples throughout the robins' range, irrespective of habitat. Robins may owe their success to their ability to feed predominately on terrestrial invertebrate taxa that happen to be widespread and abundant, not to any behavioral flexibility that has enabled them to learn new foraging skills. Although robins are generalists in one sense, they appear specialized in another sense because they are tied to certain food types.

Robins appeared more flexible with respect to fruit diet than to invertebrate diet. Only rosaceous fruits were eaten commonly in each region. The consistently high frequency of the Rosaceae in robins' diets reinforces a growing perception that fruit-eating birds may feed opportunistically on many fruit species but tend to specialize on the fruits of a few plant families, indicating selective foraging and possible coevolution at taxonomic levels above the species (Wheelwright 1983, Moermond and Denslow 1985).

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APPENDIX 1. Fruit and invertebrate taxa eaten by American Robins. Families and genera are listed for fruits; orders and families are listed for insects. Taxa are arranged alphabetically.

Fruits

- Anacardiaceae
  - *Rhus*
  - *Schinus*
- Aquifoliaceae
  - *Ilex*
  - *Nemopanthus*
- Berberidaceae
  - *Berberis*
- Caprifoliaceae
  - *Lonicera*
  - *Sambucus*
  - *Symphoricarpos*
  - *Viburnum*
- Celastraceae
  - *Celastrus*
  - *Euonyumus*
- Cornaceae
  - *Cornus*
  - *Nyssa*
- Ebenaceae
  - *Diospyros*
- Elaeagnaceae
  - *Elaeagnus*
- Empetraceae
  - *Empetrum*
- Ericaceae
  - *Gaylussacia*
  - *Oxycoccus*
  - *Vaccinium*
- Lauraceae
  - *Lindera*
  - *Persea*
  - *Sassafras*
- Liliaceae
  - *Smilax*
- Loranthaceae
  - *Phoradendron*
- Meliaceae
  - *Melia*
- Menispermaceae
  - *Menispermum*
- Moraceae
  - *Ficus*
  - *Morus*
- Myricaceae
  - *Myrica*
- Oleaceae
  - *Olea*
- Palmae
  - *Sabal*
- Pinaceae
  - *Juniperus*
- Phytolaccaceae
  - *Phytolacca*
- Rhamnaceae
  - *Berchemia*
  - *Rhamnus*
- Rosaceae
  - *Amelanchier*
  - *Crataegus*
  - *Duchesnia*
  - *Fragaria*
  - *Malus*
  - *Prunus*
  - *Pyrus*
  - *Rubus*
  - *Sorbus*
- Rubiaceae
  - *Mitchella*
- Saxifragaceae
  - *Ribes*
- Solanceae
  - *Solanum*
- Ulmaceae
  - *Celtis*
- Vitaceae
  - *Ampelopsis*
  - *Parthenocissus*
  - *Vitis*

Invertebrates

- Amphipoda
- Annelida
- Arachnida
  - Araneida
  - Pseudoscorpionida
- Chilopoda
- Coleoptera
  - Anthicidae
  - Buprestidae
  - Byrrhidae
  - Cantharidae
  - Carabidae
  - Cerambycidae
  - Chrysomelidae
  - Cicindelidae
  - Coccinelidae
  - Curculionidae
  - Dermestidae
  - Dytiscidae
  - Elateridae
  - Erotylidae
  - Haliplidae
  - Histeridae
  - Hydrophilidae
  - Lampyridae
  - Languridae
  - Miridae
  - Nitidulidae
  - Scarabidae
  - Scolytidae
  - Silphiidae
  - Staphylinidae
  - Tenebrionidae
- Decapoda
- Diplopoda
  - Julida
  - Polydesmida
- Diptera
  - Anthomyiidae
  - Bibionidae
  - Chironomidae
  - Chloropidae
  - Empididae
  - Ephydridae
  - Lonchaeidae
  - Micropezidae
  - Muscidae
  - Mycetobiidae
  - Otitidae
  - Stratiomyidae
  - Tabanidae
  - Tachinidae
  - Tipulidae
  - Sarcophagidae
- Gastropoda
- Hemiptera
  - Anthocoridae
  - Coreidae
  - Corimelidae
  - Corizidae
  - Cydnidae
  - Lygaeidae
  - Miridae
  - Nabidae
  - Pentatomidae
  - Piesmidae
  - Reduviidae
  - Rhopalidae
  - Scutelleridae
- Homoptera
  - Aphidae
  - Cicadellidae
  - Cicadidae
  - Fulgoridae
  - Membracidae
- Hymenoptera
  - Apidae
  - Braconidae
  - Chalcidae
  - Cynipidae
  - Formicidae
  - Halictidae
  - Ichneumonidae
  - Sphecidae
  - Symphyta (misc.)
  - Tenthredinidae
  - Tiphiidae
  - Vespidae
- Isopoda
- Isoptera
- Lepidoptera
  - Arctiidae
  - Bombycidae
  - Geometridae
  - Noctuidae
  - Notodontidae
  - Olethreutidae
  - Psychidae
  - Tortricidae
- Mallophaga
- Mecoptera
  - Meropidae
- Neuroptera
  - Chrysopidae
  - Corydalidae
  - Myrmelionidae
  - Raphidiidae
- Odonata
  - Anisoptera (misc.)
  - Zygoptera (misc.)
- Orthoptera
  - Acrididae
  - Blattidae
  - Gryllidae
  - Tetrigidae
  - Tettigoniidae
- Phalangida
- Trichoptera

APPENDIX 2. Frequency of co-occurrence of the most common taxa of fruits and invertebrates in American Robin stomachs.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
1. Arachnida	—																														
2. Diplopoda	21	—																													
3. Acrididae	55	25	—																												
4. Pentatomidae	44	21	37	—																											
5. Unidentified Hemiptera	42	21	32	18	—																										
6. Carabidae	117	63	167	87	79	—																									
7. Chrysomelidae	22	13	20	18	21	57	—																								
8. Curculionidae	92	60	70	82	73	258	58	—																							
9. Elateridae	67	32	45	50	27	164	36	144	—																						
10. Scarabidae	81	38	82	73	59	222	45	196	135	—																					
11. Unidentified Coleoptera	38	31	42	24	31	111	20	102	64	76	—																				
12. Noctuidae	11	3	11	5	9	54	10	40	19	28	47	—																			
13. Unidentified Lepidoptera	140	68	112	94	99	330	64	258	161	256	132	17	—																		
14. Unidentified Diptera	14	18	8	12	13	46	16	40	24	32	32	13	49	—																	
15. Formicidae	72	34	74	50	53	164	38	169	105	140	96	21	179	22	—																
16. Unidentified Hymenoptera	23	15	28	17	33	67	16	61	35	41	27	3	71	13	49	—															
17. Unidentified insects	262	118	201	199	153	616	160	519	326	418	267	100	614	121	315	126	—														
18. *Smilax*	7	8	9	3	3	23	1	21	7	5	18	1	14	1	3	1	28	—													
19. *Celtis*	0	1	0	1	0	6	3	4	0	1	5	0	5	1	0	0	9	3	—												
20. *Morus*	7	3	10	6	0	19	6	14	9	10	8	2	14	2	10	3	29	0	0	—											
21. Unidentified *Prunus*	19	7	38	11	18	88	25	69	43	63	41	10	76	10	74	21	160	0	0	14	—										
22. *Rubus*	12	0	21	7	7	22	4	13	15	13	8	1	33	1	20	8	43	1	0	2	19	—									
23. *Melia*	1	3	2	0	2	25	3	1	0	2	8	0	14	2	0	0	34	2	4	0	0	0	—								
24. *Rhus*	18	7	16	14	13	19	4	25	12	17	9	2	37	2	12	6	51	4	2	0	0	0	0	—							
25. *Schinus*	0	1	1	1	1	5	1	2	2	2	2	6	2	0	1	1	7	0	0	0	0	0	0	0	—						
26. *Ilex*	0	0	1	0	1	4	1	2	3	1	6	0	6	1	1	0	10	7	7	0	0	0	0	1	0	—					
27. *Vitis*	3	2	9	3	8	17	2	8	1	9	4	1	20	1	6	0	39	0	0	0	1	0	0	1	1	1	—				
28. *Cornus*	3	1	2	1	4	3	1	2	2	1	3	1	5	1	4	2	9	0	0	0	1	2	0	2	0	1	4	—			
29. *Vaccinium*	8	3	9	7	2	15	1	9	15	13	6	0	23	2	13	3	26	0	0	0	3	4	1	0	0	0	0	0	—		
30. Unidentified fruits	158	100	132	106	90	405	68	314	196	247	197	43	407	66	231	104	844	25	10	14	86	25	8	30	2	17	16	17	11	—	
Total	1,337	696	1,179	889	799	2,740	583	2,013	1,174	1,375	916	221	1,569	246	739	275	1,992	42	23	30	110	31	9	34	3	19	20	17	11	294	—