

ANNUAL DIET OF CEDAR WAXWINGS BASED ON U.S. BIOLOGICAL SURVEY RECORDS (1885-1950) COMPARED TO DIET OF AMERICAN ROBINS: CONTRASTS IN DIETARY PATTERNS AND NATURAL HISTORY

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ABSTRACT.—The diet of Cedar Waxwings (*Bombycilla cedrorum*) is described using records of gut contents collected by the U.S. Biological Survey. Cedar Waxwings eat more fruit than most other Temperate Zone birds, including one of the most frugivorous thrushes, the American Robin (*Turdus migratorius*; 84 vs. 57% fruit in their annual diets, respectively). Cedar Waxwings are almost exclusively frugivorous in the winter and early spring. During the spring period of fruit scarcity, flowers comprise a large portion of the diet of waxwings (44% of May diet). Cedar Waxwings eat aerial and vegetation-borne animal prey, whereas American Robins eat vegetation-borne and terrestrial prey. The fruits eaten by Cedar Waxwings are characterized by high sugar and low lipid content. American Robins, like other North American thrushes, eat sugary and lipid-rich fruits, suggesting contrasting digestive strategies in waxwings and thrushes. This perspective is reinforced by the correspondence between these birds' diets, the timing of breeding in relation to availability of preferred foods, and flocking patterns. Received 24 February 1995, accepted 25 August 1995.

ECOLOGISTS OFTEN equate caloric content of foods with nutritive value without considering the specific nutrient composition of foods and the digestive characteristics of consumers (e.g. Martin 1985). Such assessments assume that animals are similar in the ways that they process and assimilate foods and that digestion of various nutrients does not vary among species. This perspective has probably resulted from the historical importance of energy in ecological theory (Elton 1927, Lindeman 1942, Schoener 1971, Krebs 1978, McKey 1975). Although knowledge of caloric content of foods can be informative in systems where animals have comparable digestive characteristics and foods are chemically similar (Pyke 1980), this approach ignores crucial information in comparisons between animals with different digestive systems eating chemically diverse diets. Detailed comparisons of dietary habits can identify specializations to particular foods and corresponding limitations imposed by such adaptations (e.g. Walsberg 1975, Milton et al. 1980, Milton 1981, Martinez del Rio 1990b).

This study describes the diet of Cedar Waxwings (*Bombycilla cedrorum*) and compares it to the diet of American Robins (*Turdus migratorius*; Wheelwright 1986). These birds are two of the principal avian frugivores of North America. They share similar ranges throughout the year and are among the few frugivorous birds that winter in the northern United States (AOU 1983). From this comparison, I develop inferences about digestive strategies and describe natural-history traits of each species that appear to be associated with their respective dietary specializations.

METHODS

This analysis is based on records of Cedar Waxwing stomach contents collected by the U.S. Biological Survey (subsequently the U.S. Fish and Wildlife Service) from 1885 to 1950, from the same data set used by Martin et al. (1951) for their comprehensive book on North American wildlife food habits. Records of gut contents of Cedar Waxwings were provided by the library of the Patuxent Wildlife Research Center in Laurel, Maryland. Each record includes: collection date, location, sex, stomach fullness, proportions of animal and vegetable foods in stomach, and description of food items. Because information from stomach contents may be influenced by collector bias in choosing collecting sites, as well as by differential preservation and retention of foods in the gizzard, care must be taken in analysis and interpretation of these re-

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cords (for discussion of potential biases, see Wheelwright 1986). Foods differ in their detectability within animals: fruits are easily identified by their seeds; earthworms become amorphous and difficult to distinguish; and liquid foods, like sap and nectar, are virtually impossible to detect. However, for birds that eat many insects and fruits, items that contain indigestible components that permit identification of foods (chitinous exoskeletons and seeds, respectively), gut contents offer a means of characterizing overall diets and evaluating seasonal changes in food habits. The collection of birds and quantification of gut contents were conducted by many of the same biologists over the same historical time period, making this a unique data set from which strong comparisons can be made. These records also establish a historical baseline from which long-term shifts in dietary habits can be evaluated.

My study is primarily based on gut contents of 212 Cedar Waxwings from the eastern United States (Atlantic Coast states westward to Minnesota, Iowa, Missouri, Arkansas, and Louisiana). Most collection sites were in New York and Pennsylvania (49%); other northeastern states comprised 35% of the sites. Information for American Robins came from comparable work from the same geographic region (Wheelwright 1986). I also describe Cedar Waxwing diets from 71 birds collected from the central and western United States (56% from California, 25% from Oregon, 13% from North Dakota).

Cedar Waxwings congregate in flocks during much of the year, characteristically foraging on local concentrations of fruit for extended periods (Bent 1950, pers. obs.). Because birds within a flock do not represent independent samples of feeding choices, it is important in statistical treatment of gut-content data to treat specimens collected from the same flock as a single replicate. I inferred flock association by locality and collection date information, defining replicates as all waxwings collected at the same site during a seven-day period ($n = 90$ replicates). Although arbitrary, this time period was used because it aggregated samples that were collected at single sites during short-term efforts by individual collectors, minimizing the potential for biases from pseudoreplication.

The mean percent of fruit in the Cedar Waxwing's diet was calculated by averaging the values from birds for each replicate and then averaging replicates for each month (an unweighted measure to avoid bias from unequal monthly sample sizes). Annual diet composition was based on mean values of proportion of fruit in stomachs, rather than median values. Wheelwright (1986) described American Robin diets with median values of the proportion of fruit in birds' stomachs because these data were bimodally distributed, as was also true for the Cedar Waxwing data. Gut contents tended to reflect whatever birds had most recently fed on, either fruits or insects. Median measures describe the condition of an "average" bird's

gut. I use mean values because they are more descriptive of the relative proportions of foods in the overall diets of Cedar Waxwings; each bird gut represents a sample from a bimodal distribution of foods that comprise the diet of waxwings. Because I am focusing on questions related to the nutritional ecology of wild birds, and a single filled gut is probably not a good representation of a bird's balanced diet, a mean measure is more appropriate. Data expressed as proportions were arcsine-transformed for parametric statistical analyses.

I calculated proportional use of fruit genera by occurrence of each fruit genus relative to total number of fruit occurrences in individual birds for each replicate; replicates thus contributed equally to monthly values of relative fruit consumption (again, an unweighted measure). Because monthly sample sizes were low from November through April, I combined data from November through December and January through April. Waxwing guts contained similar taxa of fruits and consumption of fruit relative to other diet items was constant during each of these seasonal units. Each fruit's relative occurrence was apportioned evenly only over the months during which it was found in stomach contents (e.g. *Malus* spp. fruits occurred only from February through April).

I compared morphological (fruit fresh mass, seed mass, seed mass/fresh mass, pulp dry matter/fruit, pulp dry matter/seed mass, and pulp water content) and nutritional (hexose, lipid, and nitrogen content of pulp, and caloric content of fruits) characteristics of fruits eaten by Cedar Waxwings to those not recorded in their diet, but eaten by American Robins, by linear discriminant-function analysis (Stevens 1986). The U.S. Biological Survey data were supplemented with personal observations of feeding by these birds from 1988 to 1993 in the vicinity of Ithaca, New York (see Table 1). Measurements were log-transformed and proportions were arcsine-transformed.

This analysis focused on 33 of the most common bird-dispersed fruits of the northeastern United States. Information for 21 fruits came from published sources; I analyzed fruits of 12 other species. Fruits were collected from single shrubs (12–100 fruits) for each sample. Seeds were removed from fruit pulp (pulp and skin) and the sample was freeze-dried. Samples were homogenized by grinding with a mortar and pestle. I analyzed fruits for sugars soluble in 80% ethanol (hexoses and potentially sucrose; Yemm and Willis 1954), nitrogen (Kjeldahl), and lipids (ether extraction). Literature values for nitrogen content were determined by Kjeldahl. Because nonprotein compounds may contain nitrogen, nitrogen content of fruit pulp represents an index of maximum protein/amino acid content. Dry matter was determined by drying to constant mass at 100°C in a forced-air oven. My results are replicated by samples from separate shrubs. For published data from more than one source, I calculated mean values across studies.

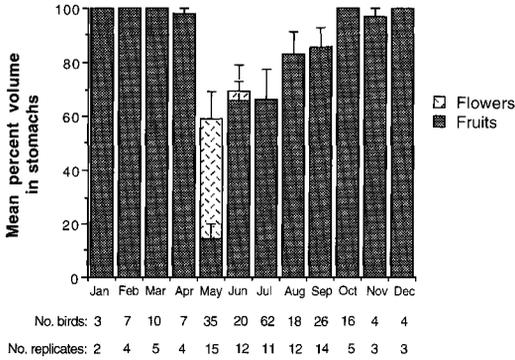


Fig. 1. Monthly diet composition of Cedar Waxwings. Whiskers indicate SE. Bars show proportions of fruit in diet; remainder of diet is animal prey, primarily insects. Data was replicated by flock, rather than individual bird (see Methods for details).

To determine relative consumption of arthropods (orders and families), I analyzed the data by replicate exactly as performed for fruit genera ($n = 41$ replicates that included animal prey); sample sizes were too small to assess monthly patterns of invertebrate prey consumption. Tachinid larvae (Tachinidae) were omitted from the analysis of arthropod prey (three guts) since they are insect parasites and, thus, do not represent prey actively chosen by waxwings. Seasonal patterns of grouping by foraging Cedar Waxwings and American Robins are reported from records of birds encountered near Ithaca, New York, from 1989 through 1993.

RESULTS

Seasonal dietary patterns.—The annual diet of Cedar Waxwings consisted of 84% fruit, 4% flowers, and 12% insects, in agreement with the estimate of Martin et al. (1951) of mean annual use of plant foods by Cedar Waxwings of 88%. Waxwings showed strong seasonal trends in the proportion of fruit in their diet (ANOVA, $F = 8.2$, $df = 11$ and 78 , $P < 0.001$; Fig. 1). There were no differences between males and females in the proportion of fruit in stomachs (two-factor ANOVA [season and sex], $F = 0.001$, $df = 1$ and 151 , $P = 0.98$) or in stomach fullness (same analysis, $F = 0.92$, $df = 1$ and 149 , $P = 0.34$). From October through April waxwings consumed almost exclusively fruit (99%). In May, a month of low fruit availability (McAtee 1914, Sherburne 1972, Thompson and Willson 1979, McPherson 1987, pers. obs.), frugivory by Cedar Waxwings declined markedly, with a dramatic increase in flower (petals and stamens) consumption (44% of May diet). Frugivory increased sharply in June with the ripening of early summer fruits (*Amelanchier* spp., *Morus* spp., and *Fragaria* spp.; Fig. 2). Waxwings ate insects from May through September, but fruit still dominated their diets during these months (Fig. 1).

Cedar Waxwings were consistently more frugivorous than American Robins throughout the year, compared by monthly median percent fruit

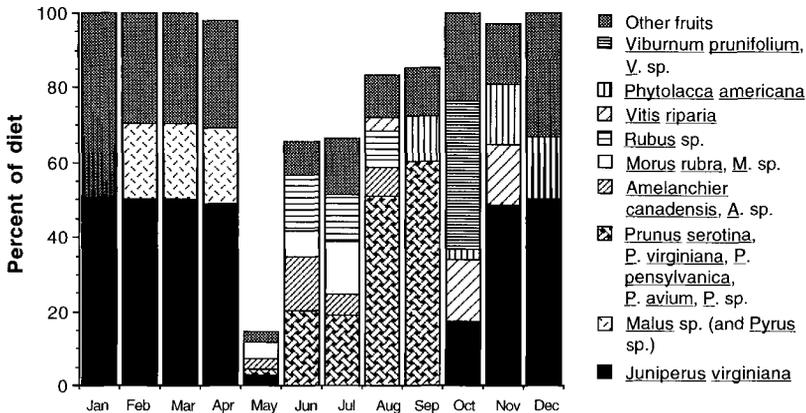


Fig. 2. Seasonal fruit consumption by Cedar Waxwings. "Other fruits" are: (Jan–Apr) *Celtis occidentalis*, *Phoradendron serotinum*, *Ligustrum japonicum*, *Berberis vulgaris*, *Berberis* sp.; (Jun) *Fragaria virginiana*, *Ribes* sp.; (Jul–Sep) *Lonicera caerulea*, *Vaccinium* sp., *Gaylussacia* sp., *Sambucus canadensis*, *S.* sp.; (Sep–Nov) *Cornus florida*, *Nyssa sylvatica*.

per gut (one-tailed, paired t -test, $df = 11$, $P = 0.009$; Fig. 3) or seasonal mean percent fruit per gut (same test, $df = 3$, $P < 0.001$; respective mean amounts of fruit in waxwing and robin diets were 56 and 38% from April to May, 72 and 39% from June to August, 93 and 77% from September to October, and 99 and 67% from November to March; Wheelwright 1986). Annually, Cedar Waxwing diets contained 84% fruit, compared to 57% for American Robins (Wheelwright 1986).

Kinds of fruits eaten.—Fruits of *Juniperus virginiana* were prominent in the Cedar Waxwing's diet over winter and spring months (40–50% of diet from October to April, 27% of annual diet; Fig. 2). Apples (*Malus* spp. [including records of "*Pyrus*"]) were the next most prominent winter fruit of waxwings (21% of diet from February to April). Cherries (*Prunus* spp.) were commonly eaten by waxwings from June through September (Fig. 2), forming 37% of their diet during this period. Naturalized *Prunus* spp. were consumed in June and July; pin cherries (*P. pensylvanica*) were eaten from July through September; and chokecherries (*P. virginiana*) and black cherries (*P. serotina*) were eaten primarily in August and September.

Cedar Waxwings and American Robins ate many of the same fruits throughout the year. *Prunus* spp. fruits were the most common fruits in both birds' diets during the summer and fall (12 and 23% of annual fruit diets of waxwings and robins, respectively). Relative consumption of *Prunus* spp. fruits by these birds was similar (Fig. 2; Wheelwright 1986:fig. 2), comprising about 50 and 69% of their fruit diets during this period, respectively. Despite broad overlap in fruit selection by robins and waxwings, their overall patterns of fruit use were different (proportional use of eight common fruit genera; $G = 61.39$, $df = 7$, $P < 0.001$). During winter and spring months, waxwings consumed more *Juniperus virginiana* fruits than did robins (45 vs. 5% of fruit diets from October through April, respectively). *Rhus* spp. fruits were eaten by American Robins during most of the year (7% of annual fruit diet), especially from January through June (Wheelwright 1986:fig. 2), but not by Cedar Waxwings. In the fall, fruits of the Cornaceae (four species) were prominent in American Robin guts (7% of annual fruit diet), whereas only *Cornus florida* was consumed by Cedar Waxwings (3% of annual fruit diet).

Nutritional characteristics of fruits eaten by Cedar

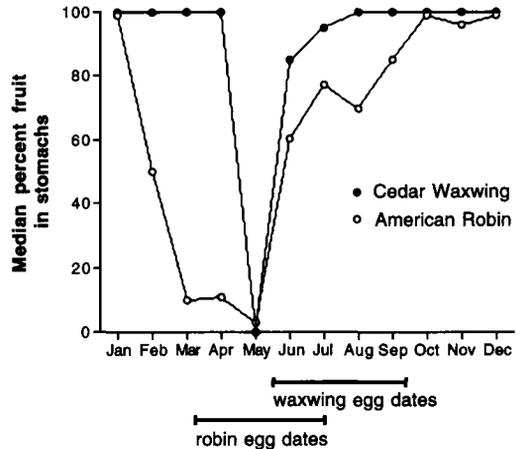


Fig. 3. Monthly proportion of fruit (by volume) in diets of Cedar Waxwings and American Robins from eastern North America. Median measure used for consistency with Wheelwright (1986), but mean measure recommended for reporting diet composition (see Methods and Fig. 1). Breeding periods for New York from Bull (1974).

Waxwings.—*Cornus racemosa*, *Viburnum dentatum*, *Lindera benzoin*, *Parthenocissus quinquefolia*, *Rhus typhina*, and *Myrica pensylvanica* were avoided by Cedar Waxwings, whereas virtually all bird-dispersed fruits were eaten by American Robins (Table 1). The contemporary diet of Cedar Waxwings differed from the U.S. Biological Survey data in the inclusion of several naturalized species (*Lonicera morrowii*, *Viburnum opulus*, and *Rhamnus cathartica*).

The results of linear discriminant-function analysis were qualitatively the same whether or not my recent observations were included; therefore, I report a single analysis for the combined results (see Table 1). Fruits eaten by Cedar Waxwings were distinguished from those avoided by (in decreasing strength of association with the discriminant function): low lipid and high hexose content of fruit pulp (Fig. 4), larger fruit mass, higher water content, and more dry pulp per fruit (Table 2). Bird-dispersed fruits in the eastern United States are segregated into these two general syndromes: sugary fruits tend to be relatively large with high water content in their fruit pulp, whereas lipid-rich fruits tend to be small with drier pulp (White 1989). Lipid content was redundant in the analysis (low discriminant-function coefficient), suggesting that fruit selection was cued more to the presence

TABLE 1. Traits of fruits of northeastern United States from literature (means of all reports) and my study (\pm SD). Feeding records from Biological Survey data and my observations. Dashes represent fruits I did not encounter. Robin data are from Beal (1915a). Fruits grouped in table by seasonal availability: (species 1-8) summer, (9-18) fall, (19-33) persistent.

Fruit ^a	Fruit mass (mg)	Seed mass (mg)	Pulp dry mass (mg)	Water (%)	Hexose (%)	Fat (%)	Nitrogen (mg/g)	Cedar Waxwing		American Robin			
								vey data	New data	vey data	New data		
1. <i>Amelanchier arborea</i> (W)	507	3	93	82	42	<1	4.5	12	7	X	19	4	X
2. <i>Fragaria virginiana</i> (W)	1,140	0.5	92	92	92	1	1.9	1	2	X	6	0	X
3. <i>Lonicera morrowii</i> (n = 6)	310 \pm 57	15 \pm 3	36 \pm 8	88 \pm 2	74 \pm 3	2 \pm 2	5.3 \pm 2.0	0	42	X	0	10	X
4. <i>Morus rubra</i> (S)	780	2	112	86	66	1	9.4	17	1	X	19	0	X
5. <i>Prunus virginiana</i> (n = 4)	502 \pm 5	82 \pm 20	103 \pm 11	76 \pm 2	58 \pm 2	3 \pm 5	5.8 \pm 1.7	6	5	X	12	2	X
6. <i>P. serotina</i> (n = 2)	618 \pm 54	135 \pm 41	108 \pm 1	78 \pm 0	71	<1	5.6	24	2	X	28	4	X
7. <i>Rubus occidentalis</i> (W)	639	1	61	90	71	<1	3.7	11	0	X	47	0	X
8. <i>Vaccinium</i> spp. (W)	230	1	43	81	56	1	5.0	3	-	X	42	-	X
9. <i>Cornus racemosa</i> (n = 2)	206 \pm 16	43 \pm 8	43 \pm 7	74 \pm 3	37 \pm 3	37	7.8 \pm 1.4	0	0	O	3	4	X
10. <i>Lindera benzoin</i> (n = 3)	341 \pm 71	129 \pm 26	51 \pm 17	76 \pm 7	7 \pm 3	49 \pm 5	17.0 \pm 2.1	0	0	O	3	0	X
11. <i>Viburnum dentatum</i> (n = 2)	92 \pm 11	31 \pm 10	16 \pm 9	67 \pm 11	9 \pm 1	44 \pm 3	6.1 \pm 1.2	0	0	O	3	3	X
12. <i>Parthenocissus quinquefolia</i> (J, S, W)	203	35	29	77	14	26	9.0	0	0	O	21	0	X
13. <i>Phytolacca americana</i> (n = 4)	393 \pm 59	88 \pm 6	47 \pm 3	84 \pm 2	73 \pm 10	0	31.5 \pm 18.7	5	1	X	15	0	X
14. <i>Sambucus canadensis</i> (J, W)	69	18	7	86	28	4	13.0	0	4	X	8	0	X
15. <i>Cornus florida</i> (S, W)	297	71	65	69	24	29	7.0	3	0	X	59	0	X
16. <i>C. amomum</i> (W)	203	43	34	79	55	2	7.7	0	1	X	0	0	O
17. <i>Nyssa sylvatica</i> (W)	438	128	81	73	46	15	6.0	4	-	X	11	-	X
18. <i>Vitis riparia</i> (n = 3)	524 \pm 98	79 \pm 14	104 \pm 17	76 \pm 2	72 \pm 1	5 \pm 3	8.3 \pm 3.1	3	5	X	1	3	X
19. <i>Berberis vulgaris</i> (H)	148	20	26	80	69	6	8.0	2	0	X	1	0	X
20. <i>Celtis occidentalis</i> (J, W)	436	192	141	42	37	1	5.0	1	-	X	22	-	X
21. <i>Crataegus crus-galli</i> (W)	786	81	217	69	31	1	4.0	0	7	X	2	5	X
22. <i>Ilex verticillata</i> (W)	277	6	63	77	43	4	4.0	0	4	X	3	2	X
23. <i>Juniperus virginiana</i> (W)	46	9	19	48	72	7	6.0	24	1	X	18	0	X
24. <i>Ligustrum vulgare</i> (H)	163	24	18	87	74	3	9.0	3	2	X	0	0	O
25. <i>Malus</i> sp. (n = 2)	809 \pm 112	116 \pm 4	225 \pm 67	68 \pm 5	54	2	3.0	5	26	X	9	17	X
26. <i>Myrica pensylvanica</i> (W)	30	13	12	32	0	44	9.8	0	-	O	6	-	X
27. <i>Phoradendron serotinum</i> (S)	48	6	15	64	33	6	18.0	2	-	X	3	-	X
28. <i>Rhamnus cathartica</i> (n = 2)	374 \pm 21	67 \pm 1	82 \pm 8	73 \pm 1	65 \pm 1	2 \pm 3	5.0 \pm 0.7	0	25	X	0	12	X
29. <i>Rhus typhina</i> (W)	16	9	7	5	3	16	4.0	0	0	O	3	3	X

TABLE 1. Continued.

Fruit ^a	Fruit mass (mg)	Seed mass (mg)	Pulp dry mass (mg)	Water (%)	Hexose (%)	Fat (%)	Nitrogen (mg/g)	Cedar Waxwing		American Robin	
								Biological Survey data	New Eithers ^b	Biological Survey data	New Eithers ^b
30. <i>Sorbus americana</i> (W)	134	4	23	82	29	2	6.0	0	1	7	0
31. <i>Viburnum lentago</i> (n = 3)	449 ± 38	85 ± 15	123 ± 9	66 ± 7	63 ± 7	7 ± 1	3.3 ± 0.3	0	4	0	3
32. <i>V. opulus</i> (n = 10)	454 ± 85	69 ± 8	53 ± 12	86 ± 2	58 ± 7	1 ± 1	2.1 ± 0.2	0	43	0	1
33. <i>V. prunifolium</i> (W)	350	97	106	58	20	2	2.8	3	—	2	—

^a H. Herrera (1987); J. Johnson et al. (1985); S. Skeate (1985); W. White (1989).
^b X, represented in Biological Survey records or new data (my observations); O, not represented in either data set.

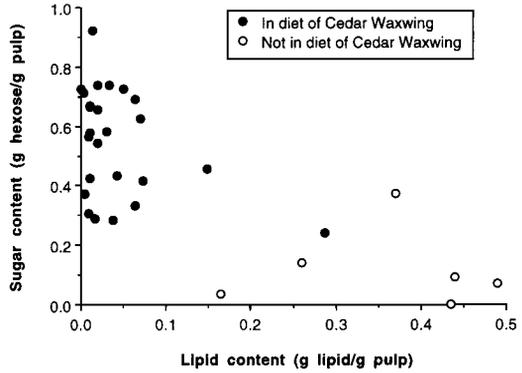


Fig. 4. Sugar and lipid content of fruit pulp (dry pulp and skin) of fruits eaten by Cedar Waxwings compared to those not eaten by waxwings. Fruits represent most of bird-dispersed fruits available in northeastern United States.

of sugar. This is consistent with intuitive conclusions based on the observation that the only lipid-rich fruits eaten by Cedar Waxwings also contain about as much (*Cornus florida*) or more (*Nyssa sylvatica*) sugar (Table 1).

The absence of lipid-rich fruits in the diet of Cedar Waxwings is not likely to be a result of inadequate sampling or seasonal bias. Like American Robins, the diets of other thrushes sampled by the Biological Survey contained sugary and lipid-rich fruits, even when sample sizes were lower than for Cedar Waxwings (*Hyalocichla mustelina*, n = 171; *Catharus fuscescens*, n = 176; *C. minimus*, n = 111; *C. ustulatus*, n = 403; *C. guttatus*, n = 551; Beal 1915b). Sixty Cedar Waxwing specimens were collected from August through October, a period during which lipid-rich fruits are abundant and eaten by other birds (Thompson and Willson 1979, pers. obs.). Other lipid-rich fruits that occurred in American Robin guts, but not in those of Cedar Waxwings, were (from Beal 1915a; number of records in parentheses): *Persea borbonia* (1), *Sassafras variifolium* (1), *Rhus glabra* (19), *Rhus copallina* (10), *Rhus radicans* (3), and *Olea europaea* (1).

Insects.—Five insect orders (Coleoptera, Hymenoptera, Diptera, Lepidoptera, and Hemiptera) comprised 81.7% of the animal diet of Cedar Waxwings (Table 3, Fig. 5). The most common coleopteran families were Scarabaeidae and Chrysomelidae (Table 3, Fig. 6). Scale insects (Coccoidea) occurred in waxwing guts in May and June. The scarabaeid beetles identified in

TABLE 2. Discriminant-function analysis of characteristics of fruits eaten by Cedar Waxwings compared to fruits not eaten. Traits of fruits in each category compared using two-tailed *t*-tests, with ratios and proportions arcsine-transformed ($\bar{x} \pm$ SD shown). Energy content calculated from content of sugars and lipids in fruits. Correlations are between conditional dependent variables and discriminant function. Fruit traits ordered in decreasing magnitude of correlations (declining importance of traits in discriminating fruits eaten by Cedar Waxwings). Discriminant-function correctly classified 32 of 33 fruits (*Cornus florida*, containing 29% lipid, incorrectly classified as not eaten).

Trait	Eaten (<i>n</i> = 27)	Not eaten (<i>n</i> = 6)	<i>t</i>	Correlation	Discriminant- function coefficient
Lipid (% of dry pulp)	4 ± 6	34 ± 14	-8.32***	-0.785	-0.051
Hexose (% of dry pulp)	55 ± 18	11 ± 11	5.86***	0.552	1.313
Fruit mass (mg)	412 ± 263	144 ± 125	2.47*	0.289	-2.412
Water (% of wet pulp)	75 ± 13	54 ± 29	2.79**	0.265	1.062
Dry pulp/fruit (mg)	78 ± 56	29 ± 20	2.16*	0.242	2.030
Dry pulp/seed (g/g)	15.4 ± 37.9	1.0 ± 0.7	1.74	0.155	4.206
Energy/fruit (kJ)	0.80 ± 0.53	0.50 ± 0.42	1.35	0.133	-2.632
Nitrogen (% of dry pulp)	0.7 ± 0.6	0.9 ± 0.5	-0.81	-0.079	-0.171
Seed mass (mg)	53 ± 51	41 ± 47	0.51	-0.033	4.822

*, *P* < 0.05; **, *P* < 0.01; ***, *P* < 0.001.

Cedar Waxwing guts were *Aphodius fimentarius* and *A. inguinatus* (dung beetles). *Trirhabda* spp. and *Galerucella* sp. beetles (Chrysomelidae) were eaten by waxwings in mid-July. Fragments of molluscs, probably snails, were found in waxwing guts on 25 May, 27 July, and 30 July (two sites; all three were female birds); grit was noted in five specimens from 25–28 May (three sites; three females and two males), including a male and a female each with "oyster shell."

Thirty-three birds were collected from a spruce forest in Maine from 18 June through 10 July in 1949 and 1950. Of these, 28 birds had eaten spruce budworm (*Choristoneura fumiferana*) larvae and pupae (20 and 80% of budworm prey consumed, respectively). Gut contents averaged 82.5% insect prey, compared to 33.6% for all specimens from July (Fig. 1). Other insect prey at this site were spruce coneworm larvae (*Dioryctria reniculelloides*; five guts), spruce bud moth larvae (*Zeiraphera canadensis*; one gut), and spruce bud scale (*Physokermes piceae*; one gut).

Cedar Waxwings and American Robins showed strong differences in selection of insect prey at the taxonomic level of order ($G = 34.3$, $df = 8$, $P < 0.001$; Fig. 5). Consumption of prey of different families within the Coleoptera ($G = 13.7$, $df = 5$, $P = 0.018$) and Hemiptera ($G = 41.9$, $df = 3$, $P < 0.001$) also were different (Fig. 6). Waxwings concentrated on aerial and vegetation-borne prey (characterizations of arthropod prey from Table 3), whereas robins ate ter-

restrial and vegetation-borne prey ($G = 16.5$, $df = 3$, $P = 0.002$; Fig. 7). The aerial prey of waxwings included ant alates (three of six records of ant prey noted ant wings, gravid female ants, and male ants), mayfly alates, crane flies, ichneumonid wasps, cicindelid beetles, scarabaeid beetles, and chrysomelid beetles, whereas prey gleaned from the vegetation included the same beetle families, scale insects, aphids, and spiders (Table 3, Figs. 5 and 6). Adult *Trirhabda* spp. and *Galerucella* spp. beetles (Chrysomelidae) were eaten in mid-July, when adult beetles undertake mass dispersal flights during the day (Johnson 1969, Messina 1982), suggesting that waxwings feed on the airborne beetles (A. Herzog, observations of waxwings catching *Trirhabda virgata*). The most common terrestrial prey of robins were carabid beetles, elaterid beetles, and stink bugs (Hemiptera; Pentatomidae), whereas their common vegetation-borne prey were scarabaeid and curculionid beetles (Wheelwright 1986:fig. 6). Cedar Waxwings did not eat the most terrestrial insects consumed by robins—stink bugs and carabid beetles.

Diets of waxwings from central and western states.—Fruits and insects eaten by Cedar Waxwings in the central and western United States were similar to those eaten in the eastern states (Table 4). Consistent with the pattern of nutrient selection in the eastern region, waxwings selected sugary fruits (Table 1; *Ribes* sp., 87% sugar and 1.3% lipid [Watt and Merrill 1963];

TABLE 3. Occurrence (%) of arthropod orders and families in guts of waxwings relative to total number of prey items identified to order, weighted equally by replicate ($n = 41$). Descriptions pertain to adult stages, except for Lepidoptera (from Borror et al. 1976, Evans 1984).

Percent	Order and family	Habitat and diet	Propensity to fly
29.4	Coleoptera		
12.2	Scarabaeidae (scarab beetles)	Vegetation, ground; eat dung, carrion, plants	Occasional flight
7.6	Chrysomelidae (leaf beetles)	Vegetation; phytophagous	Occasional flight
1.8	Curculionidae (weevils)	Vegetation; phytophagous	Occasional flight
0.8	Cicindelidae (tiger beetles)	Open areas; predaceous	Flighty; short flights
0.2	Elateridae (click beetles)	Vegetation, flowers, under bark; phytophagous	Occasional flight
15.6	Hymenoptera		
7.0	Formicidae (ants)	Ground, vegetation	Volant alates; mass flights
3.7	Ichneumonidae	Parasitic wasps	Volant; some swarm around trees infested with hosts
13.1	Lepidoptera		
12.8	Diptera	Larvae on vegetation; phytophagous	Sedentary
10.1	Tipulidae (crane flies)	Areas with damp vegetation	Volant
10.8	Hemiptera		
3.9	Aphididae (aphids)	Vegetation; sap feeders	Sedentary (volant dispersal morphs)
6.1	Coccidae (scale insects)	Vegetation; sap feeders	Sedentary
0.8	Cicadidae (cicadas)	Vegetation; phytophagous	Occasional flight
5.4	Orthoptera (grasshoppers)	Vegetation; phytophagous	Occasional flight; saltatory
4.9	Ephemeroptera (mayflies)	Riparian	Volant alates; mass flights
2.3	Araneae (spiders)	Vegetation; predaceous	Sedentary
4.5	Odonata (dragonflies)	Near water; predaceous	Volant

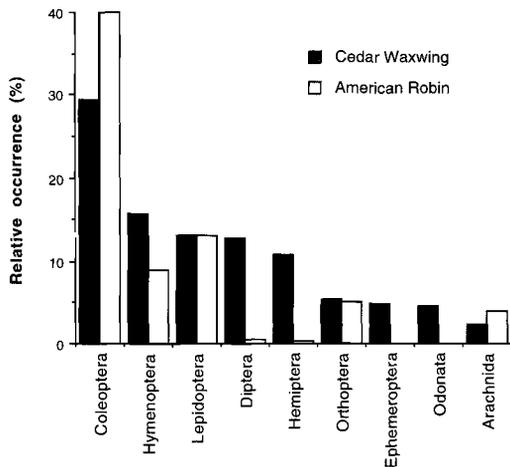


Fig. 5. Relative occurrence of arthropods (percent of total animal prey identified) in the diets of Cedar Waxwings and American Robins (robin data from Wheelwright 1986).

Schinus molle, $38 \pm 1\%$ sugar, $n = 2$ trees; *Eleagnus angustifolium*, $51 \pm 7\%$ sugar, $n = 4$ trees). *Prunus* spp. fruits also were commonly eaten by waxwings in western states (Table 4). Among insect prey, single records of sawfly larvae (Pergidae) and alderflies (*Sialis* sp.) were unique to the west/central region.

DISCUSSION

Cedar Waxwing diets are distinctive in at least three important respects. First, Cedar Waxwings eat more fruit than most other birds throughout the year (84% of annual diet, compared to 57% for American Robins; Wheelwright 1986). Among North American birds, only *Bombycilla garrulus* and *Phainopepla nitens* are similar to Cedar Waxwings in the high proportion of fruit in the diet (Martin et al. 1951). Second, Cedar Waxwings select sugary fruits. Third, waxwings capture aerial and vegetation-borne insects.

Dietary differences in fruit vs. insect foods.—Differences in the kinds of fruits versus insects selected by birds may have very different implications for feeding habits (Snow 1976). Fruit selection is likely to be based on chemical properties of fruits that have nutritional consequences for consumers (nutrients and secondary compounds) rather than foraging skills of birds because fleshy fruits are easily accessible, and crops are presented in showy displays that

advertise their presence. The kinds of arthropods consumed by birds, however, are likely to be strongly influenced by the foraging abilities of birds (e.g. wing loading, bill morphology, limb proportions) because of variation in the mobility, visibility, and location of animal prey. Chemical characteristics of arthropods also may influence their palatability. Although fruits can require different handling techniques, both Cedar Waxwings and American Robins swallow whole fruits (gulpers; Moermond and Denslow 1985, Levey 1987). Both species can ingest all of the bird-dispersed fruits available in central New York (pers. obs.).

Patterns of frugivory.—The ability of captive Cedar Waxwings to maintain body mass while eating only sugary fruits (27 days, Holthuijzen and Adkisson 1984; 64 days, Witmer 1994) corroborates the apparent exclusive use of these fruits by wild birds for extended periods. The sugar rewards of bird-dispersed fruits are hexose sugars, glucose and fructose, in approximately equal proportions (Widdowson and McCance 1935, Southgate 1976). The feeding habits of Cedar Waxwings suggest dietary specialization to a fruit diet rich in these sugars as a primary energy source, a novel dietary distinction among frugivorous birds.

Although most fruits eaten by Cedar Waxwings have high sugar and low lipid content, waxwings consume some lipid-rich foods. Two fruits eaten by Cedar Waxwings contain significant amounts of both sugars and lipids (*Cornus florida* and *Nyssa sylvatica*; Table 1). The insect portion of Cedar Waxwings diets (41% in May declining steadily to 14% in September) represents another source of seasonal lipid consumption (Spector 1956, Redford and Dorea 1984, Bell 1990). Consumption of lipid-rich foods may be related to fatty acid requirements, food item availability, and/or associated protein content of fatty insect prey.

McPherson (1987) found that fruit selection by Cedar Waxwings wintering in Oklahoma was strongly correlated with fruit abundance. She did not assess nutrient composition of fruit pulp, nor did she find that fruits avoided by Cedar Waxwings had higher pulp energy density, most likely because her study included only one lipid-rich fruit. Corroborating my results, Cedar Waxwings never ate this fruit (*Euonymus* spp., 31–38% lipid; Johnson et al. 1985, Skeate 1985) during the two-year field study (McPherson 1987).

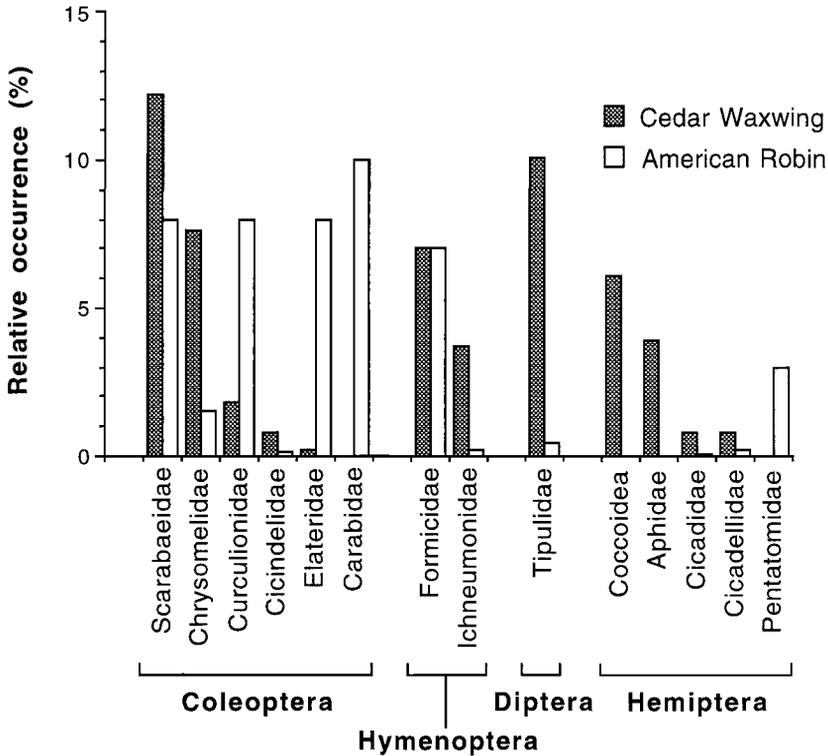


Fig. 6. Relative occurrence of insect families (percent of total animal prey identified) in diets of Cedar Waxwings and American Robins (robin data from Wheelwright 1986).

Flower consumption.—The coincidence between flower use by Cedar Waxwings in May and seasonal fruit scarcity (Sherburne 1972, Thompson and Willson 1979, McPherson 1987, pers. obs.) suggests that flowers may provide a nutritional alternative to sugary fruits at this time of year. Waxwings select both petals and stamens individually (Barrows 1912, Bent 1950, pers. obs.), indicating that they obtain nutrients from both of these flower parts. Petals may provide sugars, whereas stamens may provide protein.

Animal prey.—Because many prey taxa may occur either on the ground or in vegetation and most have volant dispersal phases, inferring foraging styles of birds from their selection of animal prey can be difficult. Differential selection of prey that are strongly aerial (Ichneumonidae, Tipulidae, Ephemeroptera, Odonata) or terrestrial (Carabidae) emphasizes the predilections of Cedar Waxwings to capture aerial prey and of American Robins to probe for terrestrial prey. Waxwings rarely take exclusively terrestrial prey and robins rarely capture exclu-

sively aerial prey (Fig. 7). For both birds, vegetation-borne insect prey are almost certainly overrepresented in this analysis. The ground foraging habits of American Robins are well known from descriptive (Bent 1949), behavioral

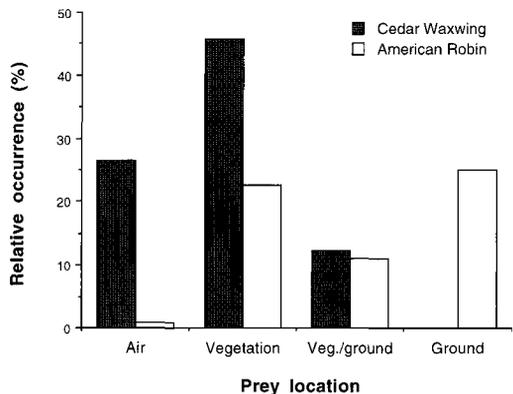


Fig. 7. Relative occurrence of animal prey in Cedar Waxwing and American Robin diets categorized by location in environment.

TABLE 4. Fruits and insects in guts of Cedar Waxwings from central and western United States.

Taxa	No. occurrences	Date
Fruits		
<i>Prunus</i> spp. (<i>P. virginiana</i> , <i>P. sp.</i>)	28	May–October
<i>Fragaria virginiana</i>	11	May–June
<i>Schinus molle</i>	15	February–May
<i>Smilax</i> sp.	1	April
<i>Crataegus</i> sp.	1	April
<i>Lonicera involucrata</i>	1	May
<i>Ribes</i> sp.	2	May–June
<i>Rubus</i> sp.	1	July
<i>Amelanchier</i> sp.	1	July
<i>Phoradendron</i> sp.	1	December
<i>Eleagnus angustifolium</i>	1	February
<i>Vitis</i> sp.	1	December
Insects		
Coleoptera (Chrysomelidae, beetle spp.)	3	May, January
Hymenoptera (Formicidae: <i>Componotus</i> sp., ant spp.)	3	June, October
Hymenoptera (Pergidae: sawfly larvae)	1	June
Odonata (dragonfly)	2	May
Diptera (Tipulidae)	1	May
Neuroptera (Sialidae: <i>Sialis</i> sp.)	1	June

(74% terrestrial prey; Paszkowski 1982), and food-habit (Hamilton 1940) studies. Cedar Waxwings often sally for aerial prey (Mearns 1879, Putnam 1949, pers. obs.), but because gleaning is a less obvious behavior than flycatching, this foraging mode may be underrated in the foraging repertoire of Cedar Waxwings. Many of the insect prey of waxwings are found only on vegetation and must be gleaned (lepidopteran larvae and pupae and scale insects; see also reports of waxwings gleaning larvae of cankerworms and elm leaf beetles; Flagg 1889, Forbes 1881, Mearns 1879, Beal 1893).

Nutritional implications of a sugary fruit diet.—The dietary reliance by Cedar Waxwings on fruits rich in hexoses suggests digestive and physiological adaptations to this diet. Glucose and fructose are water soluble and readily assimilated, either by active or passive mechanisms (Pappenheimer and Reiss 1987, Martinez del Rio and Karasov 1990).

Lipid digestion is accomplished under very different physiological conditions. Lipids are hydrophobic and their digestion requires emulsification by the action of bile secretions (bile salts and phospholipids) and hydrolysis by lipases (Gordon 1977, Ganguly et al. 1972, Stevens 1988). Digestive characteristics, such as gut morphology, bile and pancreatic fluid composition

and output, gut motility, and digestive enzymes, may differ for birds adapted to consuming such chemically different diets (Roby et al. 1989, Levey and Karasov 1992, Martinez del Rio and Restrepo 1992, Place and Stiles 1992). The feces of Cedar Waxwings fed exclusive fruit diets are more acidic than the feces of American Robins and other thrushes fed the same diets (Witmer 1994), consistent with the prediction of lower levels of bile and pancreatic fluid secretion in Cedar Waxwings. The strong negative association between sugar and lipid content of fruits appears to be a general phenomenon for bird-dispersed fruits (Herrera 1987, White 1989, Jordano 1995, this study), and may be explained by the contrasting physiological mechanisms required for the digestion and assimilation of these two nutrient types.

Waxwings produce sucrase and can digest sucrose, whereas thrushes lack this intestinal enzyme and cannot digest sucrose (Martinez del Rio et al. 1989, Karasov and Levey 1990, Martinez del Rio 1990a). Sucrose is the most abundant soluble carbohydrate in plants (Van Soest 1994). Dietary sources of sucrose for Cedar Waxwings include flowers, sap-feeding insects (aphids and scale insects), and perhaps some in fruits (Southgate 1976). Waxwings sometimes feed on maple (*Acer* sp.) sap in the spring (Beal

1882, Rogers 1907, Leatherman 1992), another dietary source of sucrose that may be important when fruits are scarce.

Protein requirements.—The ability of Cedar Waxwings to thrive on sugary fruits that typically contain only small amounts of protein (Table 1) suggests that they may have low protein requirements, as do hummingbirds which are specialized to a nutritionally comparable diet (Brice and Grau 1991). Many fruits are also limited in essential amino acid composition (Burroughs 1970), suggesting that Cedar Waxwings may be physiologically specialized in the use and metabolism of amino acids.

American Robins include no less than 23% animal prey in their diets during any season (Wheelwright 1986). Thrushes commonly mix fruit and animal prey in their diets (White and Stiles 1990). Captive American Robins fed fruit diets generally lose body mass (Levey and Karasov 1989, Witmer 1994) and show net nitrogen (protein) losses (Witmer 1994), suggesting that robins are nutritionally limited by the low protein content of fruit diets. The apparent dietary requirement of American Robins for proteinaceous animal matter may explain the northern limit of their winter range (Speirs 1953).

Phenolics.—Fruits, as well as flower petals, often contain phenolics (Goldstein and Swain 1963, Van Buren 1970, Robbins et al. 1987). Phenolics probably function in enhancing fruit persistence on the plant by their anti-fungal effects (Cipollini and Stiles 1992, 1993). Phenolics may have negative effects on digestion and palatability, by binding to proteins or systemic toxicity (Butler 1989). Waxwings may ameliorate the effects of phenolics by diet mixing with proteinaceous food items. Physiological mechanisms, such as proline-rich salivary proteins (Robbins et al. 1987, Butler 1989) or enhanced liver detoxification capacity are also possible. Because pH may influence the activity of phenolics, their physiological effects may be different in waxwings and robins.

Chrysomelid beetles are often chemically protected, some by phenolic compounds (Pasteels et al. 1988). If Cedar Waxwings are physiologically specialized for detoxifying the secondary compounds in fruits, this may predispose them to detoxification of insect secondary compounds.

Minerals.—It is likely that females ingest snails and grit during egg production as sources of

calcium and phosphorous for shell formation. The dietary demand for these minerals rises during egg production (Heuser and Norris 1946, Robbins 1993, J. McCarty unpubl. data).

Diets and breeding seasons.—The correspondence between the timing of breeding and the occurrence of animal prey in the diet of American Robins and fruit in the diet of Cedar Waxwings suggests contrasting nutritional specializations by these birds (Fig. 3). American Robins initiate egg laying in late April as consumption of animal prey dramatically increases. The arthropod diets of American Robins and Cedar Waxwings may be partially distinguished at this time of year by the ability of robins to probe for terrestrial prey. In contrast, breeding by Cedar Waxwings is coincident with increasing frugivory during the summer months (Fig. 3) as fruits ripen (Sherburne 1972, Thompson and Willson 1979). Frugivory by American Robins also increases during this season, but their breeding season is waning; fruits appear to provide an accessible supplement to the animal diet of robins. Breeding seasonality of Cedar Waxwings appears to be keyed to fruit availability because other aerial insectivores breed much earlier than do waxwings (Bull 1974). Breeding in many birds is timed to periods of greatest seasonal food availability (Perrins 1970, Immelmann 1971), presumably to maximize reproductive success. Reproduction requires increases in the acquisition of energy and protein, for both egg production (Robbins 1993) and growing young (Immelmann 1971). Cedar Waxwings are known to feed large amounts of fruit to their young (Saunders 1911, Putnam 1949). The correspondence between Cedar Waxwing breeding and fruit availability further implicates sugary fruits as the primary energy source for Cedar Waxwings and suggests that their breeding season is keyed to energy availability. Putnam (1949) noted the association between seasonal fruit abundance and the breeding of Cedar Waxwings in Ohio.

Grouping patterns of birds and food.—In central New York, Cedar Waxwings flock for a greater portion of the year and in much greater numbers compared to American Robins (Fig. 8). These grouping patterns probably result from dispersion patterns of preferred foods. Fruits are patchily distributed in large crops, while insects are usually more ubiquitously dispersed at low densities. The flocking behavior of Cedar

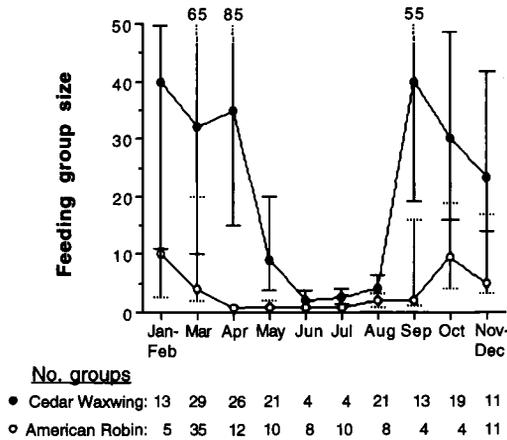


Fig. 8. Median sizes of foraging flocks of Cedar Waxwings and American Robins from 1988 through 1992 in vicinity of Ithaca, New York. Whiskers indicate upper and lower quartiles.

Waxwings foraging on widely-dispersed, abundant fruit crops (McPherson 1987) appears to extend to flock-feeding on insect prey that occur in localized concentrations (leaf beetles, ant alates, mayfly alates, spruce budworm larvae and pupae, scale insects; Mearns 1879, Forbes 1881, Flagg 1889, Bent 1950, pers. obs.). Waxwings often congregate near streams and ponds during the summer months where emerging insects are abundant (pers. obs.). Cedar Waxwings sometimes nest in close association, suggesting the possibility that they forage in flocks even when breeding (Saunders 1911). The dispersion and abundance of fruit and animal foods probably interact with digestive traits in determining the dietary patterns of these birds.

Ecological and evolutionary implications.—Coevolutionary and ecological models of the relationships between fruiting plants and fruit-eating birds have been strongly influenced by an underlying notion that frugivorous birds prefer fruits with high digestible energy density, leading to the perception of lipid-rich fruits as high quality fruits (Snow 1971, McKey 1975, Howe and Estabrook 1977, Stiles 1980, 1993). Early coevolutionary musings suggested relatively tight mutualisms between plants producing lipid-rich fruits and dietarily specialized frugivores (Snow 1971, McKey 1975, Howe and Estabrook 1977). The dietary patterns described here contradict these conceptions in several respects. Strongly frugivorous Cedar Waxwings are dietarily specialized to sugary fruits, con-

tradicting a positive relationship between degree of frugivory and specialization to lipid-rich fruits. This point has also been made by Fuentes (1994), who found that among Spanish frugivorous birds, two of the more moderately frugivorous species showed the strongest preferences for lipid-rich fruits. For American Robins, as well as many other frugivores, lipid-rich fruits are not necessarily more valued as foods compared to sugary fruits; they are consumed with sugary fruits and/or animal prey in the wild (Martin et al. 1951, Wheelwright 1986, White and Stiles 1990), and in captivity (Borowicz and Stephenson 1985, Borowicz 1988, Levey and Karasov 1989, Witmer 1994). Omnivorous frugivores appear to consume fruits opportunistically, as a supplement to animal foods.

Dietary specializations in frugivorous birds appear varied, ranging from birds that feed exclusively on lipid-rich fruits (e.g. *Steatornis caripensis*; Snow 1962), to omnivorous frugivores that consume fruits of mixed nutrient types, to birds that feed extensively on sugary fruits. The nutritional properties of fruits and dietary habits of frugivores are no doubt even more complex than a simple sugar/lipid dichotomy. Lipids in fruits may be triglycerides or waxes, compounds requiring specialized digestive traits for assimilation (Place 1992), as Place and Stiles (1992) have shown for Tree Swallows (*Tachycineta bicolor*) and Yellow-rumped Warblers (*Dendroica coronata*) eating bayberries (*Myrica pennsylvanica*). The diversity of nutrient mixtures in fruits is likely to be important in determining the array of birds that eat particular fruits and the nutritional roles of fruits for birds. Most fruits are nutritionally imbalanced and contain secondary compounds, suggesting critical nutritional interactions with other fruit and animal foods, both positive (sugar, lipid, and protein) and negative (secondary compounds; see Bairlein and Gwinner 1994).

Nutrient-based differences in fruit selection among frugivorous birds provides supportive evidence for diffuse coevolutionary patterns between fruits and dispersers. Recent studies assert that phylogenetic conservatism of many fruit traits, including nutrient content, constrains reciprocal adaptive responses in this system (Herrera 1987, 1992, Jordano 1995). Although phylogenetic conservatism is often interpreted as an evolutionary constraint, antagonistic to adaptation, effective functional traits should be phylogenetically conserved because they are retained by descendent species sub-

jected to the same selective pressures (phylogenetic niche conservatism; Harvey and Pagel 1991, Lord et al. 1995). Occasional variation from conservative patterns of nutrient composition among congeneric fruiting plants (*Cornus* fruits tend to be lipid-rich, but *C. ammomum* fruits are sugary; *Viburnum* fruits are usually sugary, but *V. dentatum* is lipid-rich) suggests a lack of absolute constraints, implicating niche conservatism as the cause of the phylogenetic conservatism of this trait. Phylogenetic information, rather than competing with adaptive interpretations, is complementary in determining evolutionary congruence between novel life-history characteristics and derived functional traits.

The diffuse patterns of association between fruiting plants and frugivorous vertebrates (Wheelwright and Orians 1982, Witmer and Cheke 1991) are likely to be explained by phylogenetic niche conservatism on both sides of the mutualism. This process can account for the observation that associations in the fruit/frugivore mutualism appear to occur at taxonomic levels higher than species (Moermond and Denslow 1985, Wheelwright 1986). Complex nutritional interactions between frugivorous animals and fruits, as well as among fruits and other foods, are also likely to be responsible for diverse interactions between fruiting plants and dispersers. Identification of nutrient-based differences among the diets of frugivorous birds provides an initial step towards an understanding of fruit selection based on chemical constituents of fruits and the physiology of animals.

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