

A FIELD STUDY OF WINTER FRUIT PREFERENCES OF CEDAR WAXWINGS¹

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Abstract. Winter field censuses of Cedar Waxwings (*Bombycilla cedrorum*) in an urban area of central Oklahoma were used to evaluate which fruit characteristics influence avian choice. Abundance estimates (g/ha) of fruits of each species in the study area were made to determine the resource base available to waxwings. I hypothesized that waxwing foraging preferences would be correlated with one or more of the following fruit characteristics: (1) abundance, (2) color, (3) size, (4) height, (5) pulp-to-seed ratio, (6) percent water, (7) percent protein, and (8) caloric content. Preliminary data from 1983-1984 indicated that waxwings were selective; they ate mostly mistletoe (*Phoradendron serotinum*) and one species of a relatively small crab apple (*Malus* sp.) from the 16 species available. During the winter of 1984-1985, waxwings used mistletoe heavily, along with hackberry (*Celtis* sp.), until these species were mostly depleted. Yaupon and deciduous hollies (*Ilex vomitoria* and *I. decidua*) then were used heavily and became the most important overall food sources during the winter. Waxwings generally ate abundant species and seldom ate rare ones. Among the fruits consumed, the order of waxwing preference was related only to fruit abundance, size, and caloric content. Comparisons of the results with other studies of frugivorous birds shows only partial agreement on the fruit characteristics most influential in avian choice, suggesting that a number of factors interact to determine foraging preferences and that these factors are not constant for all frugivorous species.

Key words: Cedar Waxwings; censuses; dispersers; foraging preferences; fruit; gape width; nutrition; resource abundance.

INTRODUCTION

Many plants produce seeds that must be carried away from the parent plant for successful germination and growth (Howe and Estabrook 1977, Howe and Smallwood 1982, Stiles 1984). Animals, especially birds, often serve as effective dispersal agents by ingesting seeds and depositing them intact at sites distant from the seed source. Seeds of some plants are enclosed in a pulpy fruit that provides the nutritional and energetic benefits necessary to attract dispersers (Snow 1971, McKey 1975, Herrera 1981).

Production of nutritious fruits by plants might not, in itself, guarantee dispersal of seeds (Snow 1965, Howe and Estabrook 1977, Herrera 1981). Thus, plants that not only produce rewards but also advertise them effectively (Snow 1971, Willson and Thompson 1982, Willson and Melampy 1983) may gain an advantage because of competition to attract dispersers (Snow 1965, Howe and Estabrook 1977). Dispersers are under selective pressure to be perceptive and discrimi-

natory because individuals that make the "wrong" choice may receive little or nothing in return for the cost of carrying a seed.

Numerous fruit characteristics can influence avian choice. Abundance of fruits has been proposed as a factor important to foraging birds (Snow 1971), but relatively few investigators have included an analysis of the resource base available to birds over the course of a season (exceptions are Sherburne 1972, Baird 1980, Sorensen 1981). Conspicuous, brightly colored fruits and/or accessory structures have been recognized as potential cues to frugivorous birds (Davison 1962, Turček 1963, Snow 1971, Morden-Moore and Willson 1982, Stiles 1982, Willson and Thompson 1982). Water content and nutritional content of fruits—including protein, calories, and pulp-to-seed ratio—may also attract avian dispersers (Snow 1971; Sherburne 1972; Berthold 1976a; Stiles 1980; Herrera 1981, 1982; Sorensen 1981; Johnson et al. 1985). However, abundance, conspicuousness, and nutritional rewards can be overridden by fruit size due to the limits imposed by gape width (Wheelwright 1985). Risk of predation is also an important factor (Bertram 1978, Howe 1979) that may cause birds to prefer for-

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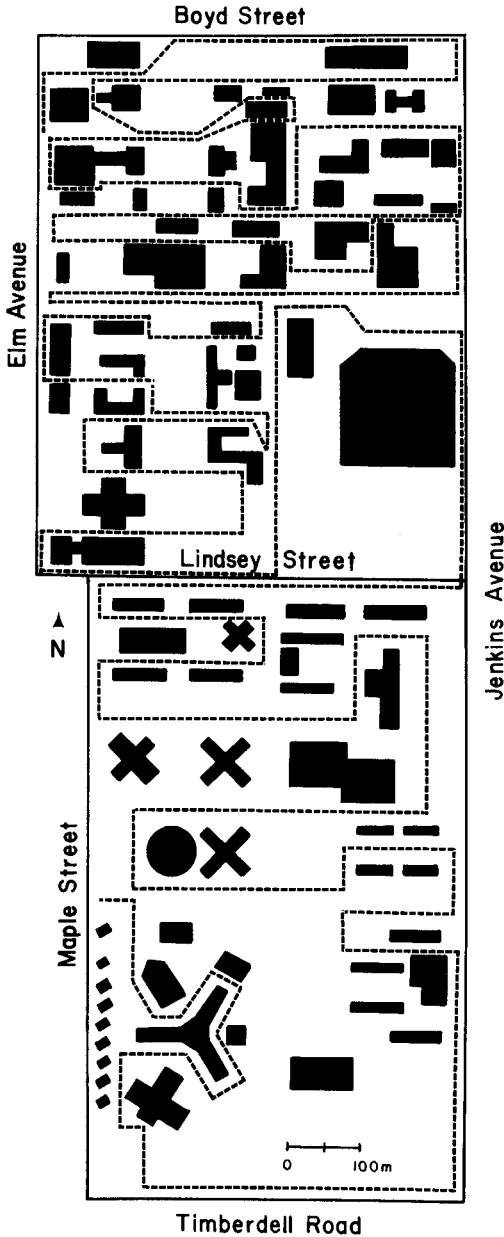


FIGURE 1. Map of study area and census route. Solid figures represent buildings.

aging in certain sites, such as high above the ground.

As a means of examining the relationship between plants and avian dispersers, I present data on foraging patterns of Cedar Waxwings (*Bombycilla cedrorum*), as well as on the fruits that form the resource base for waxwings during the

winter in Oklahoma. The specific objectives of this study were: (1) to determine if waxwings show a preference for certain fruits in the field; and (2) if any preferences were found, to determine which of the fruit characteristics form the basis for the observed preferences.

Cedar Waxwings spend much of the winter and early spring in south-central United States, including Oklahoma where they are usually present from December to May. Fruits comprise about 70% of their diet during the year (Stiles 1984), and anecdotal reports describe how quickly they can strip a plant of its fruit crop (Bent 1950, Sutton 1967). Their unusually strong flocking tendencies (Putnam 1949, Sutton 1967) and conspicuous foraging behavior make them especially suitable for field observations.

STUDY AREA AND METHODS

The study area was located in central Oklahoma on the University of Oklahoma campus in Norman, Cleveland County. The boundaries of the site were five major streets forming a 88.6-ha rectangle (Fig. 1). The study area was urban and encompassed buildings, sidewalks, and streets. Also included were over 4,600 trees and shrubs of more than 70 species, some naturally occurring and some cultivated ornamentals. Fruits were available from 16 of these species during the winter (Table 1).

FRUIT DATA

All trees and shrubs in the study area were identified and mapped. To assess availability of fruits to waxwings, I estimated the total number of fruits of each species in the study area approximately once every five weeks on the following dates: 1 to 8 December 1984, 1 to 8 January, 4 to 15 February, 19 to 25 March, and 27 to 29 April 1985. Each census took about one week to complete, and it was assumed that the number of fruits did not change significantly during a census period. For all fruiting plants (ca. 600 individuals), except mistletoe, I estimated fruit numbers by counting the number of fruits on one portion of the plant, and multiplying by the number of such sections on the individual to obtain a total. The number of mistletoe berries was estimated by tallying the number of clumps that had approximately one to 100 berries, 101 to 200 berries, etc., by units of 100. Clumps with one to 100 berries were then assigned 50, those with 101 to 200 were assigned 150, etc., and a

TABLE 1. Fruit abundance for each species available in the study area, expressed as biomass per hectare (g/ha) and number of fruits per hectare (in parentheses). Values given for the 15th of each month, 1984–1985, based on interpolation from field estimates.

Fruit species	December	January	February	March	April
Hackberry (<i>Celtis</i> spp.)	267.9 (1,175.0)	73.0 (320.4)	48.5 (212.7)	16.3 (71.6)	2.9 (12.8)
Euonymus (<i>Euonymus</i> spp.)	3.7 (77.1)	2.4 (49.8)	0.3 (6.9)	0.1 (1.4)	0 (0)
Chinese holly (<i>Ilex cornuta</i>)	229.5 (591.4)	158.3 (408.1)	69.1 (178.1)	28.6 (73.7)	6.9 (17.7)
Deciduous holly (<i>I. decidua</i>)	246.9 (972.1)	233.5 (919.4)	187.9 (739.9)	45.6 (179.6)	3.6 (14.2)
American holly (<i>I. opaca</i>)	27.2 (57.7)	24.5 (52.0)	18.9 (40.0)	6.3 (13.4)	2.5 (5.3)
Yaupon holly (<i>I. vomitoria</i>)	440.2 (2,684.1)	307.8 (1,877.0)	183.9 (1,121.1)	80.2 (488.9)	25.9 (158.0)
Chinese juniper (<i>Juniperus chinensis</i>)	125.3 (513.7)	121.3 (497.2)	117.8 (483.0)	113.8 (466.6)	111.4 (456.7)
Eastern redcedar (<i>J. virginiana</i>)	227.1 (2,950.0)	136.2 (1,768.6)	96.2 (1,249.7)	53.2 (691.1)	25.3 (328.6)
Privet (<i>Ligustrum sinense</i>)	5.0 (86.2)	4.5 (77.7)	3.8 (66.1)	0.8 (13.2)	0 (0)
Crab apple, small (<i>Malus</i> sp. 1)	157.5 (158.6)	137.1 (138.0)	105.2 (106.0)	21.9 (22.1)	0.4 (0.4)
Crab apple, large (<i>Malus</i> sp. 2)	12.0 (2.9)	0.5 (0.1)	0.4 (0.1)	0.1 (0.02)	0 (0)
Nandina (<i>Nandina domestica</i>)	31.4 (126.7)	26.6 (107.2)	28.3 (68.6)	3.6 (14.7)	0.1 (0.4)
Mistletoe (<i>Phoradendron serotinum</i>)	77.8 (695.0)	51.7 (461.9)	7.4 (66.5)	1.5 (13.3)	0 (0)
Photinia (<i>Photinia serrulata</i>)	3.2 (28.2)	0.1 (0.9)	0.01 (0.1)	0.01 (0.03)	0 (0)
Cherry laurel (<i>Prunus caroliniana</i>)	14.6 (22.7)	8.0 (12.6)	6.3 (9.9)	1.3 (2.0)	0 (0)
Pyracantha (<i>Pyracantha coccinea</i>)	29.0 (137.2)	19.9 (94.3)	13.7 (64.8)	2.7 (12.9)	0 (0)

total was calculated. The number of fruits of each species was converted to biomass per unit area (g/ha) using the mean weight of individual fruits of each species. For each species of fruit, I calculated the resources available on the 15th of each month by linear interpolation from the periodic estimates made throughout the winter. Thus, when I pooled waxwing census data by month, I was able to evaluate statistically the relationship between resource availability and food use by birds.

A Haga altimeter and a meter stick were used to measure the maximum height of 10 randomly selected individuals of each tree or shrub species that produced fruit during the 1984–85 winter. If there were fewer than 10 individuals of a given

species, a mean was calculated using all available individuals of that species.

Ripe fruits were collected to determine fruit size and weight for each species. To compensate for individual variation within a species, I gathered 10 fruits from each of 10 plants for a given species when possible. For species with fewer than 10 individuals, I sampled from all available plants. Fruit weight was determined by weighing all collected fruit of one species to the nearest 0.001 g and calculating the mean weight per fruit. For 10 fruits of each species (except Chinese holly, where $n = 30$), I measured (to the nearest 0.01 mm) the distances perpendicular to (length) and parallel to (width) the insertion of the pedicle. The greater of these was called the maximum

diameter and the lesser was the minimum. An index of fruit volume was calculated as width \times width \times length.

For each species, I collected enough fruits to produce sufficient dried pulp to conduct nutritional analyses (minimum of about 1 g). No desiccated fruits were collected. I separated the pulp from the seeds and used their separate wet weights to calculate the pulp-to-seed ratio and the percentage of whole-fruit weight comprised by seeds. The pulp was dried at 60°C, weighed, and temporarily stored in a desiccator at room temperature. The percent water was calculated using the wet versus dry weight of pulp. I ground the pulp to a fine powder, which was stored in a freezer (for a maximum of 10 months) until used for nutritional analyses.

The Lowry assay (Cooper 1977) was used to determine protein content of the fruits, with the following additional procedures. Frozen, dried pulp samples were allowed to reach room temperature in a desiccator to prevent absorption of water. Before beginning the assay, the 40-mg samples were extracted with 8 ml of 80% ethanol to remove phenols that would interfere with the spectrophotometric readings. Samples were centrifuged for 30 min, and the supernatant containing the extracted phenols was discarded. Protein was solubilized by adding 6 ml of 1.0 N NaOH to each sample and boiling for 4.5 min. Particulate matter was removed by centrifuging. Subsamples of 0.25 ml (or 0.10 ml if the sample were highly colored) were pipetted from the clear supernatant and transferred to a clean test tube. Distilled water and 1.0 N NaOH were added to bring the sample to 0.5 ml of distilled water plus 0.5 ml of NaOH with solubilized protein. A standard of bovine serum albumin was run with each assay.

Absorbances of the samples at 540 nm were taken using a spectrophotometer. The fruit samples often were highly colored even before the reaction with reagents; therefore, a control containing an equal amount of sample material as the assays, but no reagents, was run for each species to determine absorbance by the fruit color alone. These values were subtracted from the assay before calculating percent protein.

Caloric content was determined using a Parr 1241 adiabatic oxygen bomb calorimeter. Duplicate samples of 0.5 to 1.0 g were run for each species.

BIRD DATA

I collected data on waxwing foraging patterns by periodic censuses of the study area. Censusing began before waxwings arrived in early winter and continued until after their spring migration. I conducted 29 censuses, approximately twice a week from 19 December 1983 through 17 April 1984, to serve as preliminary data for the following field season. From 28 November 1984 through 19 May 1985, 83 censuses were conducted virtually every other day. The 12-km route zig-zagged through the study area (Fig. 1), allowing easy detection of birds at any point on the entire site. I rode a bicycle except during severe weather when I walked and/or drove portions of the route by car. I recorded: number of waxwings, number of flocks of waxwings, activity of the birds, plant species on which birds were observed, and location (i.e., specific plant identification number on map) of birds when first sighted.

To determine mean waxwing gape width, the distance between commissural points (Wheelwright 1985) was measured on 13 skeletal specimens (six males, seven females) housed in the Stovall Museum of Science and History, Norman, Oklahoma.

STATISTICAL ANALYSES

I ran statistical tests on data collected during the 1984–1985 season using SAS computer programs. Based on waxwing census data, fruit species were classified as: those eaten by waxwings, and those not eaten. Analysis of variance (ANOVA; PROC GLM in SAS 1985a, 1985b) was used to determine statistical differences between groups in any of the measured fruit characteristics. ANOVAs were run on the two groups (“eaten” and “not eaten”) based on: (1) consumption by waxwings over the entire winter, (2) February consumption only, and (3) March data only. I used December biomass data when testing overall “eaten” versus “not eaten” as the maximum initial biomass available, and biomass data corresponding to the appropriate month for the other ANOVAs (Table 1).

The remaining statistical analyses involved tests of the distribution of waxwings on plant species. When sample sizes allowed, I analyzed both the number of individual waxwings per plant species and the number of waxwing flocks per

plant species. Because waxwings are highly social, the occurrence of one individual on a plant is not independent of the presence of other individuals. Nevertheless, the realized impact on a fruit crop depends on how many birds are actually present. The number of flocks observed per plant species, however, may serve as a better indicator of preference because the locations of individual flocks are independent at any one time. Each "group" choice is given the same weight, despite the flock size.

To compare waxwing foraging patterns with the resource base, I conducted a goodness-of-fit test (*G*-test) using the null hypothesis that the proportion of waxwings observed per fruit species should equal the proportion of the total fruit biomass for that species. I tested only those species with sufficient biomass to produce expected values greater than five individual waxwings (or five waxwing flocks) per fruit species. The remaining rare fruit species were lumped together under the heading "other."

Correlation coefficients were calculated to determine if, among those species consumed by waxwings, there was a relationship between the number of individuals (or flocks) on a given species and the fruit characteristics of that species. I used Pearson's product-moment and Spearman's rank correlations (PROC CORR; SAS 1985a, 1985b) both on the number of individuals and the number of flocks.

The relationship between waxwing consumption and fruit size also was analyzed. Because gape width may set an upper limit on the sizes of fruits that could be consumed, waxwings might show a pattern of use that would not be a simple linear association with increasing fruit size. Therefore, a *G*-test for goodness-of-fit was used to test the hypothesis that the pattern of waxwing consumption for different fruit size classes (based on maximum diameter) was proportional to fruit abundances for those size classes based on December biomass data.

RESULTS

1983–1984

During late December 1983, extremely cold weather damaged fruits of many plants, including yaupon holly, Chinese holly, nandina, and photinia. Some other fruits, including mistletoe berries, were frozen solid but were not discolored

or shriveled. Although the extreme cold reduced the number of choices available to waxwings, the waxwings were still selective in their foraging choices. During censuses, I saw waxwings eat six different types of fruit (Fig. 2): deciduous holly, mistletoe, yaupon holly, Chinese holly, and two types of crab apple ("large" = ca. 19 mm, and "small" = ca. 13 mm). By far, the two most frequently used species were mistletoe and the small crab apple. While photinia was available only for a short time in December before the freeze, noncensus observations indicated that it was an important food source during that time. Although most yaupon holly berries were damaged during the freeze, waxwings still ate fruits of that species, usually selecting berries that were not ruined. No waxwings were observed on the study area after 18 February 1984, although censuses continued through late March.

1984–1985

The most abundant fruits in December were yaupon holly, hackberry, and deciduous holly (Table 1). Eastern redcedar, Chinese holly, and the small crab apple also were relatively abundant during December and January. The remaining species, including mistletoe, each contributed less than 10% to the total biomass available at the start of the winter. The number of hackberries dropped dramatically from December to January, while the number of yaupon holly and deciduous holly berries stayed about the same. By February, these two hollies were still the most abundant species. Mistletoe was virtually absent by late February. The amount of Chinese juniper fruits remained almost unchanged from December through February but, due to the drop in numbers of fruits of other species, it became the most abundant species in March and April.

Five species of fruits were consumed by waxwings both winters: yaupon holly, Chinese holly, deciduous holly, mistletoe, and the small crab apple (Table 2). Eastern redcedar, pyracantha, hackberry, and Chinese juniper were eaten only in 1984–1985. The most common color for fruits (seven of 16 plant species) was red. The largest fruits in diameter, volume, and weight were the two crab apples and cherry laurel; the smallest were euonymus, privet, photinia, and eastern redcedar. The mean maximum heights of plants in the study area were greatest in hackberry and mistletoe, and least in nandina and euonymus.

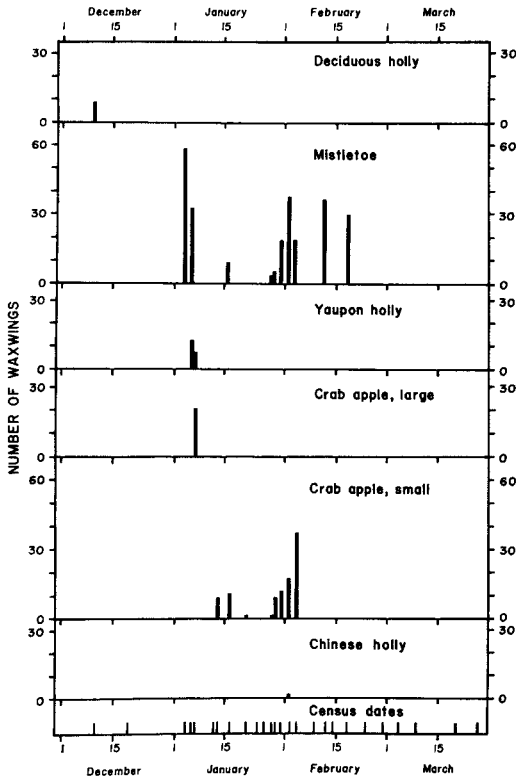


FIGURE 2. Number of waxwings foraging per fruit species from 10 December 1983 through 20 March 1984. Lines in bottom panel indicate days on which censuses were taken.

Chinese holly also had a low mean height, but varied greatly, with some individuals the size of small trees (approximately 4 m) and others low shrubs (<1 m).

The ratio of fresh pulp mass to seed mass ranged from 0.75 in hackberry to 11.0 in mistletoe (Table 3). Hackberry and mistletoe also represented the extremes of the range in percent water with 12.4% and 72.4%, respectively. Percent protein was highest in the small crab apple and lowest in pyracantha. The standard deviation of protein data was generally high (Table 3). The number of calories per gram of dried pulp was highest in euonymus, second highest in yaupon holly, and lowest in hackberry.

During the second field season (1984–85), only one waxwing flock was seen in the study area before late January (Fig. 3). Waxwings were most abundant in February, reaching a peak on 27 February when 673 waxwings (7.6 waxwings/ha) were seen. I observed more waxwings, both in total numbers and numbers of flocks, on yaupon holly than any other fruit species in 1984–1985. Deciduous holly was the second most commonly eaten fruit over the entire winter. The other species eaten by waxwings were: mistletoe, small crab apple, hackberry, eastern redcedar, Chinese holly, and pyracantha. I saw waxwings consume Chinese juniper once, but not during a census.

TABLE 2. Morphological data for 16 fruit species available in study area, and indication of species consumed by waxwings.

Fruit species	Consumption ^a		Color ^b	Diameter ^c (mm)		Volume (mm ³)	Weight (g)	Height ^d (m)
	1983–84	1984–85		Maximum	Minimum			
Hackberry	0	1	Br	8.21 (0.60)	7.23 (0.43)	429.43	0.228	15.97 (2.68; 10)
Euonymus	0	0	R–O	5.23 (0.32)	3.77 (0.23)	74.38	0.048	1.81 (0.53; 10)
Chinese holly	1	1	R	9.82 (0.31)	9.38 (0.52)	864.36	0.388	1.98 (0.53; 10)
Deciduous holly	1	1	R	7.33 (0.51)	6.66 (0.43)	357.98	0.254	4.18 (0.71; 10)
American holly	0	0	R	9.02 (0.25)	8.35 (0.20)	629.64	0.472	5.10 (1.08; 6)
Yaupon holly	1	1	R	7.05 (0.13)	6.13 (0.11)	264.68	0.164	3.67 (1.86; 10)
Chinese juniper	0	2	Bl–G	8.99 (0.59)	7.74 (0.50)	625.63	0.244	8.09 (2.14; 10)
Eastern redcedar	0	1	Bl	6.15 (0.36)	5.35 (0.56)	175.85	0.077	8.11 (2.14; 10)
Chinese privet	0	0	Pu	6.24 (0.29)	4.88 (0.22)	148.33	0.058	5.57 (0.98; 7)
Crab apple, small	1	1	Pi	13.28 (1.03)	11.55 (1.01)	2,035.44	0.993	5.48 (1.09; 6)
Crab apple, large	1	0	R	19.11 (1.27)	17.27 (1.57)	6,305.18	4.166	7.30 (–; 1)
Nandina	0	0	R	8.45 (1.19)	8.32 (1.05)	585.49	0.248	1.38 (0.65; 10)
Mistletoe	1	1	W	6.67 (0.34)	5.36 (0.31)	191.54	0.112	12.01 (2.80; 10)
Photinia	2	0	Pi	6.05 (0.33)	5.72 (0.36)	197.81	0.112	4.03 (0.81; 3)
Cherry laurel	0	0	Pu	10.80 (0.27)	9.30 (0.20)	993.03	0.641	6.44 (1.15; 7)
Pyracantha	0	1	O	9.19 (0.80)	7.34 (0.71)	720.65	0.211	2.49 (1.06; 10)

^a 0 = Never eaten by waxwings; 1 = observed eaten during census; 2 = observed eaten, but not during census.

^b Bl = Blue; Bl–G = blue-green; Br = brown; O = orange; Pi = pink; Pu = purple; R = red; R–O = red-orange; W = white.

^c SD given in parentheses.

^d SD, *n* given in parentheses.

TABLE 3. Nutritional data for 16 fruit species available in study area.

Fruit species	Pulp-to-seed ratio	%			Calories* (kcal/g)
		Water	Protein ^b		
Hackberry	0.75	12.38	4.63 (0.72; 4)		3.94 (0.057)
Euonymus	0.84	24.89	11.36 (0.59; 4)		6.26 (0.209)
Chinese holly	1.53	42.95	—		—
Deciduous holly	1.77	41.25	4.31 (1.41; 8)		4.58 (0.016)
American holly	2.30	41.69	5.39 (0.23; 4)		4.30 (0.003)
Yaupon holly	1.58	40.63	2.54 (0.05; 4)		5.13 (0.025)
Chinese juniper	3.13	48.28	5.17 (0.43; 8)		4.64 (0.003)
Eastern redcedar	3.31	—	3.14 (0.25; 8)		4.43 (0.016)
Chinese privet	1.35	23.85	4.75 (0.18; 4)		4.55 (0.010)
Crab apple, small	6.36	64.52	12.46 (0.43; 4)		4.18 (0.010)
Crab apple, large	6.54	66.80	2.99 (0.25; 4)		4.04 (0.001)
Nandina	1.37	42.00	5.09 (0.17; 4)		4.42 (0.038)
Mistletoe	11.00	72.37	5.25 (0.60; 8)		4.39 (0.016)
Photinia	5.46	58.86	8.49 (0.29; 4)		4.56 (0.022)
Cherry laurel	0.79	30.94	4.27 (0.23; 4)		4.16 (0.019)
Pyracantha	8.62	71.94	1.64 (0.04; 4)		4.08 (0.013)

* SD in parentheses.

^b SD, *n* in parentheses.

In late February, the birds began foraging on flowers, seeds, and insects.

Waxwings showed no consistent preference for fruits of a particular color, eating fruits that were red, white, orange, blue, brown, and pink. However, the two most heavily-used fruits (yaupon and deciduous hollies) were red, and seven of the 16 species available were red.

Waxwings changed their use of food resources during the winter (Fig. 3). Despite the wide selection of fruits available when the birds first arrived, waxwings foraged mostly on only three species—mistletoe, hackberry, and crab apple—for about four weeks. Although flocks present early in the winter were relatively small, more flocks (16 of 52) were seen on mistletoe than any other fruit species during January and February. Waxwings continued to eat mistletoe until they had consumed virtually all of the available berries by mid-February. Likewise, hackberries were consumed, not only by waxwings but also heavily by American Robins (*Turdus migratorius*), until less than 30% of the fruits were left by mid-February. The small crab apple was eaten only in mid-February, and much of its crop persisted into March.

During February, more waxwings were observed eating yaupon holly than any other species. Although less than 20% of the original crop of yaupon holly was left in March, the birds continued to feed on it through late March. Like

yaupon holly, eastern redcedar abundance declined steadily, but waxwings were observed eating it only from mid-February to 1 March. The crop of deciduous holly berries, however, persisted much longer. In mid-February, about 76% of its original crop remained, and it had become the most abundant species. Waxwings used deciduous holly extensively between 24 February and 1 March, resulting in a substantial decline in the crop size of this holly.

From late February through March, most fruits became scarce while flowers, seeds, and insects became more abundant. After 1 March, waxwings fed largely on the flowers of hackberry, American elm (*Ulmus americana*), and eastern cottonwood (*Populus deltoides*), as well as on elm seeds. In April, waxwings frequently were seen foraging on insects by flycatching and gleaning. The number of waxwings observed declined during late March and April, and no waxwings were seen after 15 April. Censuses continued through May.

The two groups of fruit species used in the ANOVAs ("eaten" and "not eaten") differed significantly only in fruit biomass (g/ha) using census data for 1984–1985 ($F = 15.02$; $P < 0.01$), February data alone ($F = 5.16$; $P < 0.05$), and March data alone ($F = 4.71$; $P < 0.05$). Fruits eaten had a higher biomass than those not eaten. No other variables were significantly different.

Insufficient numbers of waxwings were re-

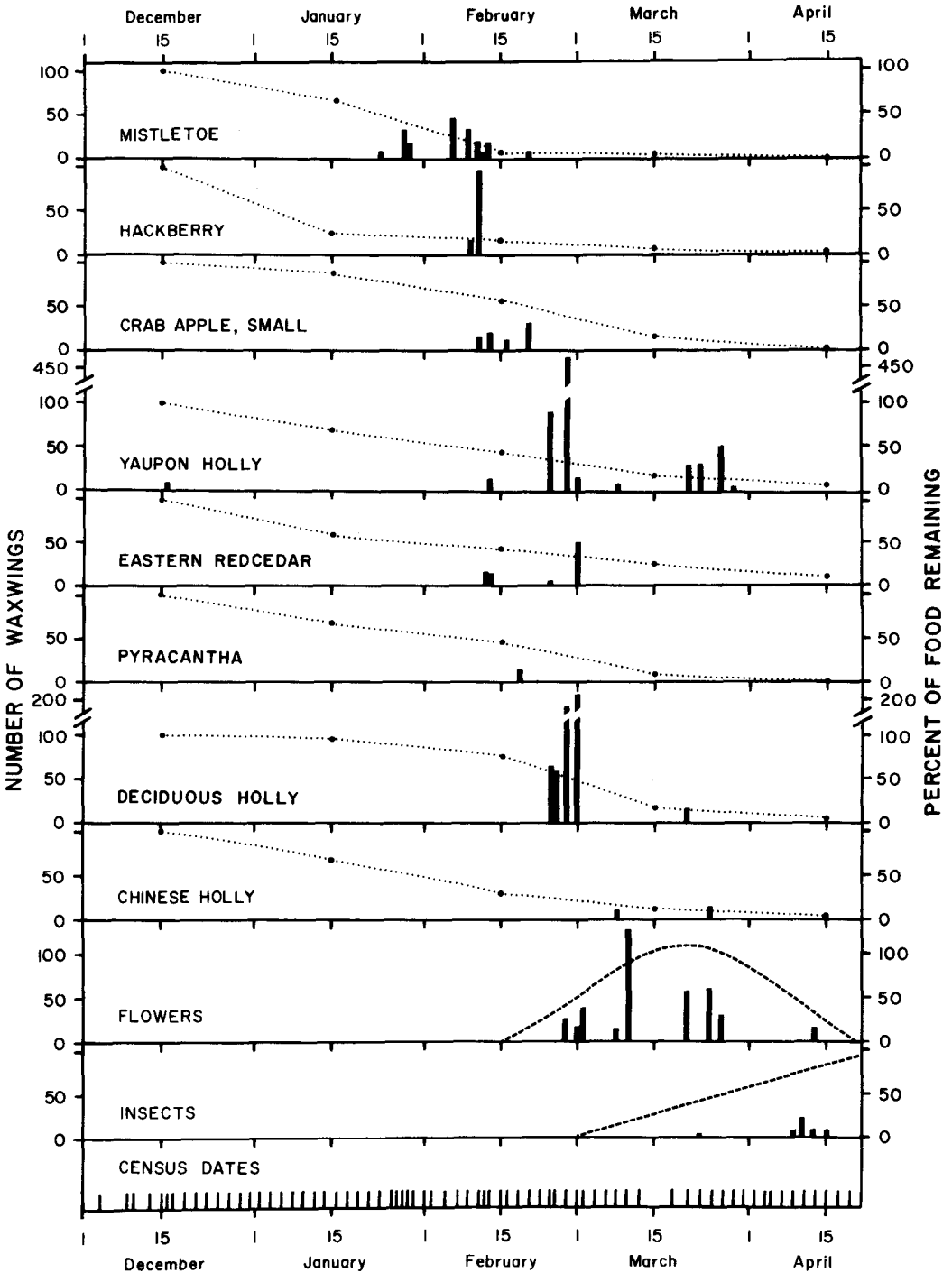


FIGURE 3. Number of waxwings foraging per fruit species (bars) from 28 November 1984 through 19 May 1985. Availability of major food resources through time graphed as percent of total available for that resource (dotted lines). Percent remaining for fruits based on percent of fruit biomass given in Table 1. Dashed lines represent qualitative estimates of availability of flowers and insects over time.

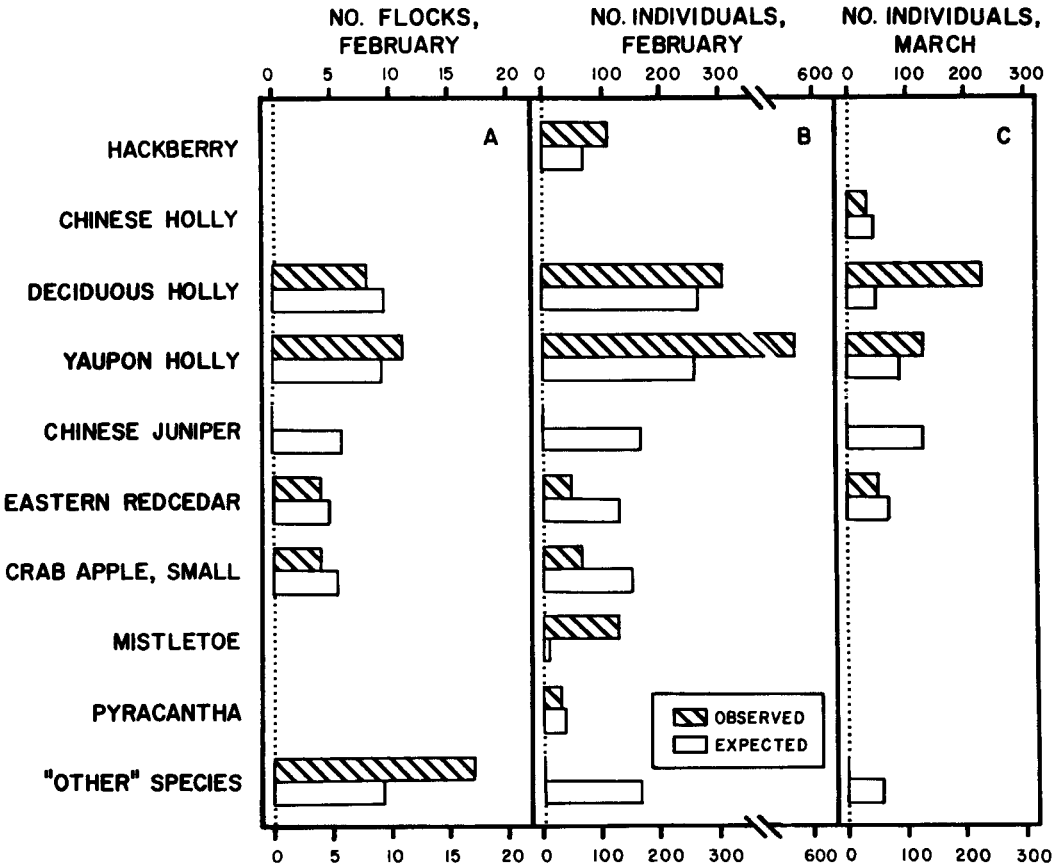


FIGURE 4. Observed versus expected values for waxwings per fruit species tested using G -test for goodness-of-fit. Expected values based on proportion of biomass per fruit species. (A) Observed values based on numbers of waxwing flocks seen per fruit species during February 1985 ($G = 17.96$, $P < 0.005$). (B) Observed values based on total number of waxwings seen per fruit species during February 1985 ($G = 1,483.22$, $P < 0.001$). (C) Observed values based on total number of waxwings seen per fruit species during March 1985 ($G = 710.69$, $P < 0.001$).

recorded in December and January for goodness-of-fit tests. In February, the number of flocks observed per fruit species was significantly different ($P < 0.01$; Fig. 4A) from the expected distribution. The observed number of flocks was greater than expected for yaupon holly and for the group of less abundant species called "Other." The high observed value for Other was primarily due to numerous flocks of waxwings feeding on mistletoe. The remaining species had fewer flocks than predicted. Chinese juniper was not eaten, although it had a relatively high expected value (large biomass).

I also analyzed the February data using the actual number of birds seen per fruit species and found a significant difference between observed

and expected distributions based on fruit crop biomass (Fig. 4B). Yaupon holly, deciduous holly, hackberry, and mistletoe had more waxwings than predicted whereas all other species had fewer birds than expected. Despite high expected values, no waxwings were observed on Chinese juniper, nor any of the species in the group Other.

In March, expected values greater than five were generated only when numbers of individual waxwings were used (Fig. 4C). Waxwings were observed more often than predicted on yaupon holly and deciduous holly. Fewer birds than expected were observed on all other species.

Based on the results of the G -tests, the null hypothesis that waxwing foraging patterns match resource availability was rejected. In general, the

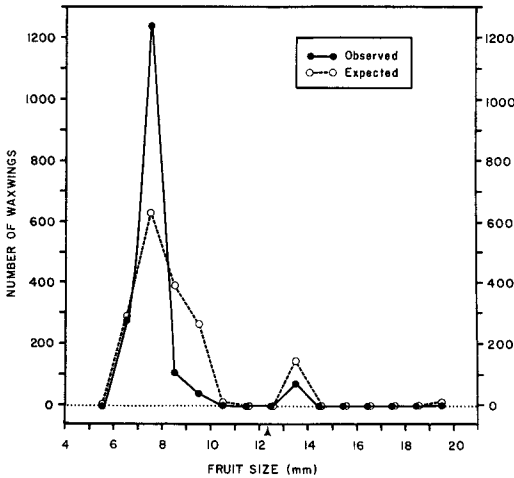


FIGURE 5. Observed versus expected values for waxwings per fruit size class tested using G -test for goodness-of-fit. Assignment of species to size classes based on mean maximum diameter. Expected values based on proportion of biomass for each size class; observed values based on total number of waxwings seen per size class in 1984–85 ($G = 1,129.8$, $P < 0.001$). Arrow indicates mean gape width ($12.3 \text{ mm} \pm 1.21 \text{ SD}$).

abundant species were most heavily used, sometimes more than expected (e.g., yaupon holly), and rare species (i.e., Other) were consumed much less than predicted. Notable exceptions were mistletoe (only moderately abundant but eaten much more than expected) and Chinese juniper (fairly abundant but rarely consumed).

When all census data were pooled, there was a significant rank correlation between fruit calories and number of waxwing flocks ($r = 0.857$; $P < 0.05$). Tests using product-moment correlations showed a significant relationship between calories and number of flocks ($r = 0.847$; $P < 0.05$), as well as between calories and number of individual birds ($r = 0.893$; $P < 0.01$). Biomass and number of flocks were significantly correlated using product-moment tests ($r = 0.709$; $P < 0.05$). February data showed a product-moment correlation between number of calories and number of birds ($r = 0.888$; $P < 0.01$), as well as biomass and number of birds ($r = 0.759$; $P < 0.05$). No other tests of correlation between fruit characteristics and waxwing patterns were significant.

The observed number of waxwings per fruit size class did not equal expected values based on availability of fruits in each size class (Fig. 5). In

particular, waxwings fed heavily on fruits in the 7 to 8 mm size class (which included yaupon and deciduous hollies). Mean gape width ($12.3 \text{ mm} \pm 1.2 \text{ SD}$) was exceeded by only two types of fruit—the large and small crab apples.

DISCUSSION

Cedar Waxwings showed definite preferences for certain fruit species in the field. They also shifted their use of foods during the course of the winter, beginning with a strong preference for mistletoe and then for hackberry. In a qualitative assessment of waxwing fruit preferences during winter in Oklahoma, Sutton (1967) also listed mistletoe first and hackberry second. When fewer choices were available later in the winter, yaupon and deciduous hollies became the most heavily-used species. Other field studies of temperate frugivore foraging patterns have also quantified such pronounced shifts in food use. Sorensen (1981) found that thrushes in England consumed different types of fruits in a certain order, depleting the fruits of one species before shifting to another. In a study of frugivores in a New Jersey forest, Baird (1980) also found that certain fruit species were consumed first among a variety of choices until quantities were reduced. Previously unused fruit species then became important food sources, after remaining uneaten for weeks (Baird 1980).

ABUNDANCE

Waxwings foraged mostly on abundant fruits and seldom on rare ones, but there were some exceptions. Mistletoe was highly preferred but only moderately abundant, indicating that some characteristic(s) of that species was (were) sufficiently attractive to waxwings so that they would search out and consume mistletoe fruits even when other species were more abundant. In contrast, Chinese juniper was abundant but distinctly avoided by waxwings. Thus, some other characteristic of the fruits that was unattractive to waxwings outweighed its high abundance.

Snow (1971) suggested that fruiting plants producing many fruits would be more conspicuous, would attract more dispersers and, therefore, would have a selective advantage over plants with fewer fruits. In my study and in one by Baird (1980), the most abundant fruits generally were most heavily used. In contrast, in a study of 14 frugivorous bird species in a British woods, Sorensen (1981) found no correlation between fruit abundance and consumption by birds.

COLOR

Waxwings ate fruits of many colors but the two most heavily-used species had red fruits. Other investigators have suggested that the color red has evolved as a cue to good food sources for birds (Grant 1966, Raven 1972, Willson and Thompson 1982). Turček (1963) concluded that red was the most common color of bird-dispersed fruits in Europe, but that red and black were most common worldwide. Wheelwright and Janson (1985) found that black was the most common color of "bird fruits" in Peru, Costa Rica, and Florida. Although color may make fruits conspicuous and, therefore, attractive, choice is not based on color alone (Turček 1963). Birds may cue in on one or two colors but can learn to eat foods of a variety of colors (Stiles 1976).

Green is the most common color of unripened fruits and is generally avoided by birds (Kalmbach and Welch 1946, Turček 1963, Foster 1977). Only one species of plant in the study area, Chinese juniper, produced greenish fruit, and waxwings generally avoided these.

SIZE

In my study, the lack of association between fruit size and frequency of waxwing use can be explained by the fact that some fruits exceeded gape width and others may have been too small to provide benefits outweighing costs. When the two extremes are excluded, waxwings might be expected to prefer fruits slightly smaller in diameter than their gape width, as these could potentially provide the greatest benefit per fruit. However, waxwings foraged preferentially on fruits 7 to 8 mm in diameter, considerably less than their gape width. Waxwings might also be predicted to forage on fruits based on abundance of fruits. However goodness-of-fit tests showed that they did not do so, but rather preferred the 7 to 8 mm size.

One explanation for the observed size preference in the field is that waxwings were selecting not only among different sizes but also species of fruits. Pressures for taking the largest fruits (still under gape width) may have been overridden by factors such as nutritional content. When fruit species were controlled in the laboratory, Moermond and Denslow (1983) found that tanagers and saltators did prefer the largest fruits offered.

A second explanation for the observed size

preference is that although waxwings physically could have swallowed the larger fruits, the cost of handling them may have been too high. Martin (1985) defined the size at which handling becomes difficult for a given bird as the "critical size." In a study of Three-wattled Bellbirds (*Procnias tricarunculata*), Wheelwright (1985) also found preferential feeding on fruits that were medium sized relative to the sizes in the birds' diets.

HEIGHT

I expected waxwings to prefer foraging in taller plants as a means of reducing predation risk, but found no significant correlation between the fruit preference (based on numbers of visiting waxwings) and mean height of the plant species. The most heavily-used plants, yaupon and deciduous hollies, were only intermediate in height. However, the following observations suggest that waxwings prefer to perch before, during, and after foraging as far from the ground as possible unless drawn to lower levels by favorable food resources.

First, waxwings initially foraged on mistletoe and hackberries, the two highest species. After these fruits were virtually depleted, the birds began foraging on species closer to the ground. However, other factors besides height may also have played a role in selection of mistletoe and hackberry (e.g., nutritional content of fruits, the fact that these two species were native to the area).

Second, waxwings usually made foraging bouts to fruiting plants from the tops of tall deciduous trees, such as elms and oaks. Individuals usually stayed in the fruiting plant while consuming several fruits in rapid succession and, once full, returned to the treetop where other flock members were perched. Sutton (1967) noted the same behavior. Skeate (1984) found that waxwings showed a significant preference for deciduous trees as perch sites after foraging bouts. He suggested that these sites provided a good vantage point for flocking, foraging, and predator detection.

Third, Best (1981) determined in laboratory tests that height was the overriding factor in waxwing fruit preferences. In fact, waxwings selected fruits that were less-preferred in simple preference tests if those fruits were offered at the preferred height. From these observations, it appears that waxwings prefer high perching and

foraging sites when available. However, they will make foraging bouts to food sources closer to the ground.

PULP-TO-SEED RATIO

Herrera (1981) hypothesized that plants must compete among themselves to attract dispersers and, therefore, should reduce seed weight that is an unwanted load to birds. Birds should select fruits with the highest pulp-to-seed ratio in order to gain highest nutritional benefits per volume of fruit consumed. Although this prediction has been supported for tropical frugivores (Howe and Vande Kerckhove 1980), I found no significant correlation between waxwing choice and pulp-to-seed ratio. The birds heavily used fruits with the highest (mistletoe) and the lowest (hackberry) ratios, as well as fruits with intermediate values. Thus, other factors such as nutritional content of the pulp consumed, location of fruits, and abundance of fruits must play a more important role in food selection by waxwings.

WATER CONTENT

There was no correlation between water content and preferences of waxwings. In midtemperate latitudes, including Oklahoma, birds are probably not water-stressed during winter (Herrera 1982, Johnson et al. 1985). Water was not only available to birds in fruits but also from streams, ponds, and fountains (Sutton 1967), as well as from rainwater puddles.

PROTEIN CONTENT

Although the hypothesis that birds are more likely to consume nutritious fruits than low-quality fruits is well-accepted (Snow 1971, Johnson et al. 1985), actual studies of the relationship between nutrition and food selection by frugivores have produced conflicting results. Berthold (1976a) concluded from laboratory tests on five species of omnivorous songbirds that animal foodstuffs were vital to these birds because of the low protein content available to them in plant material, including fruits. His results indicated that birds deprived of animal material would lose weight and could eventually die from lack of protein.

Several studies (Sorensen 1981, Johnson et al. 1985), including mine, have found no correlation between protein content of fruits and selection by frugivores. There are a number of reasons for this lack of association. First, protein require-

ments may diminish with the onset of winter, and energetic requirements may become the overriding nutritional need (Stiles 1980, Herrera 1982). If this is the case, frugivores might be expected to maximize energetic intake at the expense of protein intake. Also, the lower protein requirements may be met even by the low amounts of protein in fruits. My study showed that waxwings do, in fact, select fruits with higher caloric, not protein, content.

Second, low protein content per fruit may be compensated for by increased food intake. However, Johnson et al. (1985) found that the 11 frugivorous bird species they tested rarely increased consumption when nutritional quality of food was relatively low. Finally, waxwings may be particularly adapted to survive on low levels of protein in a highly frugivorous diet. This is supported by Berthold's (1976b) observation that Bohemian Waxwings (*B. garrulus*), unlike the other songbirds he tested, were able to survive and even gain weight on an exclusively frugivorous diet. He called the Bohemian Waxwing a "frugivorous feeding specialist." In addition, Stiles (1984) observed that the diet of Cedar Waxwings is exceptionally high in fruits all year (approximately 70%) relative to other frugivores. Although I saw American Robins foraging on the ground for insects during the winter, waxwings ate only fruits until early spring. Waxwings did begin to forage on insects in March.

CALORIES

There was no significant difference in caloric content between the group of fruits that waxwings ate and the group that they did not eat, suggesting that factors other than calories (e.g., abundance) are more important in initially determining whether or not fruits are consumed by waxwings. However, among fruits that waxwings ate, species with high energy content were consumed more frequently. As suggested above, this would be expected if energetic requirements are the most important nutritional need for frugivores during winter (Stiles 1980, Herrera 1982). In contrast to my study, however, Sorensen (1981) found no relationship between fruit selection by birds and fruit caloric content.

Overall, my results indicate that Cedar Waxwings forage selectively on certain fruit species. The relative abundance of a species of fruit is related to whether or not that type of fruit will be eaten by waxwings. Among the species that

were consumed, the order of preference was related to abundance, caloric content, and fruit size. That other fruit characteristics—including color, height, pulp-to-seed ratio, percent water, and percent protein—were not significantly correlated to foraging patterns in this study does not eliminate the possibility that these characteristics are important in other fruit-disperser interactions. Lack of agreement on which fruit characteristics are most influential in avian choice suggests that a number of factors interact to determine choice and that different studies reveal true differences in the relative importance of the fruit characteristics that attract avian dispersers.

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