Wilson Bull., 105(4), 1993, pp. 604–611

HANDLING EFFICIENCY AND BERRY SIZE PREFERENCES OF CEDAR WAXWINGS

MICHAEL L. AVERY,[1] KELLY J. GOOCHER,[2] AND MARCIA A. CONE[3]

ABSTRACT.—In a series of feeding trials, Cedar Waxwings (*Bombycilla cedrorum*) preferred blueberries (*Vaccinium* spp.) having a mean diameter of 7.5 mm when the diameter of alternative berries exceeded 12 mm. Waxwings did not exhibit clear preferences among blueberries that differed by ≤3.5 mm mean diameter. For 7.5 mm fruit, observed handling times averaged 2.8 sec and increased exponentially as berry diameter increased. Because the frequency of dropped fruit also increased with fruit size, the birds' rate of sugar ingestion was maximized by feeding on the 7.5 mm berries. The rate of sugar ingestion decreased linearly as blueberry size increased. Thus, within the range of sizes tested, Cedar Waxwings preferentially selected blueberries that were more efficiently handled and that produced the highest rate of sugar intake. *Received 18 Dec. 1992, accepted 16 April 1993.*

Fruits that are abundant, accessible, and conspicuous attract a wide variety of seed dispersers (Snow 1971, Stiles 1982). The selection of individual fruits by frugivorous birds may be governed by factors such as pulp to seed ratio (Herrera 1981, Snow 1971), fruit size (Wheelwright 1985; McPherson 1987, 1988), seed size (Levey and Grajal 1991), fruit accessibility (Moermond and Denslow 1983), and total pulp mass (McPherson 1987). In addition, birds might be expected to select fruits that provide large rewards (e.g., energy gain) relative to the costs of acquiring and handling them (Martin 1985). Indeed, the selection of fruits based on pulp to seed ratio or the total pulp content may be incidental to maximizing the ratio of energetic benefit to costs associated with manipulating and swallowing the fruit (Hegde et al. 1991).

Martin (1985) suggested that larger fruits are taken up to the point where gape width limitations severely increase handling time. Similarly, Wheelwright (1985) noted that because fruits frequently are swallowed whole, the upper size limit of a food may be restricted by the gape width of the bird. Although gape-width limitation may be especially important in many small-bodied birds (Jordano 1987), others are able to circumvent this constraint (Levey 1987).

Cultivated blueberries (*Vaccinium* spp.) represent an important food source for migrating Cedar Waxwings (*Bombycilla cedrorum*). Previous

[1] USDA/APHIS, Denver Wildlife Research Center, Florida Field Station, 2820 E. University Ave., Gainesville, Florida 32601.
[2] Univ. of Florida, Office of Sponsored Research, Gainesville, Florida 32611 (Present address: 5751 N. 72nd St., Milwaukee, Wisconsin 53218).
[3] Univ. of Florida, Office of Sponsored Research, Gainesville, Florida 32611 (Present address: 116 Sir Scott Rd., Athens, Georgia 30607).

TABLE 1
BERRY SIZE CLASSES USED IN FRUIT SIZE PREFERENCE TESTS

Size class limits (mm)	N	Diameter (mm)		Height (mm)		Mass (g)	
		$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
>7 to ≤9	21	7.5	0.2	6.7	0.2	0.25	0.01
>10 to ≤12	15	11.0	0.1	10.3	0.2	0.82	0.02
>12 to ≤13.5	13	12.8	0.1	10.6	0.1	1.11	0.02
>13.5 to ≤15	15	14.0	0.1	11.1	0.2	1.38	0.03
>16 to ≤18	15	17.6	0.1	14.4	0.3	2.71	0.06
>18	15	20.5	0.1	16.1	0.1	3.91	0.07

field observations (Nelms et al. 1990) suggested that, although they consumed blueberries across a wide range of sizes, waxwings preferred the smallest ones. In this study, we sought to document the responses of individual waxwings to the various sizes of blueberries available to them. We hypothesized that Cedar Waxwings would prefer the size that maximized their rate of sugar intake.

METHODS

General.—During April and May 1989 and 1991, we collected blueberries from various cultivars at the Univ. of Florida Horticultural Unit (UFHU). We established six size classes according to berry diameters: >7 to ≤9 mm, >10 to ≤12 mm, >12 to ≤13.5 mm, >13.5 to ≤15 mm, >16 to ≤18 mm, and >18 mm. We separated berries into size classes, using specially constructed metal sorting trays. We measured the diameter, height, and mass of a subsample in each size class (Table 1).

We mist netted Cedar Waxwings at the UFHU in April 1989 and April–May 1991. Waxwings were housed communally for two weeks prior to testing. Initially, we fed the birds banana mash (Denslow et al. 1987) mixed with fresh blueberries of various sizes and then gradually accustomed them to eating AVN® (Purina Mills, St. Louis, Missouri) finch-canary feed. We tested birds individually (4 × 4 × 6 m cages), and we placed a blueberry presentation tray (4 × 8 cm, 2 cm deep) next to one perch and a cup of AVN diet at the other perch on the opposite side of the cage.

Size preference trials.—We deprived birds of food for 30 min prior to the start of a trial. Then, the observer placed two test berries on opposite sides of the blueberry presentation tray and stepped 4 m away to begin timing the bird's behavior. Handling time was recorded from when the berry was picked up until when it either was swallowed or dropped. The birds could not retrieve dropped berries. The first berry picked up was recorded as the berry chosen. If the bird did not pick up either berry within 3 min, the trial was stopped and recorded as a refusal.

We offered a given pairing of berry sizes to an individual up to 14 times. We required eight successful trials (i.e., nonrefusals) for the bird to be included in our size preference analyses. Also, individual birds received up to three different berry size pairings and were tested no more than four times in a single morning. In 1989, we tested the 7.5 mm size

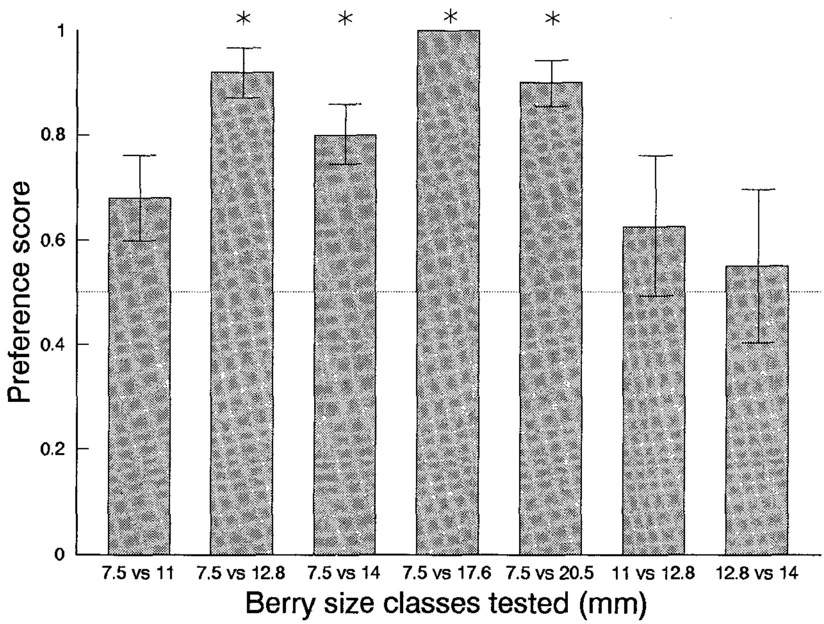

FIG. 1. Results of feeding trials (N = 5 birds/trial) with individual Cedar Waxwings expressed as the number of smaller berries selected/the total number of selections (8). A value of 0.5 indicates indifference. Asterisks denote significant difference ($P < 0.05$) from 0.5. Capped bars indicate one SE.

class against each of the five larger size classes. In 1991, we tested the 12.8 mm berries against the two adjacent sizes.

We used 20 birds to obtain five successful preference tests for each size pairing. Five birds participated in three pairings each, five birds were used for two pairings, and 10 birds were used in one pairing each. In addition, five other birds participated in the size preference tests but did not achieve our criterion of eight successful trials. We did, however, incorporate the eat and drop times from these birds in our overall evaluation of berry handling times.

Analysis.—For each size preference test, we calculated each bird's preference ratio for the smaller size class by dividing the number of smaller berries chosen (eaten plus dropped) by eight, the total number of berries handled (eaten plus dropped). We tested the null hypothesis that the mean preference ratio for the smaller berry size was not significantly different from 0.5 (each berry size chosen equally) using one sample *t*-tests on arcsine transformed preference values (Sokol and Rohlf 1969, Martinez del Rio et al. 1989). In one-way analyses of variance, we combined the data from all 25 of the study birds to compare eat and drop times among size classes and among birds.

RESULTS

Size preference.—When the difference between the mean diameters of the test berries was >3.5 mm, the waxwings demonstrated a clear preference for the smaller berry (Fig. 1). The birds showed no preference,

TABLE 2

BLUEBERRY HANDLING BEHAVIOR BY CEDAR WAXWINGS DURING FEEDING TRIALS TO ASSESS FRUIT SIZE PREFERENCE

Fruit size class (mm)	Number of berries		Eat time (sec)		Drop time (sec)	
	Eaten	Dropped	$\bar{x}$	SE	$\bar{x}$	SE
7.5	166	6	2.8	0.2	4.5	1.5
11.0	43	11	14.4	2.2	4.7	2.1
12.8	17	42	32.0	2.7	2.9	0.5
14.0	4	33	44.3	6.1	2.9	0.8
17.6	0	0	—	—	—	—
20.5	0	4	—	—	2.0	0.6

however, between berries of adjacent size classes. Large standard errors in several tests (Fig. 1) reflected the variation in responses among test birds; some consistently selected one size or the other, while others displayed no preference. Two of the birds that showed indifference to fruit size in the 7.5 mm vs 11.0 m test, strongly preferred the smaller berry when it was tested against the 12.8 mm class. Berries in the 7.5 mm and 11.0 mm classes were eaten 97% and 80% of the time, respectively (Table 2). In contrast, berries in the larger size classes were dropped 79% of the time. The 17.6 mm size class was never chosen.

Handling time and sugar intake.—The time required to swallow a berry increased significantly with berry size ($P < 0.001$; $F = 128.9$), as did the frequency with which berries were dropped (Table 2). Among berry sizes, drop time did not differ ($P = 0.67$; $F = 0.59$). Waxwings swallowed berries in the two smallest size classes with little or no manipulation. Occasionally, a bird flew to another part of the cage before swallowing the fruit, but extended handling was unnecessary. The birds were able to eat the larger fruit only by mashing them repeatedly in their bills until the soft fruit could pass through the somewhat distensible gape and mouth to the esophagus. Among the 12.8, 14.0, and 20.5 mm size classes, 79 berries were picked up and dropped, 56 (71%) within 2 sec. The birds appeared to assess and to reject immediately such berries as unsuitable. Other large berries, however, were dropped apparently by accident after being manipulated for as long as 22 sec.

There were significant differences ($F = 9.04$, $P < 0.001$) in handling times among the 10 birds that ate 7.5 mm berries. This result was due, however, to extended handling times by three birds that habitually changed perches or flew briefly around the cage before swallowing the fruit. These three birds averaged 4.8 sec/berry compared to the overall mean of 2.8

TABLE 3

ESTIMATED SUGAR INTAKE OBTAINED BY CEDAR WAXWINGS PER 100 BLUEBERRIES OF FOUR DIFFERENT SIZE CLASSES

Factor	Blueberry size class			
	7.5 mm	11.0 mm	12.8 mm	14.0 mm
Number of berries[a]				
Eaten	97	80	29	11
Dropped	3	20	71	89
Total handling time (sec)[a]				
Berries eaten	272	1152	928	487
Berries dropped	14	94	206	258
Total time invested (sec/100 berries)	286	1246	1134	745
Sugar content (mg/berry)[b]	27.2	90.2	121.0	154.0
Sugar intake				
Total (mg/100 berries)	2638	7216	3509	1694
Rate (mg/sec)	9.2	5.8	3.1	2.3

[a] Determined from frequencies of eating and dropping and handling times given in Table 2.
[b] Based on an average of 110 mg sugar/g fresh berry; R. L. Darnell, K. E. Koch, P. M. Lyrene, unpubl. data.

sec/berry (Table 2). There were no differences ($F = 1.04$, $P = 0.44$) among the 14 birds that ate 11.0 mm berries. Drop times among birds did not differ for either the 12.8 mm (15 birds; $F = 0.45$, $P = 0.94$) or the 14.0 mm (10 birds; $F = 0.76$, $P = 0.65$) size classes.

For the four smallest berry size classes, we estimated the birds' rate of sugar ingestion by dividing the mg of sugar/berry by the handling time, corrected for the observed size-specific frequency of drops (Table 3). Sugar ingestion decreased in a negative linear fashion with increasing berry size (Fig. 2). Although 11.0 and 12.8 mm berries provided greater absolute amounts of sugar, the 7.5 mm size class clearly provided the highest rate of sugar ingestion.

DISCUSSION

Foraging theory predicts that animals will maximize energy gain (benefit) per unit time spent foraging (cost) (Stephens and Krebs 1986). Part of the foraging cost is the time spent handling food items (Martin 1985, Hegde et al. 1991). Hegde et al. (1991) defined handling time as the time from picking up a food item to swallowing it. They found that for Red-vented Bulbuls (*Pycnonotus cafer*), the handling time per fruit increased exponentially with an increase in fruit size. Our findings corroborate their result.

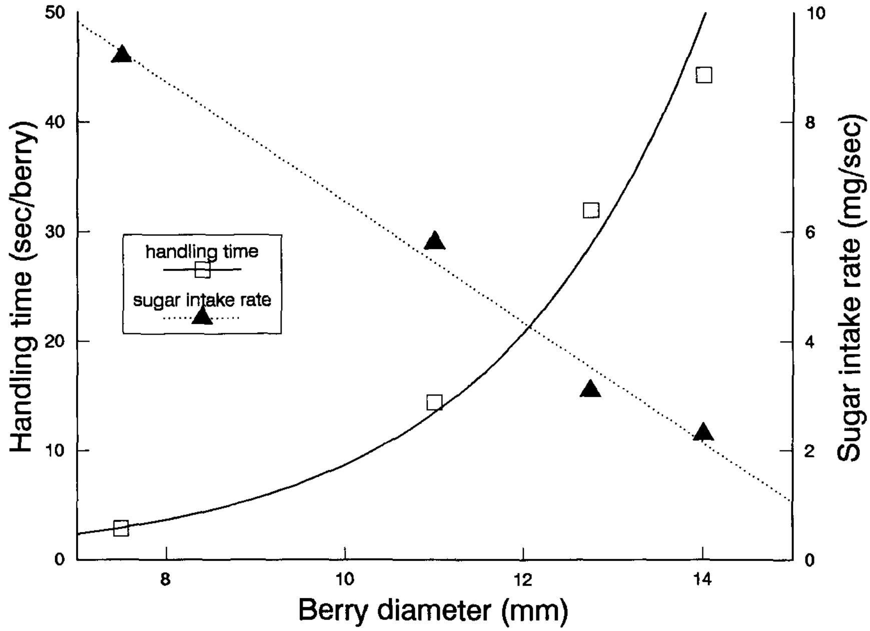

FIG. 2. The effect of blueberry diameter on the handling time and rate of sugar intake of captive Cedar Waxwings. Handling time (Y) increases exponentially with berry size (X) according to the equation, $Y = 0.11\ e^{0.44X}$ ($R^2 = 0.99$). Rate of sugar intake (Z) decreases linearly with increased berry size according to the equation, $Z = 17.51 - 1.01X$ ($R^2 = 0.98$).

On the other hand, our findings differ somewhat from those of White and Stiles (1991) who found that feeding efficiency (fruit biomass harvested per time) of American Robins (*Turdus migratorius*) increased with fruit size. Their study, however, included fruit only up to 9 mm in diameter, considerably less than the robins' mean gape width (White and Stiles 1991). It is likely, therefore, that handling time was uniformly low and that accidental dropping was infrequent, so profitability (net energy gain) would be expected to increase with fruit size (Martin 1985).

In contrast, the size range of blueberries offered to waxwings in our preference tests may represent the downside of the profitability curve (Martin 1985). The 7.5 mm berries are at or near the peak of the curve, with the larger sizes being increasingly less profitable (i.e., yielding less net energy) due to increased handling costs. For each bird there probably is a "critical fruit size above which handling becomes difficult" (Martin 1985:566). Birds should, therefore, prefer larger fruits only to the point at which the diameter does not exceed this critical size.

McPherson (1988) found that two groups of captive Cedar Waxwings (mean gape width 12.3 mm) preferred 6-mm diameter cantaloupe bits to 9-mm and 12-mm pieces, a result consistent with field observations of waxwing fruit size selection (McPherson 1987). We departed from McPherson's (1988) study design by focusing on the behavior of individual Cedar Waxwings instead of groups and by testing a broader range of fruit sizes representative of those available. Also, we used actual fruit to reduce the possibility of other factors (e.g., secondary chemical compounds, color) interacting with fruit size to confound the results. We found that although Cedar Waxwings can eat fruit equal to or greater than their gape width, they become increasingly inefficient as fruit diameter exceeds 7.5 mm. We suggest that increased handling difficulty, not gape width per se, sets the upper limit on the size of soft fruits like blueberries that Cedar Waxwings can efficiently handle.

ACKNOWLEDGMENTS

We greatly appreciate the review comments of D. J. Levey and K. E. Brugger. P. Nol, C. Newman, and M. Kress provided animal care services. L. A. Whitehead prepared the manuscript. D. G. Decker constructed the berry sorting trays and assisted in many ways.

LITERATURE CITED

DENSLOW, J. S., D. J. LEVEY, T. C. MOERMOND, AND B. C. WENTWORTH. 1987. A synthetic diet for fruit-eating birds. Wilson Bull. 99:131–135.

HEGDE, S. G., K. N. GANESHAIAH, AND R. UMA SHAANKER. 1991. Fruit preference criteria by avian frugivores: their implications for the evolution of clutch size in *Solanum pubescens.* Oikos 60:20–26.

HERRERA, C. M. 1981. Fruit variation and competition for dispersers in natural populations of *Smilax aspera.* Oikos 36:51–58.

JORDANO, P. 1987. Frugivory, external morphology and digestive system in mediterranean sylviid warblers *Sylvia* spp. Ibis 129:175–189.

LEVEY, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. Am. Nat. 129:471–485.

——— AND A. GRAJAL. 1991. Evolutionary implications of fruit-processing limitations in Cedar Waxwings. Am. Nat. 138:171–189.

MARTIN, T. E. 1985. Resource selection by tropical frugivorous birds: integrating multiple interactions. Oecologia (Berlin) 66:563–573.

MARTINEZ DEL RIO, C., W. H. KARASOV, AND D. J. LEVEY. 1989. Physiological basis and ecological consequences of sugar preferences in Cedar Waxwings. Auk 106:64–71.

MCPHERSON, J. M. 1987. A field study of winter fruit preferences of Cedar Waxwings. Condor 89:293–306.

———. 1988. Preferences of Cedar Waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. Anim. Behav. 36:961–969.

MOERMOND, T. C. AND J. S. DENSLOW. 1983. Fruit choice in neotropical birds: effects of fruit type and accessibility on selectivity. J. Anim. Ecol. 52:407–420.

NELMS, C. O., M. L. AVERY, AND D. G. DECKER. 1990. Assessment of bird damage to early-ripening blueberries in Florida. Proc. Vertebr. Pest Conf. 14:302–306.

SNOW, D. W. 1971. Evolutionary aspects of fruit eating by birds. Ibis 113:194–202.

SOKOL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Company, San Francisco, California.

STEPHENS, D. W. AND J. H. KREBS. 1986. Foraging theory. Princeton Univ. Press, Princeton, New Jersey.

STILES, E. W. 1982. Fruit flags: two hypotheses. Am. Nat. 120:500–509.

WHEELWRIGHT, N. T. 1985. Fruit size, gape width and the diets of fruit-eating birds. Ecology 66:808–818.

WHITE, D. W. AND E. W. STILES. 1991. Fruit harvesting by American Robins: influence of fruit size. Wilson Bull. 103:690–692.

SAFRING NEWS AVAILABLE ON SUBSCRIPTION

Safring News, the biannual journal of the South African Bird Ringing Unit (SAFRING), has been in publication since 1972. The journal publishes articles reporting the results of ringing activities in southern Africa, ageing and sexing guides to southern African birds, and book reviews. Many of these papers relate to migratory birds, and therefore their immediate interest transcends a purely southern African relevance. Papers in *Safring News* are included in *Wildlife Review* and similar services. Previously, *Safring News* has had a limited circulation, with copies being sent only to SAFRING ringers and to ringing offices. In response to requests from researchers and institutions in many parts of the world, it has been decided to make *Safring News* available on subscription. The subscription rate for volume 23, 1994, has been set at 30 U.S. dollars for individuals and 60 U.S. dollars for institutions. Orders for subscriptions should be sent to SAFRING, Avian Demography Unit, Department of Statistical Sciences, Univ. of Cape Town, Rondebosch 7700, South Africa.