

male displaying towards a receptive female in another male's territory. Also, territory switches occur during the season. There was also an instance in which a male Dickcissel left his territory for 3 weeks and returned with a female. Some female Red-winged Blackbirds on territories of vasectomized males have still been known to produce young (Bray et al., *Wilson Bull.* 87:195–197, 1975). Keller (M.S. thesis, Univ. North Dakota, Grand Forks, North Dakota, 1979) suggests that in Chipping Sparrows (*Spizella passerina*) an alternative strategy to holding a good territory could be to sneak copulations, provided that the male does not spend much time off his territory or his female may be inseminated by other wandering males. The role of distant flight and switching territories needs further investigation. In birds such as the Dickcissel, both strategies could increase fitness.

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Passage rate, energetics, and utilization efficiency of the Cedar Waxwing.—The Cedar Waxwing (*Bombycilla cedrorum*) is noted for its intensive foraging on fleshy fruits (Nice, *Condor* 43:58–64, 1941; Tyler, *U.S. Natl. Mus. Bull.* 197:79–102, 1950). Flocks of Cedar Waxwings have been reported to deplete entire fruit crops of red cedar (*Juniperus virginiana*) over a period of 2 days (Parker, Ph.D. diss., Duke Univ., Durham, North Carolina, 1949). In summer the diet of the Cedar Waxwing is composed largely of insects and fleshy fruits and in winter their food consists almost exclusively of fruits (Beal, pp. 197–200 in *Ann. Rept. Dept. Agric.* 1892, and *Farmer's Bull.* 54:38–39, 1904; Nice 1941; Tyler 1950; Martin et al., *American Wildlife and Plants*, Dover Publ. Inc., New York, New York, 1951). The Cedar Waxwing is therefore considered a major frugivore (Thompson and Willson, *Evolution* 33:973–982, 1979; Stiles, *Am. Nat.* 116:670–688, 1980). However, the extent to which the Cedar Waxwing can subsist on fruits alone has not been investigated.

Nutritional studies of fruit-eating passerines in Europe have shown that all species except the Bohemian Waxwing (*Bombycilla garrulus*) rapidly lose weight and die in captivity if supplied only with fruits (Berthold, *J. Orn.* 117:145–209, 1976a; *Experientia* 32:1445, 1976b; *Ardea* 64:140–154, 1976c; *J. Orn.* 118:202–203, 1977). Therefore, Berthold (1976b) considered the Bohemian Waxwing a fruit specialist, as opposed to an opportunistic frugivore. A similar adaptation to a frugivorous diet may be expected from the Cedar Waxwing, since this bird closely resembles the Bohemian Waxwing in its food habits (Bent, *U.S. Natl. Mus. Bull.* 197:62–79, 1950; Tyler 1950).

In this study we assessed the energy requirements, the rate and efficiency of digestion, and the ability of captive Cedar Waxwings to survive on a diet of fleshy fruits during autumn. The investigations were part of a larger research project on the role of Cedar Waxwings as seed dispersers of red cedar, a common woody tree species in eastern North America.

Materials and methods.—Cedar Waxwings were caught on the campus of the Virginia Polytechnic Institute and State University, Blacksburg, Montgomery Co., Virginia, in the autumn of 1980 (N = 5) and 1981 (N = 6). Each bird was placed in a separate, wire mesh (0.5 cm) cage, measuring 80 × 60 × 45 cm. The Cedar Waxwings were kept in an unheated room allowing free circulation with outside air (\bar{x} = 12°C during the day; \bar{x} = 5°C at night), on an 11-h light, 13-h dark cycle, simulating the natural photoperiod. The birds were supplied ad libitum with water and a mixture of fruits, including those of cork-tree (*Phellodendron sachalinense*), cherry (*Prunus* sp.), mountain ash (*Sorbus americana*), viburnum (*Viburnum* sp.), privet (*Ligustrum vulgare*), multiflora rose (*Rosa multiflora*), honeysuckle (*Lonicera morowii*), flowering dogwood (*Cornus florida*), and red cedar (*Juniperus virginiana*). All foodstuff was collected locally and stored in a refrigerator.

Observations on feeding and defecation rates were made on four Cedar Waxwings provided with red cedar cones in the autumn of 1980; the observations were repeated with four different birds in 1981. In 1981, similar observations were made on two Cedar Waxwings supplied with flowering dogwood fruits. All food was removed from the cages on the evening before each observation period. The next morning, 14–16 h later, the birds were weighed and provided with fruits. Direct observations, made at a distance of 1–2 m from the birds, included time of feeding, number of fruits ingested per feeding bout, and time of defecation. The birds were supplied with a mixture of fruits upon termination of each experiment. The passage rate of red cedar and dogwood seeds in the alimentary tract of Cedar Waxwings was estimated by applying 1–2 cc of an inert marker (ferric-oxide in solution) directly into the bird's esophagus immediately before the start of an experiment. The passage rate represented the time between ingestion of the first fruit at the start of the experiment and the appearance of the first colored dropping.

The energy requirements of the Cedar Waxwing were determined using five birds caught in 1980. An estimation of the existence metabolism can be obtained, if captive birds sustain their weight, as shown by Kendeigh (Wilson Bull. 81:441–449, 1969; Condor 72:60–65, 1970; Am. Nat 106:79–88, 1972). The existence metabolism is a reasonable approximation of the energy requirements of a bird under free living conditions (Kendeigh 1969, 1970). The five Cedar Waxwings were starved for 16 h prior to the start of the experiment. Their daily energy requirements were determined over a period of 6 days. The birds were weighed each morning and supplied with known amounts of mountain ash, cork-tree and *Viburnum* sp. fruits in excess of the bird's daily use as established prior to the start of the experiment. The first 2 days of the experiment were excluded from the analysis to allow the birds to adjust to their diet (Sibbald, pp. 38–43 in Standardization of Analytical Methodology for Feeds, W. J. Pigden et al., eds., Workshop Proc., 12–14 March 1979, Ottawa, Ontario, 1980). Each morning, all fecal material and remaining fruits were collected from the cages and weighed. Fecal material was stored in plastic bags in a refrigerator. Percent dry matter of fecal material and fruits was determined according to procedures described by the Association of Official Agricultural Chemists (Methods of Analysis, Washington, D.C., 1975). The fecal material and samples of the foodstuff (including seeds) were ground in a Wiley mill after drying, sieved (mesh size 600 μ m), and pelleted for caloric determination (kcal/g dry weight) in a Parr adiabatic oxygen bomb calorimeter. The metabolized energy was determined by subtracting the caloric fecal energy (kcal/g dry weight) from the gross energy intake. The average energy metabolized over 4 days provided an estimate for the existence metabolism of the Cedar Waxwing (Kendeigh 1972). Utilization efficiencies of Cedar Waxwings

TABLE 1
METABOLIZED ENERGY (ME IN KCAL/DAY), UTILIZATION EFFICIENCY (%), AND BODY WEIGHT (G) OF CEDAR WAXWINGS IN CAPTIVITY CALCULATED OVER A 4-DAY PERIOD* IN NOVEMBER 1980

Bird	ME	Utilization efficiency (%)	Bird weight (g)	
	(kcal/day)		$\bar{x} \pm SD$	N
1	30.5	53.1	24.8 ± 0.5	4
2	17.8	26.6	35.5 ± 0.7	4
3	25.3	36.1	30.3 ± 0.4	4
4	23.7	35.2	28.2 ± 0.9	4
5	21.2	31.3	31.5 ± 0.5	4
\bar{x}	23.7	36.5	30.1 —	—
SD	4.8	10.0	3.6 —	—
N	5	5	20 —	—

* Referred to as existence metabolism (Kendeigh 1969). Birds were fed with a mixture of fruits (*Sorbus* sp., *Viburnum* sp., *Ligustrum* sp., and *Phellodendron sachalinense*).

fed on a diet of mixed fruits were calculated according to the formula $(E_i - E_e)/E_i$, where E_i = ingested energy content of the food (kcal) and E_e = fecal energy (kcal) (Walsberg, Condor 77:169–174, 1975). All calculations and tests were made using the Statistical Analysis System (SAS) (Helwig and Council, The SAS User's Guide, 1979 ed., The SAS Inst. Inc., Cary, North Carolina, 1979). Means are followed by standard deviations.

Feeding, defecation, and passage rates.—The total observation time of Cedar Waxwings provided with red cedar cones or dogwood fruits amounted to 44.32 h and 10.12 h, respectively. Cedar Waxwings fed on red cedar cones approximately every 5 min (4.93 ± 4.85 min, $N = 485$) and consumed on the average 4.4 ± 3.5 ($N = 522$) red cedar cones per feeding bout. The extrapolated feeding rate is 53 cedar cones per hour. Cedar Waxwings provided with dogwood fruits foraged at shorter intervals, 3.10 ± 3.78 min ($N = 323$) ($t = -5.97$, $df = 786$, $P < 0.0001$), but only consumed one fruit per feeding bout, which resulted in a feeding rate of 19 dogwood fruits per h. The passage rate of red cedar cones was significantly shorter ($t = 6.05$, $df = 54$, $P < 0.001$) than the passage rate of dogwood fruits (11.67 ± 4.23 min, $N = 40$ and 22.92 ± 6.92 min, $N = 16$, respectively). The mean defecation rate, however, was longer ($t = -5.87$, $df = 1080$, $P < 0.0001$) for Cedar Waxwings feeding on red cedar cones than those feeding on dogwood fruits (2.82 ± 3.73 min, $N = 705$ and 2.08 ± 1.42 min, $N = 378$, respectively). Defecation rates were not different between birds administered the marker solution and those not ($t = 1.37$, $df = 696$, $P = 0.17$, for red cedar cones; $t = -0.77$, $df = 376$, $P = 0.43$, for dogwood fruits).

Existence metabolism.—Under laboratory conditions five Cedar Waxwings used, on average, 23.7 ± 4.8 kcal/day; the utilization efficiency averaged $36.5 \pm 10.0\%$ (Table 1). The body weights of the birds remained stable during the 4 days of the experiment, as indicated by a standard deviation of less than 1 g per bird (Table 1). In 1981, the six Cedar Waxwings were kept in captivity for up to 27 days. During this period their body weights fluctuated within narrow limits, up to 4.8% of the mean body weight ($\bar{x} = 31.2 \pm 1.5$ g, $N = 162$). The Cedar Waxwings did not show a change in body weight over time: no significant linear relationships ($0.01 < F < 0.68$, $df = 1$ and 24 , $0.4 < P < 0.9$) could be established between the differences in weight of individual birds on subsequent days in captivity.

Discussion.—Cedar Waxwings have been reported to digest fleshy fruits rapidly. Nice (1941) fed cherries and blueberries (*Vaccinium* sp.) to a juvenile Cedar Waxwing and reported a passage rate varying from 16–40 min. A 20-min passage rate was measured by Maynard (Bull. Northeastern Bird Banding Assoc. 4:73–76, 1928) for cherry stones, and Stevenson (Wilson Bull. 65:155–167, 1933) estimated a passage rate of 100 min for raspberries (*Rubus* sp.) fed to two juvenile Cedar Waxwings. However, Maynard (1928) and Nice (1941) did not starve their birds prior to the start of the experiments, and Stevenson (1933) did so only for 2 h. Passage rates have been investigated to a greater extent with the Bohemian Waxwing. Cvitanic (Larus 12:51–53, 1958) fed *Ligustrum* sp. fruits to a Bohemian Waxwing, which was starved for 24 h, and observed seeds in feces after 10 min. In another experiment with *Pyracantha coccinea* fruits, a mean passage rate of 11 min was recorded, but on this occasion the bird was not starved (Cvitanic 1958). Feeding trials with *Symphoricarpos albus*, *Viscum album*, *Viburnum opulus*, and *Sorbus aucuparia* conducted by Borowski (Przełaz Zoolo-giczny 10:62–64, 1966) with a Bohemian Waxwing, showed that 50% of the ingested seeds were voided after 13.5–27.5 min. Digestion of marked mistletoe berries (*Phorodendron californicum*) by the Phainopepla (*Phainopepla nitens*), a fruit specialist similar in weight to the Cedar Waxwing, took 29 min (Walsberg 1975). The above mentioned estimates of passage rates for the Cedar Waxwing, Bohemian Waxwing, and Phainopepla are of the same order of magnitude as those found in this study, in spite of considerable differences in experimental conditions (e.g., foodstuff and starvation time). Thus, the passage rate observed in these frugivores is relatively short.

Differences in passage rates of fruits found for our Cedar Waxwings (i.e., 23 min for dogwood fruits and 12 min for red cedar cones) may be partly attributed to differences in digestibility of the fleshy fruits with which the experiments were conducted. Dogwood fruits are heavier than cedar cones (0.14 g vs 0.01 g; Halls, Southern Fruit-producing Woody Plants Used by Wildlife, U.S. Dept. Agric. For. Serv. Gen. Tech. Rept. SO-16, South. For. Expt. Stn., New Orleans, Louisiana, 1977) and the fruit pulp also contains a higher percent crude fat (16.7 vs 6.8%; Halls 1977).

The metabolized energy (ME = 23.7 ± 6.1 kcal per day) found for Cedar Waxwings in captivity is within the range of the metabolized energy estimated using Pimm's (Condor 78: 121–124, 1976) functional relationship between existence metabolism and body weight, ambient temperature and photoperiod (mean body weight of five Cedar Waxwings during the experiment = 30.1 g (N = 20), mean temperature = 8°C, photoperiod = 11 h; ME = 20.5 kcal/day).

The feces of Cedar Waxwings feeding on fleshy fruits were pulpy and contained many undigested fruit skins, perhaps a reflection of their low utilization efficiency (36.5%). The low utilization efficiency is similar to that reported for two other fruit feeders (Phainopepla, 49%, Walsberg 1975; Townsend's Solitaire [*Myadestes townsendi*], 37.6%, Salomonson and Balda, Condor 79:148–161, 1977). These data support the generalization that frugivores have lower utilization efficiencies than granivores (70%–90%, Kendeigh et al., pp. 127–204 in Granivorous Birds in Ecosystems, J. Pinowski and S. C. Kendeigh, eds., Int. Biol. Prog. 12, Cambridge Univ. Press, Cambridge, Massachusetts, 1977).

During 27 days of captivity the Cedar Waxwings were able to subsist on a fruit diet, suggesting that they are fruit specialists *sensu* Berthold (1976b). Similar experiments may be conducted with other frugivores to develop a relative scale of frugivory among birds now rather arbitrarily classified as "frugivores" or "major frugivores" (Stiles 1980).

Cedar Waxwings are reported to feed extensively on red cedar cones in winter in south-eastern North America (Tyler 1950; Martin et al. 1951). Red cedar cones contain 56.4 \pm 13.1 cal/cone (N = 36), excluding the seeds (Holtuijzen, Ph.D. diss., VPI & SU, Blacksburg, Virginia, 1983). These data suggest that Cedar Waxwings would have to consume about

twice as many cones as did our captives for maintenance during inactivity (1159 cones/day vs 583 cones/11-h day in this study). Clearly, the numbers of red cedar cones required by free-living birds would be much greater, but it is not known whether they could actually digest red cedar cones rapidly enough to cover their energy requirements.

The Cedar Waxwing subsists on a large variety of woody plant fruits for most of its nutrition during the fall and winter months. Since the Cedar Waxwing has a low utilization efficiency, it probably consumes large quantities of various fruits. This also implies that large quantities of seeds may pass through the digestive tract, perhaps in a viable condition as was found for red cedar seeds (Holthuijzen and Sharik, *Virginia J. Sci.* 34:123, 1983). Thus, the Cedar Waxwing may be a major disperser of fruit-bearing plants in eastern North America.

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Short-term changes in bird communities after clearcutting in western North Carolina.—Logging practices have been under increasing scrutiny because of their effects on biotic communities. Songbird populations as integral components of such communities are subject to disturbance by logging. Two goals involving management of songbird populations have surfaced in the literature: to maximize bird species diversity and to protect habitat of endangered and threatened species (Lennartz and Bjugstad, pp. 328–333 in USDA For. Serv. Gen. Tech. Rept. WO–1, 1975). The primary objective of this study was to examine effects of clearcutting on the breeding-bird community during the early years of vegetation regrowth, when changes in the avifauna are likely to be greatest.

The relationship of avian communities to timber harvesting in eastern forests has been the subject of several studies. Clearcutting of hardwood forests usually has resulted in an increase in bird species diversity (Ambrose, Ph.D. diss., Univ. Tennessee, Knoxville, Tennessee, 1975; Conner and Adkisson, *J. For.* 73:781–785, 1975; Nyland et al., *Tappi* 60:58–61, 1977), whereas, heavy cutting of a pine-oak woodland led to decreased diversity (Conner et al., *Wilson Bull.* 91:301–316, 1979). Changes in guild structure or other community attributes were not analyzed. Thus, a second objective of the present research was to examine changes in the bird community other than species diversity.

Study areas and methods.—The study was conducted in the Highlands Ranger District, Nantahala National Forest, North Carolina. The Highlands Plateau lies adjacent to the Blue Ridge Escarpment and contains an unusually diverse biota in comparison with the remainder of the southern Appalachians (Oosting and Billings, *Am. Midl. Nat.* 22:333–350, 1939). The Highlands Biological Station has provided a base from which the distribution and ecology of the avifauna have been studied for many years (see Johnston, J. Elisha Mitchell Sci. Soc. 80:29–38, 1964; and Holt, *Wilson Bull.* 86:397–406, 1974, for summaries). With an average elevation of 1200 m, the plateau's forests attract typically northern species such as Golden-crowned Kinglets (*Regulus satrapa*), Rose-breasted Grosbeaks, and Dark-eyed