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HOW DO FRUGIVORES PROCESS FRUIT? GASTROINTESTINAL TRANSIT AND GLUCOSE ABSORPTION IN CEDAR WAXWINGS (*BOMBYCILLA CEDRORUM*)

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ABSTRACT.—We used image-intensification radiology to examine gut function in six Cedar Waxwings (*Bombycilla cedrorum*) fed artificial fruits that contained barium-labeled pulp and seeds. Despite the absence of an anatomical crop, waxwings were able to store fruits orad to the gizzard in a distensible portion of the esophagus. By doing so, they were able to increase meal sizes above what their gizzards could contain at any one time. Thus, they could partially overcome the digestive bottleneck that results from a bulky diet. Gizzard contraction increased in frequency with gizzard fullness. Seeds and pulp were separated in the gizzard; most pulp passed into the intestine before the seeds. Once in the intestine, however, seeds moved especially quickly ($\bar{x} = 0.14$ cm/s) into the rectum. Both pulp and seeds resided for a relatively long time in the rectum, where antiperistalsis was clearly visible. Unlike other birds that have been studied, the functions of antiperistalsis in waxwings probably do not include cecal filling, since ceca of waxwings are minute. We hypothesize that the function of antiperistalsis in waxwings (and other fruit-eating birds) is to mix digesta in the intraluminal zone adjacent to the rectal mucosa, thereby increasing nutrient absorption. This hypothesis is consistent with the observation that fruit-eating birds typically have low digestive efficiencies. In particular, absorption of nutrients in the rectum may be important, given that digesta therein may still contain significant amounts of nutrients. Indeed, active uptake of D-glucose, a primary constituent of fruit pulp, was as high in the rectum as elsewhere in the gut. We also found that waxwings typically defecated only the distal 50% of rectal contents. Presumably, digesta in the proximal portion was higher in nutrients and so was retained longer for more thorough absorption. This pattern contrasts to most other vertebrates in which the rectum empties completely and sugar uptake in the rectum is negligible. We suggest that functional adaptations to frugivory (i.e. how fruit is processed) are likely more important than structural adaptations. *Received 9 May 1991, accepted 15 December 1991.*

FRUITS ARE a unique food source that combine a large proportion of well-protected seeds with a nutritious, easily digestible covering. Presumably, fruit-eating birds possess gut adaptations that allow them to efficiently process this mix of high and low digestibility components. Many studies have attempted to find such adaptations, but there is little agreement among them. For example, some researchers report that fruit-eating birds have especially short guts (e.g. Walsberg 1975, Pullainen et al. 1981), others that they have long guts (e.g. Al-Dabbagh et al. 1987, Jordano 1987), and yet others that they have guts of normal length (Herrera 1984). Apparently, there are few (if any) general morphological adaptations of avian guts to frugivory. The major adaptations may be functional, relating to how fruit is processed rather than to gut structure (Herrera 1984, Karasov and Levey 1990).

Little is known about functioning of the gut in fruit-eating birds. Most studies have simply treated birds as "black boxes"—patterns of ingestion and defecation are compared, then transit and digestive processes are inferred (Johnson et al. 1985, Bairlein 1987, Worthington 1989, Levey and Grajal 1991). For example, retention time is one of the most important parameters of food processing (Van Soest 1982, Penry and Jumars 1987). The statistic that is usually reported is the mean time from ingestion to defecation. Yet, what is needed for accurate interpretation is the time a meal spends in each segment of the gut (Penry and Jumars 1987, Martínez del Rio and Karasov 1990). This type of information can yield new insights. In the case of hummingbirds, for example, if crop-emptying time determines foraging bout frequency, these birds would likely be energy maximizers rather than foraging-time minimizers (Diamond et al. 1986, Karasov et al. 1986).

Image-intensification radiology (IIR) allows continuous viewing of barium-labeled meals as they move through the digestive tract. Although this technique has been used to study gastric motility in several orders of birds (Dziuk and Duke 1972, Rhoades and Duke 1977, Duke et al. 1989), it has only been applied once to a passerine (Duke 1989a) and has not been used on a frugivore. Here we use IIR to examine gut processing of fruits by Cedar Waxwings (*Bombycilla cedrorum*), one of the most heavily frugivorous species in North America (Martin et al. 1951). Our goal was to relate gut function to patterns of fruit digestion. More specifically, we wanted to determine whether pulp and seeds are treated differently in the gut, quantify retention times in the gizzard and intestine, measure gizzard contraction frequency, and determine the presence, timing, and location of intestinal antiperistalsis. We also used an in vitro technique to measure intestinal and rectal uptakes of D-glucose, a primary constituent of fruit pulp.

METHODS

Five Cedar Waxwings were captured with mist nets in Alachua County, Florida and held for approximately 10 months on a synthetic fruit-based diet (Denslow et al. 1987) before this study began. All regained their initial body mass and maintained good health. Birds were housed individually in cages (approximately 50 × 50 × 50 cm) at a constant temperature (21°C) and photoperiod (12 h dark, 12 h light).

Image-intensification radiology.—We observed food passage via IIR on a Technomed 1250 fluoroscopy machine. During trials, each bird was held in a small cardboard box (30 × 20 × 15 cm) with a translucent plastic top to allow illumination. The bird usually sat on the box's single perch, thus giving a consistent lateral view when the box was placed with its perch parallel to the *x*-ray beam.

To track food through the gastrointestinal tract, we used artificial fruits (6-mm diameter) composed of 2% agar, 15% glucose, 10% barium sulfate, "seeds" (4-mm plastic beads), red food coloring, and water. The "pulp" and "seeds" of these artificial fruits are passed through the gastrointestinal tract of captive waxwings at rates similar to those found in wild birds eating natural fruits (Levey and Grajal 1991). Barium sulfate, which is radio-opaque, was also packed into the bore of each bead and held in place with a drop of superglue. This made the seeds easily visible in the gut.

Each day, within 30 min after "dawn" in the holding room, a waxwing was fed three to four fruits without barium sulfate or seeds, enough to fill its foregut and initiate digestive processes. It was then placed in the box and taken to the radiology area, where approximately 15 min later it was force-fed a barium-labeled meal of one fruit without a seed and two fruits with seeds. The seedless fruit had much more barium-containing pulp than the seeded fruits and served to coat the gut with barium for easier viewing. We followed the meal through the gut until most barium had been excreted or until the equipment was needed for clinical cases. At least three trials were completed for each individual. We timed gizzard contractions and rectal antiperistalsis, estimated percent of pulp in the gizzard, intestine, and rectum at 1-min intervals, recorded passage times of seeds through the gizzard and intestine, and estimated percent of rectum emptied by each defecation.

Mean retention time of pulp in the gizzard was calculated by multiplying the proportion of the meal leaving the gizzard during each 1-min interval by elapsed time and then summing these products over all intervals (see Castle 1956, Warner 1981).

Because our birds were not feeding continually, their barium-labeled meal probably resided in the small intestine and rectum longer than if another bolus of food had been immediately behind it. Consequently, we present residence times of pulp in the rectum only up to 25 min postingestion, which is approximately the retention time of the artificial fruit pulp in freely-feeding waxwings (Levey and Grajal 1991). Even though pulp and seeds often resided in the intestine for longer than 25 min, we feel that reporting such times would be misleading. Instead, we focus on processing time in the gizzard. This measurement was probably less affected by the short-term fast, because the rest of the gut was full at the time, and gizzard emptying appeared to be a necessary precursor for ingesting another meal (D. Levey and G. Duke pers. observ.; also see Worthington 1989).

Except where noted we report statistics (average and standard deviations) calculated from mean values of each individual (i.e. $n = 5$ in most cases).

Glucose uptake.—We measured uptake of D-glucose across the brush-border membrane (not transmural flux) of four waxwings. Methodology is detailed in Karasov and Diamond (1983). In brief, the digestive tract from gizzard to vent was removed from an anesthetized bird and everted in ice-cold Ringer solution over a 4-mm diameter rod. The 1-cm sleeves were then mounted individually on 4- or 5-mm diameter steel rods and, after a 5-min preincubation in 37°C Ringer, were vertically suspended several millimeters above a stir bar (1,200 rpm) for 30 s in a 50 mM D-glucose solution containing tracer concentrations of ^{3}H D-glucose and ^{14}C L-glucose. (Justification of concentration and incubation time is provided in Karasov and Levey 1990.) Tissues were then blotted on tissue paper, removed from the rod, weighed, solubilized, and counted for disintegrations per minute. In calculations of uptake rate, we corrected for D-glucose absorbed passively and in adherent mucosal fluid by using uptake of L-glucose, a stereoisomer of D-glu-

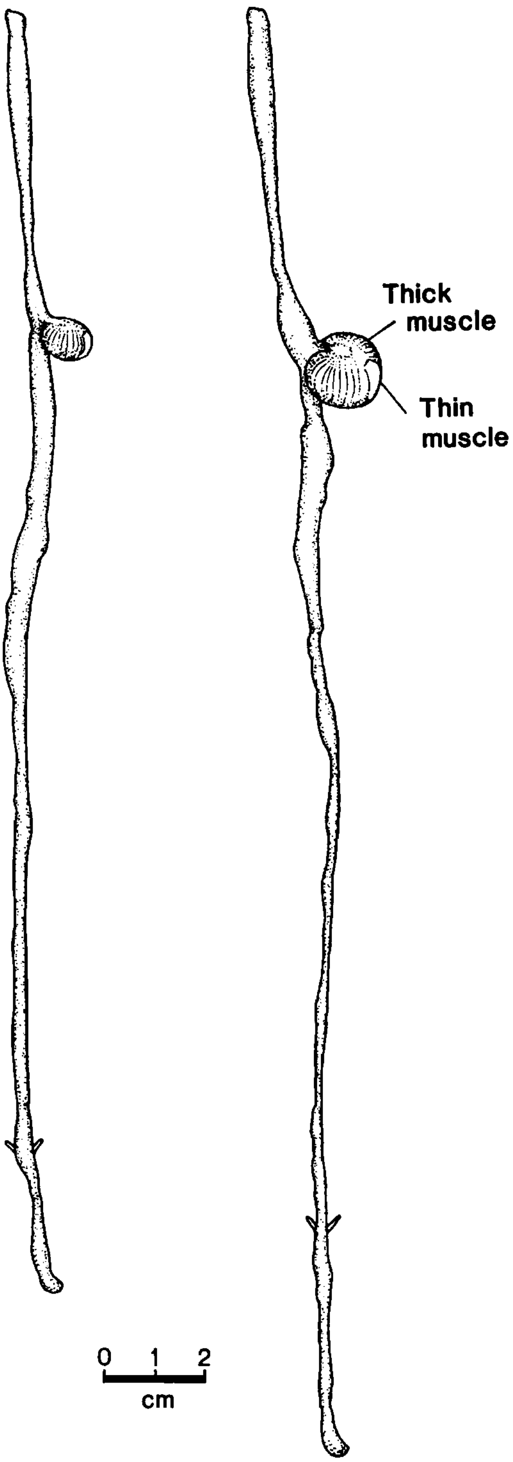

Fig. 1. Gastrointestinal tracts of long-term-captive waxwing (left) and wild waxwing (right). Note larger gizzard and longer intestines in wild individual, and the large duodenum in both. Drawn from specimens.

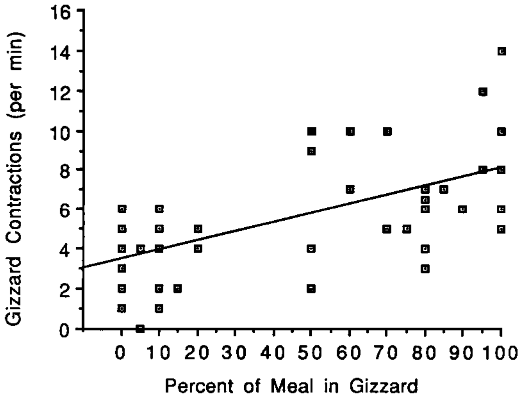

Fig. 2. Gizzard contraction frequency as function of percent of a three-fruit meal in gizzard ($r^2 = 0.43$, $P < 0.05$; data from all birds combined).

cose that is not actively transported (see Karasov and Diamond 1983). Uptake values were normalized to 1 cm of intestinal length. We were able to mount and measure uptakes in one to two sleeves from midintestine, distal intestine, and rectum (postceca).

RESULTS

General morphology.—The entire gastrointestinal tract weighed approximately 11% of total body mass. The esophagus was distensible, but lacked a crop. A small but obvious proventriculus led into the gizzard (muscular stomach), which was comprised of thin and thick muscle pairs, as described in other birds (Fig. 1; Duke 1989b). The duodenum was approximately twice the diameter of the proximal ileum. Rudimentary ceca were found upon close examination.

Image-intensification radiology.—Despite the absence of an anatomical crop, fruits were often stored in the distensible region of the esophagus before entering the gizzard. In 54% of the trials, all seeds moved directly into the gizzard within 3 min of feeding. In the remaining trials, fruits were retained in the esophagus for 27 ± 9 min. Typically, two or three fruits moved into the gizzard at approximately the same time, after it had mostly emptied the previous meal and at the end of the thick-muscle contraction. Fruits always passed rapidly through the proventriculus. Almost immediately upon entering the gizzard, pulp and seeds were separated and thoroughly mixed by the alternating contractions of the thin and thick muscles. Contraction frequency was initially high, averaging 7.9 ± 2.3 contractions/min, and contraction rates were

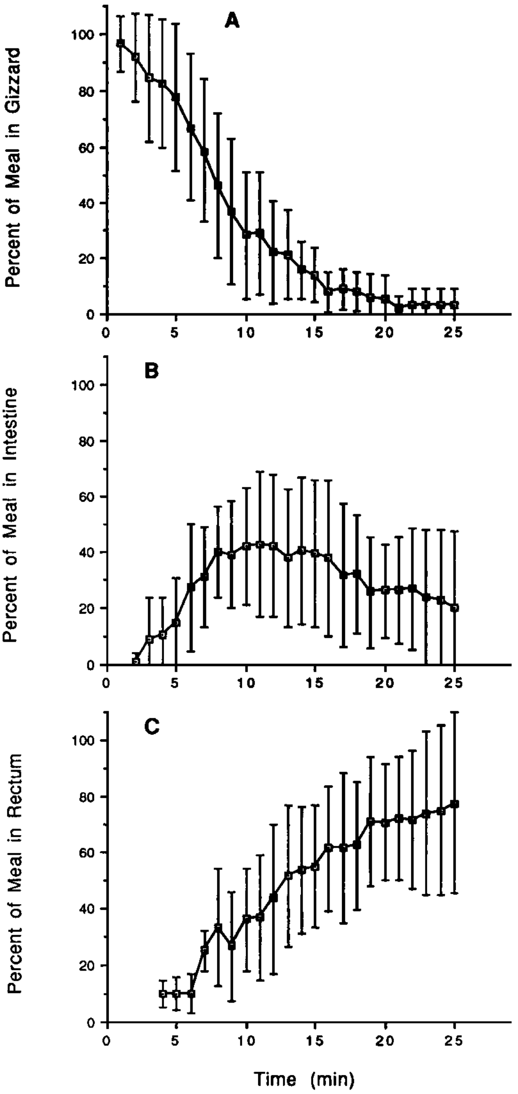

Fig. 3. Percent of single meal remaining in (A) gizzard, (B) intestine, and (C) rectum as function of time since ingestion. Bars represent SD. Note relatively small percent in intestine at any one time, and rapid accumulation in rectum.

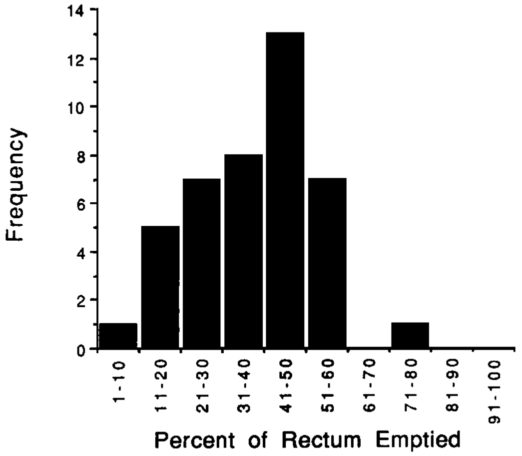

Fig. 4. Frequency distribution of defecations that emptied specified percent of material from rectum. Data from all birds combined.

positively correlated with gizzard fullness (Fig. 2).

Gizzard contents emptied at the end of the thin-muscle contraction. Mean retention time of pulp in the gizzard was 7.7 ± 2.2 min (Fig. 3). In contrast, seeds remained in the gizzard for $\bar{x} = 27 \pm 12$ min. Once seeds exited the gizzard, however, they moved extremely rapidly through the intestine at approximately 0.14 cm/s (or 155 ± 40 s to transverse the entire intestine; $n = 25$). Because the seeds nearly filled the lumen of the intestine, any pulp in the intestine was pushed ahead of them.

Despite the large size of the duodenum, we rarely saw pulp there because it moved so rapidly. Also, it was often hard to distinguish the duodenum from the adjacent gizzard. Duodenal refluxes (Duke 1989b) were rare; we saw two in 30 h of observation. Peristalsis was evident in the ileum and, although pulp generally moved through it at a steady pace, we frequently observed extremely rapid orad or aborad flow over 1- to 2-cm segments of intestine. Pulp rapidly accumulated in the rectum, which often contained 30 to 40% of the meal within 10 min after feeding (Fig. 3). Once the rectum was more than approximately 30% full, antiperistaltic waves became obvious, starting at the cloaca and usually traveling the full length of rectum to the ileocecalrectal junction. Contraction frequency was 18 ± 5 per min and was not significantly correlated with rectal fullness ($r^2 = 0.12$, $P > 0.5$). Defecations were preceded by a gradual packing of pulp in the cloaca and distal rectum. Nevertheless, defecation volume was often small compared to the amount of pulp in the rectum. Usually only 50% of the rectum was emptied, and often much less (Fig. 4). We never observed the rectum empty entirely in one defecation.

Following defecation the bird would usually become more active than it had been for the previous 5 to 10 min. Often a fruit left the "crop" or a seed left the gizzard within 1 min after a defecation, presumably freeing the foregut for

TABLE 1. Gut dimensions and masses (±SD) of waxwings held in captivity ($n = 2$) for 10 months or collected from field (window-killed birds; $n = 9$).

	Intestine		Gizzard	
	Length (cm)	Mass (g)	Diameter (cm)	Mass (g)
Captive birds	14.5 ± 0.5	0.32 ± 0.09	0.85 ± 0.05	0.14 ± 0.02
Wild birds	18.6 ± 2.1	0.27 ± 0.09	1.32 ± 0.10	0.43 ± 0.14

another meal. Our sample sizes, however, were too small to determine whether these actions were significantly associated with defecation.

Because the waxwings used in this study processed our artificial fruits more slowly than similarly treated waxwings that had not been in captivity as long (see Levey and Grajal 1991), we became concerned that the pattern of gut function described above might not be typical of wild individuals. We captured one additional waxwing, which adjusted to captivity within five days. We then ran an identical series of trials on it. Mean retention times of pulp and seeds in the gizzard indeed were shorter for this individual than for the others (4.4 vs. 7.7 min for pulp and 6.8 vs. 27 for seeds), although not statistically different (values for new bird fell within 95% but outside 85% confidence intervals of other five birds). We stress that the overall pattern of processing was essentially identical between the two groups. The only noticeable difference was that in the recently captured individual, seeds left the gizzard ahead of much of the pulp.

To examine possible changes in gut morphology associated with the 10-month period of captivity, we sacrificed two of our long-term captives and measured gizzard diameter, intestine length, and dry mass of both organs. We then compared these measurements to those collected from eight window-killed waxwings (Table 1). Intestine length of the captive waxwings was approximately 22% shorter than in the window-killed individuals (Mann-Whitney $U = 17.5$, $P = 0.042$), although intestine dry mass of the two groups was not significantly different. Gizzard diameter and dry mass were significantly smaller in the captive individuals (Mann-Whitney $U = 18$, $P < 0.05$ and $U = 16$, $P < 0.05$, respectively).

Glucose uptake.—Active uptake rate of D-glucose in the rectum was relatively high compared to rates in the midintestine and distal intestine; uptake rates did not vary significantly from midgut to rectum ($F_{2,11} = 0.5$; $P = 0.39$; repeated-measures ANOVA). We doubt that this result is an artifact of low sample size ($n = 4$ birds) because no trends in uptake rates within or among birds were apparent (Fig. 5).

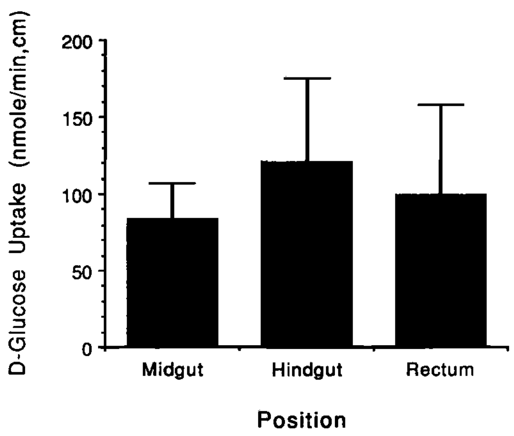

Fig. 5. Carrier-mediated D-glucose uptake at 50 mM in everted sleeves of waxwing gut ($n = 4$ birds).

DISCUSSION

Storing fruits and process-rate limitation.—Many fruit-eating vertebrates appear process-rate limited (i.e. their rate of ingestion is limited by the rate at which their guts can process the previous meal; Sorensen 1984, Tedman and Hall 1985, Worthington 1989, Levey and Grajal 1991). One way to alleviate this constraint is to increase gut size (Sibly 1981). However, volant frugivores generally do not have large gut volumes, presumably because of the associated increase in the cost of flight that such large guts would entail. A surprising observation in the present study was that, although waxwings have short, simple guts with no anatomically distinguishable crop, they nonetheless have functional crops. By storing ingested fruits, their distensible esophagi allow them to consume more fruits per feeding bout than their gizzards and intestines can process at any one time. In short, waxwings appear to offset the problem of process-rate limitation by storing fruits orad to the gizzard. Phainopeplas (*Phainopepla nitens*), another highly frugivorous species, apparently store fruit in a similar way (Walsberg 1975). More generally, these results demonstrate the danger of the simple and often dogmatic notion that function depends on structure; waxwings do not require a special storage organ to store fruits.

Note that the mean retention time of pulp from small meals (i.e. meals in which fruits pass directly to the gizzard) is approximately 25 min (Levey and Grajal 1991). This agrees quite closely with the average time fruits from larger meals are stored in the "crop" ($\bar{x}$ = 27 min). Thus, it appears the distensible esophagus allows waxwings to ingest approximately two meals of fruit in a single foraging trip.

Gut morphology.—Waxwings have a short gut with a relatively wide lumen, a type of gut found in other frugivores (Berndt and Meise 1959, *in* Cvitanic 1967). However, the structure of our waxwings' gastrointestinal tract differed from that reported for waxwings by Walsberg (1975). In particular, the duodenum of our birds (both captive and window-killed individuals) was distinctly larger than the rest of the intestine, whereas Walsberg's specimens showed no such contrast. This difference may be due to regional and seasonal variation in diet. Intraspecific changes in gut structure are often correlated with dietary shifts, which are usually seasonal (Ziswiler and Farner 1972, Miller 1975, Savory and Gentle 1976, Al-Dabbagh et al. 1987). Indeed, the gut morphology of wild individuals and our long-term captives was conspicuously different (Table 1). The smaller guts of the captive birds may have been due to their unusual diet, which was relatively low in bulk and well-balanced nutritionally. Birds on poorer-quality diets are known to increase gut volume (Savory and Gentle 1976, Al-Joborae 1980).

The difference in gut structure between the long-term captives and the newly captured individual may explain their differences in fruit processing. The latter bird passed both the seeds and pulp much more rapidly than did the long-term captives. We speculate that the larger gizzard of the newly captured individual could process the barium-labeled meal faster because the meal occupied a relatively smaller proportion of its gizzard capacity. We also observed that gizzard contraction frequency was higher in this bird. In both chickens (*Gallus gallus*; Roche and Decerprit 1977) and turkeys (*Meleagris gallopavo*; Duke et al. 1975, Duke 1986) the motility of the gizzard appears to be important in regulating motility of the small intestine, crop and esophagus. If such regulation occurs in waxwings, then their higher gastric contraction frequency would also result in higher intestinal contraction frequencies and a more rapid passage rate of contents.

The longer retention times of our five long-term captives compared to the newly captured individual clearly illustrate that rate of gut passage need not be correlated with gut length. In particular, the common assumption that short guts promote rapid passage (e.g. Ziswiler and Farner 1972) is not supported. An individual waxwing with a long gut processed fruits much more quickly than did five individuals with shorter guts.

The lack of food processing in the proventriculus and passage of food into the gizzard at the end of the thick-muscle contraction apparently are typical of other bird species (Dziuk and Duke 1972, Rhoades and Duke 1977). Gizzard-contraction frequencies, however, were much higher in waxwings than in these other species (Duke et al. 1975, Kostuch and Duke 1975, Roche and Decerprit 1977).

Rectal function in waxwings.—Rectal antiperistaltic contraction frequency is approximately the same in waxwings and domestic turkeys, 14 to 18/min (Lai and Duke 1978). Previously, the function of rectal antiperistalsis was assumed to be for urinary reflux and cecal filling. In waxwings, the latter function clearly does not occur, because the cecae are extremely small and presumably nonfunctional. We suggest an alternative explanation for antiperistalsis in waxwings—enhancement of nutrient absorption.

The intensive mixing of rectal contents through antiperistalsis suggests that the rectum is active in nutrient absorption. Karasov and Levey (1990) reported that frugivorous birds in general and waxwings in particular appear atypical in their high rates of glucose absorption in the distal third of the small intestine. Here, we extended this result by documenting high rates of glucose absorption in the rectum of waxwings. In another frugivorous species, the American Robin (*Turdus migratorius*), glucose uptake also occurs in the rectum (D. Levey and W. Karasov unpubl. data). In addition, enzymatic activity suggests nutrient uptake in the rectum of other frugivores (Ogunbiyi and Okon 1976). With the exception of hindgut fermenters, relatively high rates of nutrient absorption and enzymatic activity in the rectum of vertebrates is unusual. Typically, water and electrolytes are the principal substances absorbed rectally (Ruckebusch et al. 1991). In frugivores, rectal absorption of sugar can be explained by the low digestive efficiency of pulp, which has such a short residence time in the intestine that it is poorly assimilated (Levey and Karasov 1989, Karasov and Levey 1990, Karasov 1990). Thus, pulp in the rectum may still contain relatively high levels of sugars, which are thought to induce nutrient transport activity (Diamond and Karasov 1987, Karasov and Diamond 1987; but see Levey and Karasov 1992).

Nutrient absorption in the rectum could also help explain another distinctive feature of gut processing in Cedar Waxwings. Unlike turkeys and chickens (Duke 1986), which void virtually the entire contents of their rectum with each defecation, Cedar Waxwings typically void only the distal 50%. In most other species, relatively little absorption takes place in the colon (except for water and polyvalent ions), presumably because the contents have little nutritional value to the bird. In frugivores, however, the pulp in the colon still contains a relatively high proportion of nutrients. We suggest that only the lower portion of the rectum is voided so that nutrient absorption can continue on the pulp in the upper portion, which is probably more nutrient dense. A longer retention time of pulp in the rectum also would aid in water reabsorption, an important benefit to waxwings, who are sometimes in negative water balance (Studier et al. 1988).

Separation of pulp and seeds.—Levey and Grajal (1991) reported that waxwings internally separate pulp and seeds, and defecate the seeds before pulp. We found that, although waxwings separated the two components of fruit, they did not defecate the seeds first. Most pulp seemed to arrive in the rectum before seeds and then, typically, both were defecated together. We suggest the especially short retention times of seeds reported by Levey and Grajal were likely a statistical artifact caused by comparing a pulp marker that generates a continuous distribution (phenol red) with a discrete marker (the seeds). Even if pulp and seeds pass at the same rate, seeds may appear to pass more quickly than pulp if the pulp that follows the last seed is mixed with unlabeled pulp from the next meal, which is likely given the high rates of antiperistalsis and incomplete emptying of the rectum. This mixing would generate a long tail on the plot of marker excretion versus time and, thereby, inflate mean retention time of pulp relative to seeds, since seeds cannot be mixed in a similar fashion. The different conclusions of Levey and Grajal (1991) and this study provide a good example of the danger of examining digestive processes only on the basis of ingestion and excretion.

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