Test of a Digestion Optimization Model: Effects of Costs of Feeding on Digestive Parameters

Scott R. McWilliams*
William H. Karasov
Department of Wildlife Ecology, University of Wisconsin—Madison, Madison, Wisconsin 53706

Accepted by G.K.S. 9/12/97

ABSTRACT

We tested predictions of a chemical reactor model of digestion by manipulating the short-term costs of feeding and then measuring the effect on digestive parameters. We compared residence time of digesta and extraction efficiency of glucose in cold-acclimated waxwings (*Bombycilla cedrorum*) feeding ad lib. and in birds whose costs of feeding were increased through the addition of intervals of time when they received no food. Such a feeding schedule simulated the ecological situation in which a frugivorous bird like a waxwing encounters food in patches and experiences nonfeeding periods as it searches for new preferred food patches. None of the results were consistent with the predictions of the optimal digestion model: extraction efficiency was independent of costs of feeding, and residence times did not increase as costs of feeding increased. This empirical evidence on the passage of digesta in waxwings suggests that movement of digesta in the guts of birds is much more complex than movement of material in an ideal chemical reactor. Tests of the optimal digestion model have involved manipulating food quality or the costs of feeding, and the conclusions are similar: compensatory modulation of retention time or digesta mixing and not rate of hydrolysis and absorption seem most important in maintaining the remarkably constant digestive efficiency.

Introduction

Digestive parameters at many organizational levels are influenced by diet quality and quantity (reviewed by Karasov [1996]). For example, yellow-rumped warblers (*Dendroica coronata*) that are switched quickly from a low- to a high-protein diet increase enzyme (aminopeptidase) activity, amino acid uptake, and extraction efficiency of an amino acid (Afik and Karasov 1995; Afik et al. 1995). These changes are not, however, associated with any changes in gut morphology (Afik and Karasov 1995), although diet quality has affected gut morphology in other situations (see, e.g., Piersma et al. 1993).

Effects of diet quantity on avian digestive parameters have not been studied often, but the available evidence indicates that increased food intake primarily causes changes in gut morphology that allow digesta retention time and extraction efficiency to remain constant (Karasov 1996). However, such modulation at the level of gut morphology requires time (perhaps as long as 2–3 mo; Redig 1989). Birds may often experience short-term changes in food quantity that occur faster than the time scale required for changes in gut morphology. For example, frugivorous birds during migration may one day encounter preferred fruits that are ubiquitous, allowing relatively constant food intake, whereas the next day their preferred fruits may be patchily distributed and require much travel time between patches. In such situations, a bird's pattern of food intake may differ from day to day.

We know little about how short-term changes in food intake affect digestive performance in wild birds. Theoretical optimality models make explicit predictions about how an animal's digestive parameters should respond to short-term changes in food intake (Penry and Jumars 1986, 1987; Martínez del Rio and Karasov 1990; Martínez del Rio et al. 1994), although our study provides the first such empirical test of the models. The models predict that when costs of food acquisition are increased, for example, by adding intervals of time when the birds receive no food, the food should be held longer in the intestine, and thus nutrients in the food will be more thoroughly digested (Fig. 1). It is important to note that if retention time and extraction efficiency are modulated as predicted by the model, determining the profitability (e.g., energetic gain divided by the energetic costs) of a given food type is complicated, because digestive efficiency is not fixed but is instead conditional on the costs of acquiring the food.

We tested predictions of the model by manipulating the short-term costs of feeding and then measuring the effect on retention time and digestive efficiency. For the test, we used cedar waxwings (*Bombycilla cedrorum*) fed a semisynthetic diet rich in glucose. Cedar waxwings are ideal candidates for testing

*To whom all correspondence should be addressed. Present address: Department of Natural Resources Sciences, 237 Woodward Hall, 9 East Alumni Avenue, University of Rhode Island, Kingston, Rhode Island 02881; E-mail: srmcwill@uriacc.uri.edu.

Physiological Zoology 71(2):168–178. 1998. 0031-935X/98/7102-96116$03.00

the model's predictions because their food is principally fruits composed of readily absorbed simple sugars (Martínez del Rio et al. 1992; Witmer 1996), and many aspects of their digestive physiology have been studied (Levey and Karasov 1989; Martínez del Rio et al. 1989; Karasov and Levey 1990). We focused on glucose absorption because the kinetics of glucose absorption are well known (Fig. 1*A*) and the key assumptions of the model with regards to nutrient gain are satisified for such a nutrient (Martínez del Rio and Karasov 1990).

Material and Methods

Capture and Maintenance of Birds

Six of the 18 cedar waxwings used in this study were captured in Gainesville, Florida (29°41′ N, 82°16′ W) and sent to us on August 8, 1994. We captured the other 12 cedar waxwings on September 30–October 1, 1994, in Madison, Wisconsin (43°8′ N, 89°20′ W) using mistnets. Birds were immediately weighed and banded and then housed individually in stainless-steel cages (60 × 45 × 33 cm) under initially constant light cycle (12L : 12D, lights on at 0700 hours) and temperature (21°C). All birds were initially fed a banana-mash diet (Denslow et al. 1987) that had been used successfully for maintaining cedar waxwings and other frugivorous passerines in the laboratory (Levey and Karasov 1989; Martínez del Rio et al. 1989; Karasov and Levey 1990).

Temperature and Diet Acclimation before the Experiment

By manipulating ambient temperature, we tried to induce hyperphagia in our experimental birds and consequently maximize their rate of food intake. On October 10, we randomly assigned 10 birds to a treatment group and eight birds to a control group. All 18 birds continued on the same daily light schedule (12L : 12D). For control birds, the ambient temperature was kept constant at 21°C. For treatment birds, the ambient temperature was gradually decreased over 30 d using the following schedule: from 21°C to 1°C over 10 d (-2°C d^{-1}), held constant at 1°C for 10 d, then from 1°C to -20°C over 10 d (-2°C d^{-1}). The control birds were used to test whether the cold acclimation produced the expected increase in food intake of treatment birds. We also used the control birds to test for effects of cold acclimation on body mass changes during the experiment.

On November 18, we acclimated all birds to a new semisynthetic diet (Table 1) that simulated a fruit diet in nutrient content (65% carbohydrate : 13% protein : 6% fat, by dry mass). Cedar waxwings select fruits that contain relatively low lipid and high carbohydrate content (Witmer 1996), like the diet we formulated. The use of such a semisynthetic diet made the composition of the diet less ambiguous than diets compounded from raw foodstuffs (see also Murphy and King 1982).

Feeding Schedules and Experimental Design

Before the experiment, birds were always presented with new food and water each day at 0930–1030 hours. Each day, birds were provided with excess food ensuring ad lib. feeding conditions. For birds at -20°C, a small hotplate was placed in each cage to keep the food soft and palatable. Each day, food was placed in a glass petri dish set in a clay saucer that evenly distributed the heat from the hotplate. A wooden perch attached to each hotplate enabled birds to eat while avoiding direct contact with the hotplate or clay saucer. Once each day, we supplied birds in the cold with hot tap water in a plastic petri dish. This water was used by the birds primarily for bathing. Water content of the food (Table 1) ensured adequate consumption of water along with their regular diet.

For the experiment, each control bird continued to receive ad lib. food. Each treatment bird was tested on one of two feeding schedules on the test day, either "ad lib." (ad lib. food always available, i.e., 12 h d^{-1} with food) or "interval" (ad lib. food available for 2-h intervals separated by 1 h without food from 0700–1800 hours, i.e., 9 h d^{-1} with food). The 1-h intervals were chosen to ensure that the birds had digested and excreted most but not all of the food from the previous feeding period before being allowed to feed again (mean retention time of digesta for waxwings at +21°C on a similar diet was 32 ± 4 min; Karasov and Levey 1990). In terms of the optimal digestion models, the interval feeding schedule increased the cost of food acquisition, as compared with the ad lib. feeding schedule, because during the nonfeeding periods birds had to wait for food while maintenance and activity costs continued.

On the pretest day, food was removed at 1730 hours to ensure that birds would start the test day with a small energy deficit. On the test day, treatment birds on the interval feeding schedule had food offered or removed as prescribed every 2–3 h between 0700–1900 hours. For birds on the ad lib. feeding schedule (both control and treatment birds), food was weighed at the same time intervals as the interval feeding schedule treatment, but the food was then immediately returned to the bird's cage. This ensured that any disturbance caused by administration of the feeding schedule was the same across all treatments.

Food intake, retention time, and extraction efficiency were measured during a 4–5-h test period that began when the bird ingested about 0.5 g of diet containing radiolabeled nutrient and marker (see below). The radiolabeled food was offered to each bird at 1330 hours. This allowed birds on the interval feeding schedule to feed for 30 min before being offered the radiolabeled food. Food intake on a dry-matter basis was estimated by drying subsamples of food collected at the start and end of the test period.

Tests on all treatment birds when on the ad lib. or interval feeding schedules were conducted between December 9 and 20, 1994. Half of the treatment birds were randomly selected to be tested first on the ad lib. feeding schedule, and the other

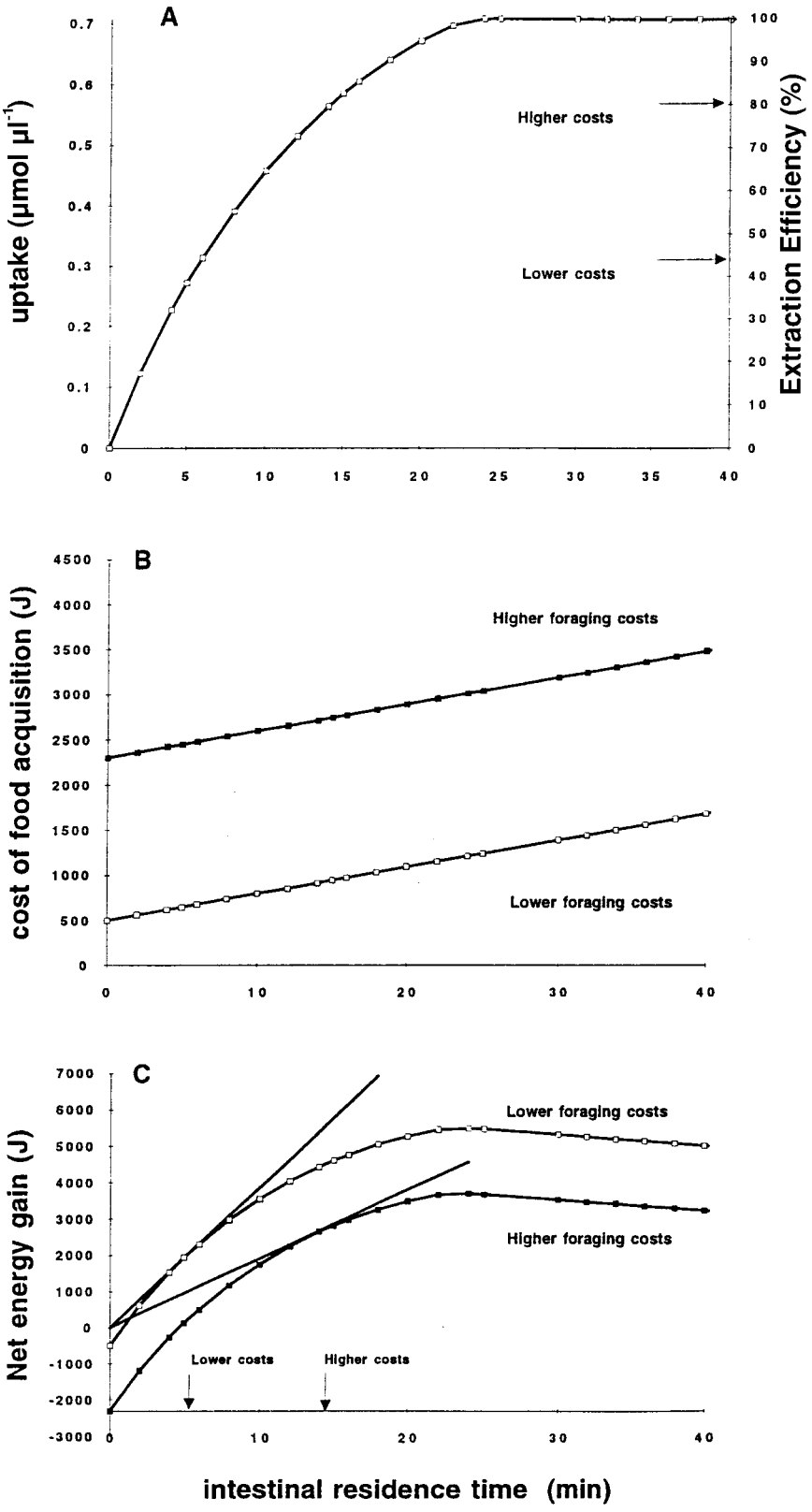

A
uptake (µmol µl-1)
Extraction Efficiency (%)
Higher costs
Lower costs
B
cost of food acquisition (J)
Higher foraging costs
Lower foraging costs
C
Net energy gain (J)
Lower foraging costs
Higher foraging costs
Lower costs
Higher costs
intestinal residence time (min)

Table 1: Composition of semisynthetic diet fed to cedar waxwings

Ingredients	% Wet Mass	% Dry Mass
Glucose	16.5	65.8
Casein[a]	2.5	10.0
Amino acid mix[b]	.7	2.8
Cellulose	.7	2.7
Vitamin and minerals[c]	.3	1.0
Salt mix[d]	1.7	6.7
Olive oil	1.5	6.0
Water	75.0	. . .
Agar	1.3	5.0

[a] Casein (high N): Teklad, U.S. Biochemical Corp., Cleveland, Ohio.
[b] Amino acid mix: Murphy and King (1982).
[c] AIN-76 Vitamin and Mineral Mix, ICN Biomedicals, Inc.
[d] Salt mix: N Salt mixture, ICN Biomedicals, Inc.

half of the treatment birds were tested first on the interval feeding schedule. All treatment birds were tested twice on each feeding schedule. One set of ad lib. and interval trials was used to test for effects of feeding schedule on extraction efficiency of glucose, and the other set of trials was used to test for effects of feeding schedule on retention time of digesta. Test days were always separated by at least 1 d and usually 2–3 d.

Figure 1. Hypothetical illustration of the effect of changing the cost of food acquisition on optimal intestinal residence time and extraction efficiency. *A,* Extraction efficiency (%) or uptake of glucose (μmol μL^{-1} of digesta volume) increases at a decreasing rate with the time that food spends in the small intestine. This decelerating gain curve is expected because passive absorption is a major pathway for glucose absorption in waxwings (Karasov and Levey 1990). Thus, intestinal absorption of glucose is fastest initially because luminal concentrations are high, but as glucose is absorbed and luminal concentrations decline, the rate of intestinal absorption also declines. In this example, the gain curve was derived exactly as described in Martínez del Rio and Karasov (1990) for a frugivorous bird like a waxwing. *B,* Cost of food acquisition is the sum of the energy expended during initial acquisition and ingestion of food (0.5 kJ) plus the energy expended during residence of food in the gut (assumed here to be the minimal rate of energy expenditure for a 30-g passerine bird, 29.6 J min^{-1}; Lasiewski and Dawson 1967). In this example, higher foraging costs were estimated by assuming that a bird goes without food for 60 min while searching for a good-quality food patch. *C,* Net energy obtained from the food is defined as the difference between the energy assimilated and the cost of food acquisition (Martínez del Rio and Karasov 1990). The bird initially suffers a net loss of energy as it searches, finds, ingests, and initiates digestion of the food. The predicted optimal residence time is the point on the net-energy curve at which a tangent line passing through the origin contacts the curve. These optimal residence times are used in panel *A* to predict extraction efficiencies when foraging costs are lower or higher.

Retention Time and Extraction Efficiency

Special observation cages were used to reduce behavioral stress associated with our presence while the birds were observed and their excreta collected (see Afik and Karasov [1995] for full description). Most important, each cage had one-way glass for observations and a roll of plastic-coated paper (S/P Absorbent Paper, Baxter Catalogue L5616-1) on a roller so that sheets of paper could be pulled across the cage's floor to collect excreta with minimal disturbance to the bird. All birds were housed in these cages for at least 1 d before the test day.

Retention time of digesta was measured using the inert marker [^{14}C] ferrocyanide (FeCN). We compared estimates of extraction efficiency using two different radiolabeled markers and nutrients because we were concerned that estimates of extraction efficiency based on tritiated nutrient might underestimate actual extraction efficiency. Such an underestimate could occur if tritiated glucose was metabolized and then partially excreted in urine as ^3H_2O, thereby confounding the calculation of extraction efficiency from collections of combined feces and urine, as is necessary in bird studies. Extraction efficiency of glucose was measured using the inert-marker method (Karasov et al. 1986). We used either [1-^{3}H] D-glucose (American Radiolabel Chemicals, Inc.) and the inert marker [^{14}C] FeCN (DuPont New England Nuclear Research Products) or [^{14}C(U)(uniformily labeled)] D-glucose (American Radiolabel Chemicals, Inc.) and the inert marker [1,2-^{3}H] polyethylene glycol (PEG; DuPont New England Nuclear Research Products) to estimate extraction efficiency. As expected, estimates of extraction efficiency using tritiated D-glucose and ^{14}C FeCN significantly underestimated extraction efficiency, compared with estimates determined with ^{14}C D-glucose and tritiated PEG (55.9% ± 2.9% vs. 92.4% ± 0.45%, respectively; $F_{1,7} = 175.1$, $P < 0.0001$, $n = 8$). Thus, we conducted separate trials for birds on both feeding schedules; retention time trials used ^{14}C FeCN as the inert marker, and extraction efficiency trials used ^{14}C D-glucose as the nutrient and ^{3}H PEG as the inert marker.

Radioisotopes were mixed into warm food mash (Table 1) at a concentration of approximately 18.5 kBq of ^{14}C D-glucose or ^{14}C FeCN and 74 kBq of ^{3}H PEG g^{-1} of food mash. After thorough mixing of the food mash and isotopes, the mash was cooled in a refrigerator. The resulting mixture had the consistency of thick gelatin. In each experiment, a bird had food available to it for at least 30 min before being offered an approximately 0.5-g cube of the radiolabeled mash. Birds usually ingested the whole cube, but when they did not, the radiolabeled food was removed 5 min after they initially consumed some of the cube. The average mass of radioactively labeled mash eaten per bird was 0.52 ± 0.06 g wet weight. After consumption of the labeled mash, all birds were resupplied with unlabeled mash, which they readily consumed; thus, a small volume of marker and nutrient was inserted into the flow of food in the bird's digestive system.

Table 2: Body mass and food intake (±SE) of cedar waxwings on two feeding schedules (ad lib., interval) and two temperature conditions

	Body Mass (g) on Pretest Day (1730 hours)	Body Mass (g) on Test Day (0700 hours)	Difference in Body Mass (g) between Pretest and Test Day	Food Intake (g dry weight) during 5-h Test Period
Treatment group (−20°C):				
Ad lib.	39.13 ± .67	34.82 ± .56	−4.32 ± .18	6.87 ± .37
Interval	38.86 ± .84	34.83 ± .54	−4.03 ± .34	6.80 ± .25
Control group (+21°C):				
Ad lib.	36.21 ± 1.31	32.97 ± 1.54	−3.24 ± .67	1.63 ± .25
Statistical comparisons:				
Ad lib. versus interval (both at −20°C)[a]	$F_{1,9} = .21$, $P = .661$	$F_{1,9} = .001$, $P = .973$	$F_{1,9} = 1.57$, $P = .242$	$F_{1,9} = .02$, $P = .885$
Ad lib. treatment versus control group	$t_{16} = 3.06$, $P = .004$	$t_{16} = 1.98$, $P = .030$	$t_{16} = 3.00$, $P = .005$	$t_{16} = 11.02$, $P < .001$

Note. See Material and Methods for definitions of each feeding schedule. Birds on the interval feeding schedule had food removed at 1730 hours on the pretest day. Sample sizes were 10 birds for ad lib. and interval feeding schedules and eight birds for the control group.

[a] Repeated-measures ANOVA ($n = 10$).

When only extraction efficiency was measured in a trial, excreta were collected 4–5 h after ingestion of the labeled diet. When only retention time was measured in a trial, excreta were collected singly for the first 30 min and thereafter every 15 min for 4–5 h. Percent recovery of inert marker 4–5 h after ingestion was 88% ± 11% ($n = 25$) for ^{3}H PEG and 95% ± 4% ($n = 27$) for ^{14}C FeCN.

Mouth-to-anus total mean retention time was calculated as the sum of the products of the proportion of inert marker excreted during each time interval multiplied by the elapsed time since ingestion of marker (Warner 1981). Residence time in the intestine was estimated in two ways: first, by recording the time since ingestion of inert marker that marker was first found in a defecation (see Penry and Jumars [1986] for rationale) and, second, by estimating mean residence time in the foregut and then subtracting this value from mouth-to-anus total mean retention time (see Discussion for important assumptions of this method of estimating residence time in the intestine). Mean residence time in the foregut was estimated from semilogarithmic plots of fecal marker concentration (ln dpm g^{-1} excreta) versus time since ingestion of the marker (Warner 1981; Karasov and Cork 1996). The terminal portions of the plots were visually inspected, and the start and end points for regression analysis were chosen using the same criteria as Karasov and Cork (1996). Mean residence time in the foregut was then calculated as the inverse of the absolute value of the slope of these regressions (Warner 1981).

Extraction efficiency was calculated as: $100 - 100[(M_f/N_f) \times (N_e/M_e)]$, where M_f is the radioactivity of the inert marker (PEG or FeCN) in food, N_f is radioactivity of the nutrient (D-glucose) in food, N_e is radioactivity of nutrient (D-glucose) in excreta, and M_e is radioactivity of inert marker (PEG or FeCN) in excreta.

Repeated-measures ANOVA was used to analyze differences in body mass, food intake, extraction efficiency, and retention time of treatment birds across the two feeding schedules. Differences in body mass and food intake between treatment and control birds feeding ad lib. were analyzed using *t*-tests. Results are given as mean ± SE unless otherwise noted.

Results

Effects of Temperature on Body Mass and Food Intake

Birds in the cold (−20°C) were on average 8.0% heavier than birds at room temperature (21°C; Table 2). Birds in the cold on the ad lib. feeding schedule lost more absolute mass overnight (Table 2) and a higher proportion of initial body mass than birds at room temperature (cold group: 11.0% of body mass; room temperature group: 9.0% of body mass; $t_{16} = 2.2$, $P = 0.04$). Removing food at 1730 hours on the pretest day had no significant effect on overnight mass loss of cold-acclimated waxwings (Table 2).

Birds in the cold consumed about 2.5 times more food each day than birds at room temperature (14.0 ± 0.5 g dry food d^{-1}, $n = 10$, compared with 5.2 ± 0.5 g dry food d^{-1}, $n = 8$, respectively; $t_{16} = 12.9$, $P < 0.0001$). During the 5-h test period, birds in the cold ate about four times more than birds at room temperature (Table 2), at least in part because birds in the cold usually increased their food intake in the afternoon as they increased their fat depots.

Effects of Feeding Schedule on Body Mass and Food Intake

Birds in the cold consumed similar amounts of food during the 5-h test period on both feeding schedules (Table 2), even

though birds on the interval feeding schedule had 1 h less time to feed. They compensated for the reduced feeding time by increasing their intake rates during the two 2-h periods when they had food available to them during the 5-h test period (interval schedule: 3.40 ± 0.12 g dry food eaten per 2-h feeding interval; ad lib. schedule: 2.72 ± 0.16 g dry food eaten per 2-h feeding interval; $F_{1,9} = 7.74$, $P = 0.021$). The 1-h interval without food apparently forced birds to wait for food, as indicated by their dramatic increase in search activity during the last 20 min of the 1-h nonfeeding period.

The 25% higher feeding rate for birds on the interval feeding schedule, however, was not great enough to compensate for the shorter feeding time available on a daily basis (interval schedule: 13.20 ± 0.40 g dry food eaten d^{-1}; ad lib. schedule: 15.29 ± 0.67 g dry food eaten d^{-1}; $F_{1,9} = 5.48$, $P = 0.044$). Despite these differences in daily food intake, birds on both feeding schedules weighed the same at 1800 hours on the test day (interval schedule: 39.3 ± 0.6 g; ad lib. schedule: 39.4 ± 0.5 g; $F_{1,9} = 0.12$, $P = 0.736$) and so had regained the mass lost the previous night (Table 2).

Retention Time and Extraction Efficiency

Excretion curves of ^{14}C FeCN for individual birds on the two feeding schedules (Fig. 2) were generally smoothly rising, reflecting the continuous feeding and defecation that we observed during the excreta collections. Bird 27 on the interval feeding schedule excreted the inert marker unusually rapidly, compared with when the same bird was on the ad lib. feeding schedule (Fig. 2), probably because it waited 25 min before eating the labeled diet and so its gut was less full when it consumed the labeled diet.

Mouth-to-anus total mean retention time and mean residence time in the foregut were similar for birds on the interval and ad lib. feeding schedules (Table 3). Inspection of the curves used in estimating mean residence time in the foregut (Fig. 3) revealed that when birds on the interval feeding schedule had no food for 1 h (ca. 90–150 min of elapsed time), there was often a dip in the usually linearly decreasing phase of this relationship (Fig. 3). As a consequence, we excluded the four points corresponding to this period (one sample every 15 min for 1 h) when we estimated the slope of the regressions.

Residence time in the intestine was estimated indirectly as the difference between mouth-to-anus total mean retention time and mean residence time in the foregut. Residence time in the intestine that was estimated by using this method was slightly higher on average when birds were on the interval feeding schedule (38.8 ± 4.0 min) than when they were on the ad lib. feeding schedule (27.3 ± 2.2 min; $F_{1,9} = 5.50$, $P = 0.044$), as predicted by the optimization model. We also directly estimated residence time in the intestine as time of first defecation that contained counts (dpm) above background level. In 18 of the 20 trials in which we measured retention time, the first defecation contained counts above background level. Thus, in this experiment, time of first appearance of the marker was also usually the time of first defecation. Contrary to the predictions of the optimization model, residence time in the intestine that was estimated by using this second method was similar for birds on the interval and ad lib. feeding schedules (Table 3).

Also contrary to the predictions of the optimization model, extraction efficiency of D-glucose did not increase when treatment birds were on the interval feeding schedule, compared with when they were on the ad lib. schedule (Table 3).

Discussion

Testing Predictions from the Optimal Digestion Model

Previous tests of the optimal digestion model have used manipulations of food quality, specifically sugar concentration, and then measured their effects on retention time and extraction efficiency (Karasov and Cork 1996). The predictions of the model have been rejected for rainbow lorikeets (Karasov and Cork 1996); changes in sugar concentration result in no significant changes in extraction efficiency, and intestinal residence time does not increase with increasing sugar concentration. That test of the model used birds in relatively benign temperature conditions, so the birds may not have been maximizing their rate of energy gain (as assumed in the model).

In our test of the optimal digestion model, we increased the likelihood that the birds were maximizing their rate of energy gain by exposing the birds to chronically low temperatures. We then tested the model by manipulating the costs of foraging by removing food every third hour on the test day. Many other researchers have used the same manipulations of intermeal intervals to increase foraging costs, especially in tests of patch use optimal foraging models (see Stephens and Krebs [1986] for review).

The predictions of the model were that extraction efficiency of glucose and intestinal residence time would increase with higher foraging costs (i.e., longer intermeal intervals). Contrary to these predictions, extraction efficiency and retention time (mouth-to-anus total mean retention time or mean residence time in the foregut) did not increase with longer intermeal intervals, although the results for intestinal residence time were ambiguous and depended on the method used to estimate intestinal residence time.

Guts as Chemical Reactors

We estimated intestinal residence time in two ways: indirectly as the difference between mouth-to-anus total mean retention time and mean residence time in the foregut, and directly as time of first defecation that contained inert marker. The predictions of the optimal digestion model were supported

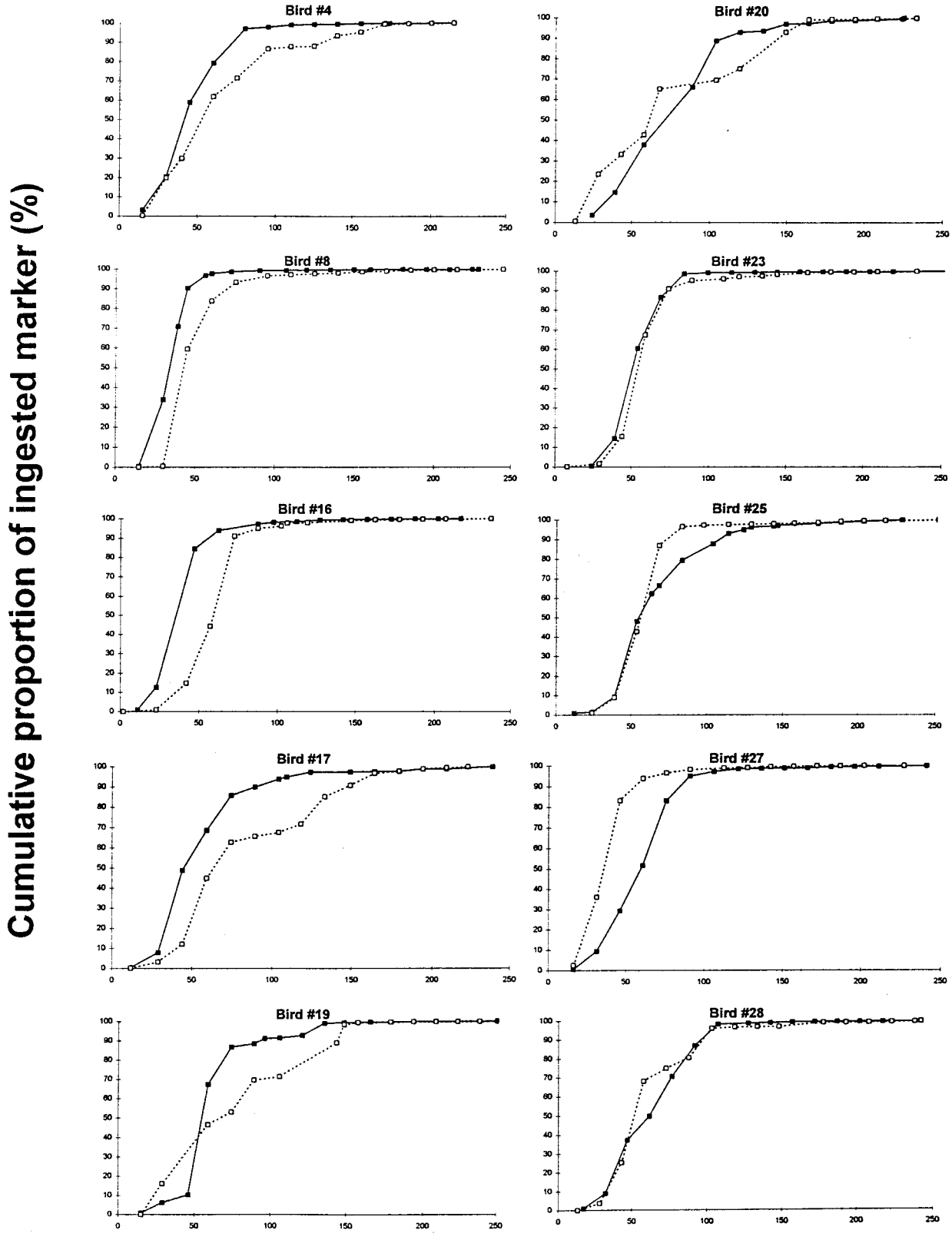

Bird #4
Bird #20
Bird #8
Bird #23
Bird #16
Bird #25
Bird #17
Bird #27
Bird #19
Bird #28
Cumulative proportion of ingested marker (%)
Elapsed time since ingestion of marker (min)

Table 3: Mouth-to-anus total mean retention time, foregut mean retention time, intestinal residence time, and extraction efficiency of glucose in cedar waxwings on two feeding schedules

Feeding Schedule	Mouth-to-Anus Total Mean Retention Time (min)[a]	Mean Residence Time in the Foregut (min)[b]	Intestinal Residence Time (min)[c]	Extraction Efficiency of D-glucose (%)[d]
Treatment group:				
Ad lib.	63.5 ± 4.1	36.7 ± 2.5	14.2 ± 1.3	93.0 ± .29
Interval	69.9 ± 4.5	31.0 ± 2.2	15.1 ± 1.8	91.2 ± .88
Statistical comparisons[e]	$F_{1,9} = 1.79$, $P = .214$	$F_{1,9} = 2.68$, $P = .136$	$F_{1,9} = 0.14$, $P = .722$	$F_{1,9} = 4.1$, $P = .074$

Note. See Material and Methods for definitions of each feeding schedule.

[a] All retention times were measured using output distributions of the inert marker ^{14}C FeCN (see Material and Methods).

[b] Calculated as the inverse of the absolute values of the slopes in Figure 3.

[c] Calculated as time of first defecation that contained counts (dpm) above background level.

[d] Extraction efficiency (%) of radiolabeled D-glucose was measured by the inert-marker technique (Karasov et al. 1986).

[e] Repeated-measures ANOVA ($n = 10$).

when residence time in the intestine was estimated indirectly but were not supported when residence time in the intestine was estimated directly. In evaluating the predictions of the optimal digestion model, we emphasize our estimates of residence time in the intestine using the direct method because they depended on fewer assumptions than estimates using the indirect method (Martínez del Rio et al. 1994).

Our estimates of residence time in the intestine depended on whether the stomach or intestine of waxwings functions as an ideal stirred-tank reactor or plug-flow reactor, respectively, in series. In stirred-tank reactors, material continuously flows into and out of the reactor, and the material in the reactor is well mixed (Martínez del Rio et al. 1994). In contrast, material in a plug-flow reactor flows continuously through the chamber, and there is little axial mixing of material during transit.

If the waxwing's gut functions as a simple combination of stirred-tank and plug-flow reactors, then mouth-to-anus total mean retention time minus mean residence time in the foregut should equal our direct estimates of residence time in the intestine (Levenspiel 1972; Martínez del Rio et al. 1994). Using the indirect approach, we estimated residence time in the intestine as about 27 min on the ad lib. feeding schedule and about 38 min on the interval feeding schedule. However, our direct estimates of residence time in the intestine were less than 15 min, on average, for birds on both feeding schedules. Using the direct approach, Karasov and Levey (1990) and Levey and Grajal (1991) also estimated residence time in the intestine at about 10 min, on average, for waxwings eating similar semisynthetic diets. Mixing of digesta in the intestine has been observed in waxwings (Levey and Duke 1992), and this may explain why the estimates of residence time in the intestine were different for the direct and indirect methods.

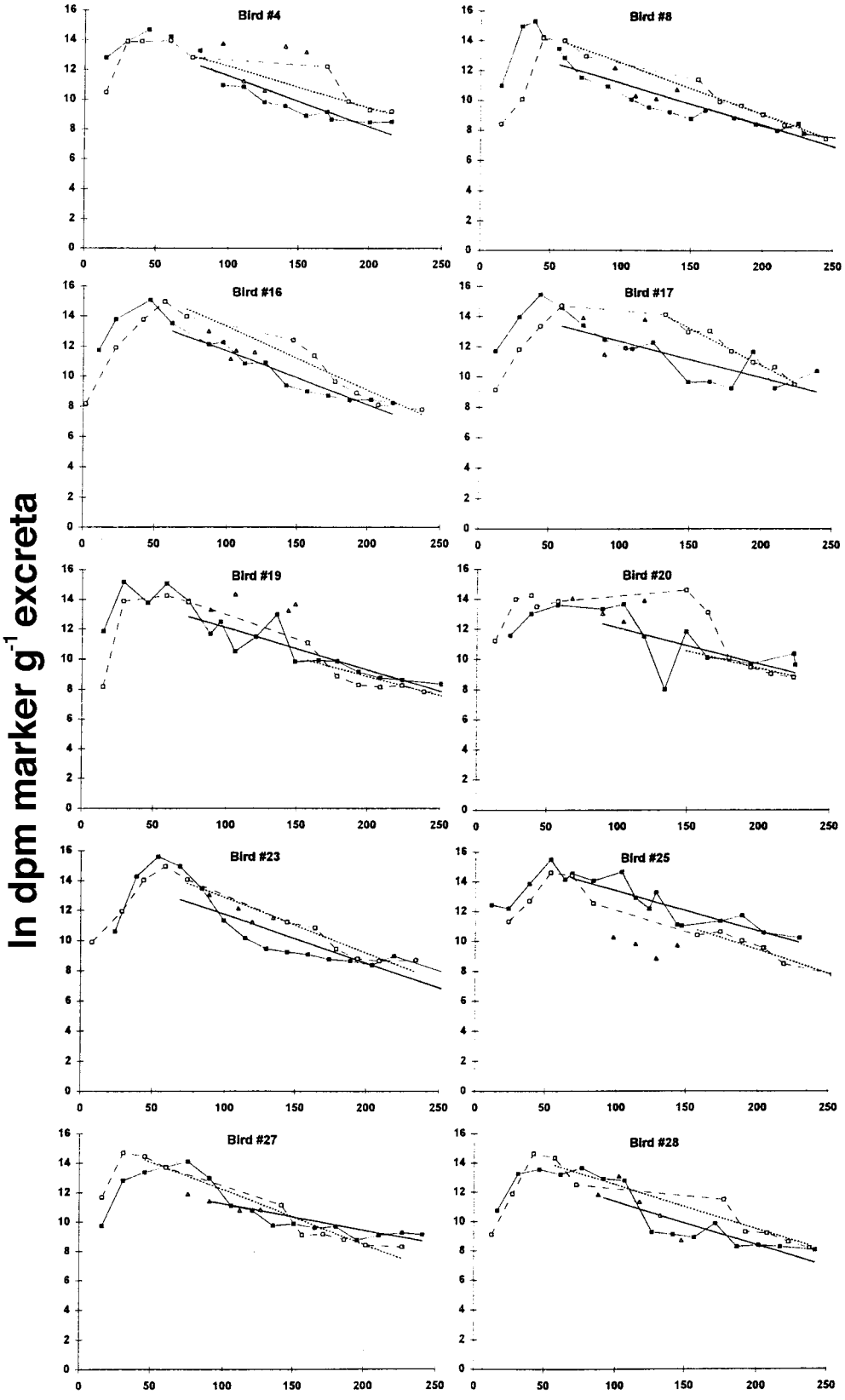
Figure 2. Cumulative output of inert marker for individual cold-acclimated waxwings on ad lib. (*solid line*) or interval (*dashed line*) feeding schedules (see Material and Methods for definitions of feeding schedules).

Modeling an animal's gut as a series of chemical reactors may be useful as a tool to describe patterns of digesta flow in particular portions of the gut. However, our inability to successfully apply chemical reactor theory to waxwings, which have quite simple guts (Martínez del Rio et al. 1994), indicates that movement of digesta in the guts of birds is much more complex than movement of material in ideal chemical reactors.

Are Animals Maximizing Their Rate of Energy Gain?

Given the lack of agreement between the results from our empirical test and the predictions of the optimal digestion model, perhaps the assumption that the net rate of energy gain is maximized is inappropriate. In fact, our results suggest that the rate of energy intake was not maximized by waxwings. Extraction efficiency of glucose in cold-acclimated waxwings was similar for birds on both feeding schedules, although short-term feeding rates were 25% higher for birds on the interval feeding schedule. If the rate of energy intake were maximized, then birds on the ad lib. feeding schedule apparently could (but did not) increase their feeding rate to at least match that of birds on the interval feeding schedule and thereby increase their daily energy intake.

Theoreticians working with optimal foraging models have long recognized that such evidence does not necessarily mean that maximization of net rate of energy gain is an inappropriate currency. Modelers of optimal diet or patch use typically assume that maximization of net rate of energy gain is the appropriate optimization criterion (reviewed by Stephens and Krebs [1986]), but they point out that the predicted pattern of feeding depends on whether the time needed to obtain a fixed amount of energy is minimized (termed a "time minimizer") or whether the energy obtained in a fixed amount of time is


Bird #4
Bird #8
Bird #16
Bird #17
Bird #19
Bird #20
Bird #23
Bird #25
Bird #27
Bird #28
ln dpm marker g-1 excreta
Elapsed time since ingestion of marker (min)

maximized (termed a "energy maximizer"; Schoener 1971, 1987). Given the difference in feeding rate between waxwings on the two feeding schedules, cold-acclimated waxwings were clearly not always behaving like energy maximizers.

The optimal digestion model predicts that digestive efficiency will be different for time minimizers and energy maximizers and so provides an additional criterion for discriminating between these two types of foragers. For an energy maximizer, the net rate of energy gain is maximized when the animal digests proportionately less of its food in favor of eating more (Fig. 1). For a time minimizer, the net rate of energy gain is maximized when the animal digests as much of the food as possible, assuming the additional time required for more thorough digestion still allows enough time for the forager to obtain its fixed energy requirements.

In our study, cold-acclimated waxwings maintained constant, high extraction efficiency. If waxwings were time minimizers, then the extraction efficiencies we measured (91%–93%) should be maximal. The two other studies that have estimated extraction efficiency of glucose in waxwings provide some support for this assumption (92%, Martínez del Rio et al. 1989; 92%, Karasov and Levey 1990). Such less-than-complete extraction of dietary glucose is apparently typical of frugivorous passerines in general (Karasov and Levey 1990).

Digestive Efficiency and Animal Ecology

Digestive efficiency is of ecological importance because it reflects the proportion of food eaten that is digested and absorbed by the animal. Digestive physiologists view digestive efficiency as a positive function of both retention time and the rate(s) of hydrolysis and absorption and as a negative function of both concentration of nutrients in the food and digesta volume (Karasov 1996). Two important assumptions are implicit in this view: that any change in one of these parameters will cause a change in digestive efficiency unless a compensatory change occurs in another parameter, and hence that there is a tradeoff between rate of digesta processing and digestive efficiency, with faster processing resulting in reduced extraction efficiency.

Given this view, how did the parameters that determined digestive efficiency in this study compensate during short-term changes in food quality and costs of feeding so that digestive efficiency remained remarkably constant? Intestinal carbohydrase activity and rates of active glucose uptake do not increase with increased glucose concentration (Levey and Karasov 1992; Afik et al. 1995; Martínez del Rio et al. 1995), although relatively few studies have focused on this type of response. In addition, such biochemical responses may be relatively unimportant if passive absorption of nutrients such as glucose accounts for a large fraction of total absorption (Karasov and Cork 1994; Caviedes-Vidal and Karasov 1996; Levey and Cipollini 1996; Afik et al. 1997) and the time scale for modulation of enzymes and uptake capacity is relatively long.

There is some evidence for modulation of retention time in response to short-term changes in food quality or costs of feeding. Rainbow lorikeets hold digesta in their stomach longer with increased sugar concentration, thereby maintaining relatively constant flow rate of sugar to the small intestine (Karasov and Cork 1994). In contrast, increased gut volume or digesta mixing apparently enabled waxwings (this study) and warblers (McWilliams and Karasov 1998) to maintain constant retention time and hence extraction efficiency, despite short-term increases in feeding rates of 25% and 50%, respectively.

In summary, the picture that emerges is that of birds minimizing feeding time by maximizing their extraction efficiency rather than maximizing their net rate of energy gain by reducing extraction efficiency in favor of eating more. Modulation of food intake, retention time, and digesta mixing may be the primary ways that high, constant extraction efficiency is maintained during short-term changes in food quality or costs of feeding. From an ecological perspective, the lack of an effect of food quality or costs of feeding on extraction efficiency suggests that estimates of digestive efficiency are robust. However, this conclusion is relevant to situations in which food type is constant (e.g., diets with constant high or low glucose concentrations). In situations in which birds switch between diets that differ in primary nutrients (e.g., between diets high in lipid and diets high in sugar), changes in extraction efficiency can be significant (Afik and Karasov 1995).

Figure 3. Output distribution of inert marker for individual cold-acclimated waxwings on ad lib. (*solid lines* and *solid squares*) or interval (*dashed lines* and *open squares*) feeding schedules. For the ad lib. feeding schedule, the regression line is based on all points after the time with maximum marker output (ln dpm g^{-1} excreta). For the interval feeding schedule, the regression line is also based on all points after the time with maximum marker output (ln dpm g^{-1} excreta) but excludes points when the birds were without food (*triangles*).

Acknowledgments

We thank Doug Levey for kindly providing some of the waxwings used in this study. Joceyln Bryant, Jean Fantle, and Jill Keen provided excellent care for the captive birds. Denise Dearing, Doug Levey, and Carlos Martínez del Rio provided helpful criticisms of earlier drafts of the manuscript. We also especially thank Bruce Darken for his valuable advice and assistance. The work was supported by National Science Foundation grant IBN-9318675.

Literature Cited

Afik D., E. Caviedes-Vidal, C. Martínez del Rio, and W.H. Karasov. 1995. Dietary modulation of intestinal hydrolytic

enzymes in yellow-rumped warblers. Am. J. Physiol. 269:R413–R420.

Afik D. and W.H. Karasov. 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. Ecology 76:2247–2257.

Afik D., S.R. McWilliams, and W.H. Karasov. 1997. A test for passive absorption of glucose in yellow-rumped warblers and its ecological implications. Physiol. Zool. 70:370–377.

Caviedes-Vidal E. and W.H. Karasov. 1996. Glucose and amino acid absorption in house sparrow intestine and its dietary modulation. Am. J. Physiol. 271:R561–R568.

Denslow J.S., D.J. Levey, T.C. Moermond, and B.C. Wentworth. 1987. A synthetic diet for fruit-eating birds. Wilson Bull. 99:131–134.

Karasov W.H. 1996. Digestive plasticity in avian energetics and feeding ecology. Pp. 61–84 in C. Carey, ed. Avian Energetics and Nutritional Ecology. Chapman & Hall, New York.

Karasov W.H. and S.J. Cork. 1994. Glucose absorption by a nectarivorous bird: the passive pathway is paramount. Am. J. Physiol. 267:G18–G26.

———. 1996. Test of a reactor-based digestion optimization model for nectar-eating rainbow lorikeets. Physiol. Zool. 69:117–138.

Karasov W.H. and D.J. Levey. 1990. Digestive system trade-offs and adaptations of frugivorous passerine birds. Physiol. Zool. 63:1248–1270.

Karasov W.H., D. Phan, J.M. Diamond, and F.L. Carpenter. 1986. Food passage and intestinal nutrient absorption in hummingbirds. Auk 103:453–464.

Lasiewski R.C. and W.R. Dawson. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69:13–23.

Levenspiel O. 1972. Chemical Reactor Engineering. 2d ed. Wiley, New York.

Levey D.J. and M.L. Cipollini. 1996. Is most glucose absorbed passively in northern bobwhite? Comp. Biochem. Physiol. 113A:225–231.

Levey D.J. and G.E. Duke. 1992. How do frugivores process fruit? Gastrointestinal transit and glucose absorption in cedar waxwings (*Bombycilla cedrorum*). Auk 109:722–730.

Levey D.J. and A. Grajal. 1991. Evolutionary implications of fruit processing and intake limitation in cedar waxwings. Am. Nat. 138:171–189.

Levey D.J. and W.H. Karasov. 1989. Digestive responses of temperate birds switched to fruit or insect diets. Auk 106:675–686.

———. 1992. Digestive modulation in a seasonal frugivore, the American robin (*Turdus migratorius*). Am. J. Physiol. 262:G711–G718.

Martínez del Rio C., H.G. Baker, and I. Baker. 1992. Ecological and evolutionary implications of digestive processes: bird preferences and the sugar constituents of floral nectar and fruit pulp. Experientia 48:544–551.

Martínez del Rio C., K.E. Brugger, J.L. Rios, M.E. Vergara, and M. Witmer. 1995. An experimental and comparative study of dietary modulation of intestinal enzymes in the European starling (*Sturnis vulgaris*). Physiol. Zool. 68:490–511.

Martínez del Rio C., S.J. Cork, and W.H. Karasov. 1994. Modelling gut function: an introduction. Pp. 25–53 in D.J. Chivers and P. Langer, eds. The Digestive System in Mammals: Food, Form and Function. Cambridge University Press, Cambridge.

Martínez del Rio C. and W.H. Karasov. 1990. Digestion strategies in nectar- and fruit-eating birds and the sugar composition of plant rewards. Am. Nat. 136:618–637.

Martínez 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.

McWilliams S.R. and W.H. Karasov. 1998. Test of a digestion optimization model: effect of variable-reward feeding schedules on digestive performance of a migratory bird. Oecologia (in press).

Murphy M.E. and J.R. King. 1982. Semi-synthetic diets as a tool for nutritional ecology. Auk 99:165–167.

Penry D.L. and P.A. Jumars. 1986. Chemical reactor analysis and optimal digestion. Bioscience 36:310–315.

———. 1987. Modelling animal guts as chemical reactors. Am. Nat. 129:69–96.

Piersma T., A. Koolhaas, and A. Dekinga. 1993. Interactions between stomach structure and diet choice in shorebirds. Auk 110:552–564.

Redig P.T. 1989. The avian ceca: obligate combustion chambers or facultative afterburners? The conditioning influence of diet. J. Exp. Zool. Suppl. 3:66–69.

Schoener T.W. 1971. Theory of feeding strategies. Annu. Rev. Ecol. Syst. 2:369–404.

———. 1987. A brief history of optimal foraging ecology. Pp. 5–67 in A.C. Kamil, J.R. Krebs, and H.R. Pulliam, eds. Foraging Behavior. Plenum, New York.

Stephens D.W. and J.R. Krebs. 1986. Foraging Theory. Princeton University Press, Princeton.

Warner A.C.I. 1981. Rate of passage of digesta through the gut of mammals and birds. Nutr. Abstr. Rev. 51:789–820.

Witmer M.C. 1996. Annual diet of cedar waxwings based on U.S. Biological Survey records (1885–1950) compared to diet of American robins: contrasts in dietary patterns and natural history. Auk 113:414–430.