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Test of a digestion optimization model: effect of variable-reward feeding schedules on digestive performance of a migratory bird

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Abstract Birds on migration often alternate between feeding and nonfeeding periods, in part because food resources may be patchily distributed and in part because birds on migration may adopt a risk-prone foraging strategy characterized by selection of variable rather than constant food rewards. Optimal digestion models predict that increases in intermeal interval like those encountered by some migratory birds should result in longer retention time of digesta and higher digestive efficiency if birds are maximizing their rate of energy intake. We tested these predictions by comparing residence time of digesta and extraction efficiency of lipid for captive yellow-rumped warblers (*Dendroica coronata*) feeding *ad libitum* and when we added intervals of time when the birds received no food. We increased the likelihood that the warblers were maximizing their rate of energy intake by increasing light levels during spring to induce hyperphagia (treatment birds (16L:8D light: dark cycle) ate 2.13 ± 0.14 g dry food day^{-1} ($n = 8$) while control birds (10L:14D) ate 1.25 ± 0.03 g dry food day^{-1} ($n = 6$)). Treatment birds offered food only every other 2–3 h ate 50% more during the 4-h test period than when they were always feeding *ad libitum*. Despite these differences in food intake, extraction efficiency of glycerol trioleate remained high and constant (93%), and mouth-to-anus total mean retention time (TMRT) did not change (overall mean: 54.8 ± 6.0 min). Residence time of lipid in the stomach increased whereas residence time of lipid in the intestine decreased when birds fed only every other 2–3 h compared to when birds always fed *ad libitum*. None of the results were consistent with the predictions of the optimal digestion model unless we assume that birds were minimizing their feeding time rather than maximizing their rate of energy gain. Furthermore, the ability of yellow-rumped warblers to maintain high extraction efficiency with no change in TMRT suggests some spare digestive capacity when food intake increases by as much as 50%.

Key words Bird migration · Risk-sensitive foraging · *Dendroica coronata* · Feeding schedule · Optimal digestion model

Introduction

The distribution and abundance of prey and foraging strategy are two factors that influence when a predator eats. For instance, if prey are patchily distributed, then the predator may consume plenty of food when in a patch but while traveling between patches it may eat little if at all. For migratory birds that travel far, the interval of time between feeding and nonfeeding periods may be relatively short when at a stopover site where prey are uniformily distributed, relatively long when at a stopover site where prey are patchily distributed, or very long when the bird moves between stopover sites.

The foraging strategy of a migratory bird also influences when and what the bird eats (Moore and Simm 1985, 1986; Berthold 1996). Risk-prone and risk-averse foragers have been identified using experiments in which birds choose between two feeding schedules that offer the same average amount of food over some short time interval (e.g. an hour) but in different quantities each meal (e.g. Caraco et al. 1980; Caraco 1981). In this experimental context, risk-prone foragers preferentially choose a feeding schedule comprised of bouts with no food or lots of food whereas risk-averse foragers choose the alternative feeding schedule comprised of bouts with constant amounts of food each meal (reviewed in Stephens and Krebs 1986). In an ecological context, a bird

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such as a warbler that adopts a more risk-prone behavior may experience longer bouts between meals as it searches for rich food patches which, when found, result in faster consumption rates. In contrast, risk-averse warblers that choose patches less selectively may feed more continuously but at relatively lower consumption rates. Thus, an important consequence of these two foraging strategies is that short-term intake rates will be more variable for risk-prone foragers compared to risk-averse foragers.

The consequences and tradeoffs associated with such foraging patterns are typically assessed in terms of benefits such as the energy or nutrient content of the food and costs such as the time or energy used in capturing and consuming the prey (reviewed by McNamara and Houston 1992). These assessments ignore potential changes in digestive efficiency associated with different feeding patterns. If risk-prone and risk-averse foragers get the same average food reward but they differ in their abilities to extract nutrients from each meal, then energy gained for each strategy is not simply gross energy in the food minus the capture and consumption costs.

We know little about how short-term changes in feeding schedule affect digestive performance in migratory birds. Theoretical optimality models make explicit predictions about how an animal's digestive features should respond to short-term changes in feeding schedule (Penry and Jumars 1986, 1987; Martinez del Rio and Karasov 1990; Martinez del Rio et al. 1994), although only one other test of such models has been published (McWilliams and Karasov, in press).

We chose to test the optimal digestion model using yellow-rumped warblers (*Dendroica coronata* Linnaeus) during their hyperphagic, spring migratory period because yellow-rumped warblers in migratory-state adopt a risk-prone foraging strategy (Moore and Simm 1986) and are likely maximizing their rate of energy gain (Moore and Simm 1985) as assumed by the model. We compared food intake, digestive efficiency, and retention time in warblers presented with either food available continuously or food available for only short intervals of time. The intermeal intervals were chosen to simulate the ecological situation in which a bird encounters and consumes food when in patches and experiences non-feeding periods as it searches for other preferred food patches. In our test of the model, we assume intestinal capacity is constant (as would be the case with short-term changes in food intake, see Discussion), so that changes in residence time of digesta can only be achieved by altering food intake or processing rate of digesta. The models (e.g., Cochran 1987; Martinez del Rio and Karasov 1990; Martinez del Rio et al. 1994) predict that short-term increases in intermeal interval like those used in this experiment should result in longer retention time and increased digestive efficiency if the birds are maximizing their rate of energy gain.

Materials and methods

Capture and maintenance of birds

Yellow-rumped warblers were captured on 27–28 September 1994 near Chippewa Falls, Wisconsin (45°00′N latitude, 91°30′W longitude) using mist-nets. Birds were immediately weighed and banded, and then placed in groups of 6–10 individuals in 50 cm square cages for transport on 29 Sept. to our laboratory in Madison. After capture and during transport, birds were given *ad libitum* water and waxworms (*Galleria mellonella*). In the laboratory, birds were housed individually in stainless-steel cages (60 × 45 × 33 cm) under initially constant light cycle (12L:12D light:dark cycle) and temperature (21°C). Prior to the experiment, birds were fed a semisynthetic high-glucose diet (Table 1) that had been used successfully for maintaining yellow-rumped warblers in the laboratory (Afik and Karasov 1995).

Diet and light cycle changes for the experiment

By manipulating daily light schedules, we tried to induce hyperphagia in our treatment birds and consequently maximize their rate of food intake. On 17 February 1995, eight birds were randomly assigned to a treatment group and six birds to a control group.

The daily light schedule for treatment birds was then changed from 12L:12D to 16L:8D (lights on at 500 h) by increasing light 1 h d^{-1} over four consecutive days, while the light schedule for control birds was changed from 12L:12D to 10L:14D (lights on at 800 h) by decreasing light 1 h d^{-1} over two consecutive days. Increasing daylength in the laboratory has caused yellow-rumped warblers or other passerine birds to eat more (e.g. Bairlein 1985), deposit fat (King and Farner 1963), be more selective feeders (Moore and Simm 1985), and to switch to a risk-prone foraging strategy (Moore and Simm 1986). The control birds in this experiment were used to test whether increasing daylength produced the expected increase in food intake of treatment birds.

Table 1 Composition of semisynthetic diets fed to yellow-rumped warblers

Ingredients	High-Glucose Diet		Insect Diet	
	% Wet mass	% Dry mass	% Wet mass	% Dry mass
Dextrose	10.01	65.27	1.31	10.04
Casein[a]	1.54	10.04	6.04	46.44
Amino acid mix[b]	0.58	3.77	0.76	5.86
Vitamin & Minerals[c]	0.26	1.67	0.22	1.67
Calcium Phosphate	0.13	0.84	0.00	0.00
Salt mix[d]	0.77	5.02	0.76	5.86
Corn or Olive Oil[e]	1.03	6.69	2.61	20.08
Water	84.67		87.00	
Agar	1.03	6.69	1.31	10.04

[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.

[e] corn oil in the High-Glucose Diet, olive oil in the Insect Diet

On 24 February, all birds were acclimated to a newly formulated diet (Table 1) that simulated an insect diet in nutrient content (10% carbohydrate:53% protein:20% fat by dry mass) (Bairlein 1987). This diet had the same carbohydrate and protein content but less fat than the insect diet composed mostly of mealworms used by Afik and Karasov (1995). We used less fat in our diet because many of the insects eaten by warblers during spring contain about 20% fat (Bairlein 1987).

Feeding schedules and experimental design

Prior to the experiment, birds were presented with new food and water each day at 1600–1700 h. Each day birds were provided with excess food ensuring *ad libitum* feeding conditions. For the experiment, each control bird continued to receive *ad libitum* food. On the day before a test day, each treatment bird was offered food following one of two feeding schedules, either "Ad Lib" (*ad libitum* food always available, i.e., 16 h d^{-1} with food) or "Interval" (*ad libitum* food available only during 500–730 h, 1030–1300 h, and 1600–1800 h, i.e., 7 h d^{-1} with food). The Interval feeding schedule included variable-length feeding and nonfeeding periods so that short-term intake rates of birds on the Interval feeding schedule were more variable and less predictable than when birds were on the Ad Lib feeding schedule. Food was removed at 1800 hours to ensure that birds would start the test day with a small energy deficit. For birds on the Ad Lib feeding schedule, food was weighed at the same time intervals as the Interval feeding schedule, 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. The 2–3 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 warblers on a similar diet was 62 ± 6 min; Afik and Karasov 1995). The Interval feeding schedule simulates the ecological situation where a bird encounters and consumes food when in patches and experiences nonfeeding periods as it searches for other preferred food patches.

On the test day, treatment birds on the Interval feeding schedule were provided food during 500–700 h and again starting at 900 h. For birds on the Ad Lib feeding schedule, food was weighed at the same time intervals as the Interval feeding schedule but the food was then immediately returned to the bird's cage. Food intake, retention time, and extraction efficiency were measured during a 4-h test period that began when the bird was gavaged at 930 h with a solution containing radiolabelled nutrient and marker (see below). Food intake on a dry matter basis were estimated by drying subsamples of food collected at the start and end of the test period. Treatment birds were tested on the Ad Lib feeding schedule between 29 March–10 April and on the Interval feeding schedule between 19–21 April.

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 importantly, the cages 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 birds. All birds were housed in these cages for at least one day before the test day.

We chose to measure retention time and extraction efficiency of triglycerides in yellow-rumped warblers because these warblers often eat foods that contain much fat during spring (Martin et al. 1951; Place and Stiles 1992; Afik and Karasov 1995) and because the key assumptions of the optimal digestion model with regards to nutrient absorption kinetics are satisfied for such a nutrient (see Discussion). Extraction efficiency of triglycerides in yellow-rumped warblers can be quite variable and low (18–82% depending on diet and retention time (Afik and Karasov 1995)). Thus, triglycerides are a potentially good nutrient for detecting increases in assimilation efficiency in response to short-term increases in feeding interval.

Retention time of digesta was measured using the inert lipid-phase marker glycerol triether (GTE, received from A. Place, University of Maryland). This single lipid-phase marker was used for estimating retention time because Afik and Karasov (1995) found no difference in estimates of retention time for lipid (GTE) or aqueous markers making it unnecessary to use both. Extraction efficiency of lipids was measured using the inert marker method (Karasov et al. 1986) with GTE used as the inert marker and glycerol trioleate (GTO, Amersham Corporation, Arlington Heights, Illinois) used for the digestible lipid.

A mixture of 18.5 kBq of [^{14}C] GTO and 74 kBq of [^{3}H] GTE in 15 μL of carrier solution was gavaged into a bird's esophagous at the start of each 4-h test period. All birds on the Ad Lib and Interval feeding schedules had food available to them for at least 30 min prior to being gavaged. Preliminary experiments showed that total mean retention time was shorter in six of seven birds that were on the Interval feeding schedule but were gavaged immediately after the 2–3 h without food (TMRT: 44 ± 6 min) than in birds gavaged after the 30 min feeding period provided here (TMRT: 55 ± 7 min; $F_{1,6} = 1.26$, $P = 0.31$). All birds were returned to the special observation cages and began feeding soon after being gavaged; thus, a small volume of marker was inserted into the flow of food in the bird's digestive system.

Excreta were collected every 15 min for 4 h. Preliminary experiments revealed that GTE marker activity in the excreta reached the background level at about 4 h (Afik and Karasov 1995). Each excreta sample was placed in a preweighed sealed vial, reweighed with the excreta, and then 10 ml of a 2:1 mixture of chloroform:methanol was added to each vial (Place and Stiles 1992). The vials were vortexed daily for three days to ensure solubilization of probes and then processed after Roby et al. (1989). Briefly, each sample was filtered in a vacuum system using glass microfiber filter (Whatman Limited, GF/A, Catalogue No. 1820 024), and the solvent was removed by N_2 evaporation. Scintillation cocktail (Ecolume, ICN Biomedical, Incorporated) was added to each vial, the vials were vortexed, and then they were counted for disintegrations per minute (dpm) by liquid scintillation with corrections for variable quenching and spill of ^{14}C into the channel where ^{3}H was counted. Phase specificity for these markers has been reported by Afik and Karasov (1995), and lack of metabolizability of the GTE marker has been demonstrated by Roby et al. (1989).

Mouth-to-anus total mean retention time (TMRT) 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). Mean retention time in just the foregut (FMRT) was estimated from semilogarithmic plots of fecal marker concentration (ln dpm g^{-1} excreta) versus time since ingestion of the marker (Warner 1981; Martinez del Rio et al. 1994). 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). FMRT was then calculated as the inverse of the absolute value of the slope (k) of these regressions (i.e., $1/k$) (Warner 1981). Residence time in the intestine (TT) was then estimated by subtracting FMRT from TMRT (see the Discussion for important assumptions of this method of estimating TT).

Extraction efficiency was calculated as $100 - 100[(M_f/N_f)*(N_e/M_e)]$, where M_f is radioactivity of the inert marker (GTE) in food, N_f is radioactivity of the nutrient (GTO) in food, N_e is radioactivity of nutrient (GTO) in excreta, and M_e is radioactivity of inert marker (GTE) in excreta.

Repeated measures ANOVA was used to analyze differences in body mass, food intake, extraction efficiency, and retention time of treatment birds across feeding schedules. Differences in food intake and body mass between treatment and control birds feeding *ad libitum* were analyzed using t-tests. Results are given as mean ± SE unless otherwise noted. Degrees of freedom for each statistical test are presented as subscripts next to the symbol for each test.

Results

Mass balance and food intake prior to experiments

As expected, treatment birds increased in body mass by 18.4 ± 4.9% within three weeks of exposure to the 16L:8D schedule (paired *t*-test: $t_7 = 3.35$, $P = 0.006$) while control birds did not change their body mass after exposure to the 10L:14D schedule (paired *t*-test: $t_5 = 1.38$, $P = 0.22$). During the period of mass gain, treatment birds ate significantly more food (1.98 ± 0.02 g dry food day^{-1}) than control birds (1.54 ± 0.06 g dry food day^{-1}) ($t_{12} = 2.56$, $P = 0.012$, one-tailed). After the period of mass gain, treatment birds consistently ate more food (2.13 ± 0.14 g dry food day^{-1}) than control birds (1.25 ± 0.03 g dry food day^{-1}) ($t_{12} = 4.82$, $P = 0.0003$, one-tailed).

Mass balance and food intake during experiments

Both control birds and Ad Lib treatment birds maintained constant and similar body mass during the pre-test and test days (Table 2). Treatment birds on the Interval feeding schedule lost 13.0% of their body mass during the pre-test day.

During the 4-h test period, Ad Lib treatment birds ate 86.8% more food than control birds (Table 2). Treatment birds on the Interval feeding schedule ate 50.7% more during the 4-h test period than when on the Ad Lib feeding schedule (Table 2). Thus, the restricted feeding schedules we imposed on the treatment birds caused the expected increase in short-term rate of food intake.

Retention time and extraction efficiency

During our continuous observations of birds during each trial, we noted that all birds except Bird #70 on the Ad Lib feeding schedule always fed and defecated regularly. The smoothly rising shape of the cumulative excretion curves (Fig. 1) reflected this continuous feeding and defecation that we observed in all but the one bird. Bird #70 was excluded from further analysis because he slept from ca. 20–100 min after gavaging and so had an unusually protracted cumulative excretion curve (see Fig. 1a, Bird #70) and consequently high TMRT.

Contrary to the predictions of the optimization model, neither extraction efficiency of lipid nor TT increased when treatment birds were on the Interval compared to the Ad Lib feeding schedule (Table 3). In fact, TT tended to decrease in birds on the Interval feeding schedule compared to the Ad Lib feeding schedule (Table 3). The slope (*k*) of the terminal portion of the curves in Fig. 2 was higher in birds on the Ad Lib feeding schedule compared to the Interval feeding schedule; thus, estimates of residence time in the stomach (1/k) were lowest in Ad Lib birds (Table 3). The proportion of TMRT accounted for by the residence time in the stomach was 55% for the Ad Lib and 82% for the Interval feeding schedule.

Although extraction efficiency of lipids can be quite variable and low (18–82%; Afik and Karasov 1995), extraction efficiency of lipid was >90% in yellow-rumped warblers on both feeding schedules in our experiment. Perhaps such high extraction efficiency made it difficult for us to detect an increase in extraction efficiency for birds on the Interval feeding schedule. We calculated the statistical power to detect a 4–5 unit change in extraction efficiency (e.g., from 92% to 96–97%) assuming an alpha level of 0.05 and using the estimated within-group variance from our experiment. The power in this case is 82–96%. Thus, we can be 82–96% certain of detecting a 4–5% difference in extraction efficiency of lipid between birds on the two feeding schedules at the 5% level of significance.

Discussion

Our results have implications for physiological ecologists interested in modeling the digestive system and for

Table 2 Body mass and food intake (± SE) in yellow-rumped warblers on Ad Lib and Interval feeding schedules and two light schedules (Treatment and Control groups). Body mass was measured at 500 h on a given day

Feeding Schedule[a]	Body mass (g) on Pre-Test Day	Body mass (g) on Test Day	Difference in Body mass (g) between Pre-Test and Test Day	Food intake (g dry) during 4-hr test period
Treatment group:				
Ad Lib	11.08 ± 0.33	11.04 ± 0.31	−0.05 ± 0.09	0.71 ± 0.07
Interval	10.81 ± 0.13	9.41 ± 0.14	−1.40 ± 0.11	1.07 ± 0.07
Control group:				
ad libitum	11.18 ± 0.38	11.00 ± 0.37	−0.18 ± 0.07	0.38 ± 0.05
Statistical comparisons:				
two feeding schedules[b]	$F_{1,7} = 0.752$ $P = 0.415$	$F_{1,7} = 44.95$ $P < 0.0001$	$F_{1,7} = 89.72$ $P < 0.0001$	$F_{1,7} = 24.53$ $P = 0.002$
Ad Lib treatment vs. Control group	$t_{12} = 0.19$ $P = 0.846$	$t_{12} = 0.07$ $P = 0.943$	$t_{12} = 1.13$ $P = 0.27$	$t_{12} = 3.53$ $P = 0.003$

[a] see methods for definitions of each feeding schedule. Sample sizes were 8 birds for Ad Lib and Interval feeding schedules, and 6 birds for the control group

[b] repeated measures ANOVA ($N = 8$)

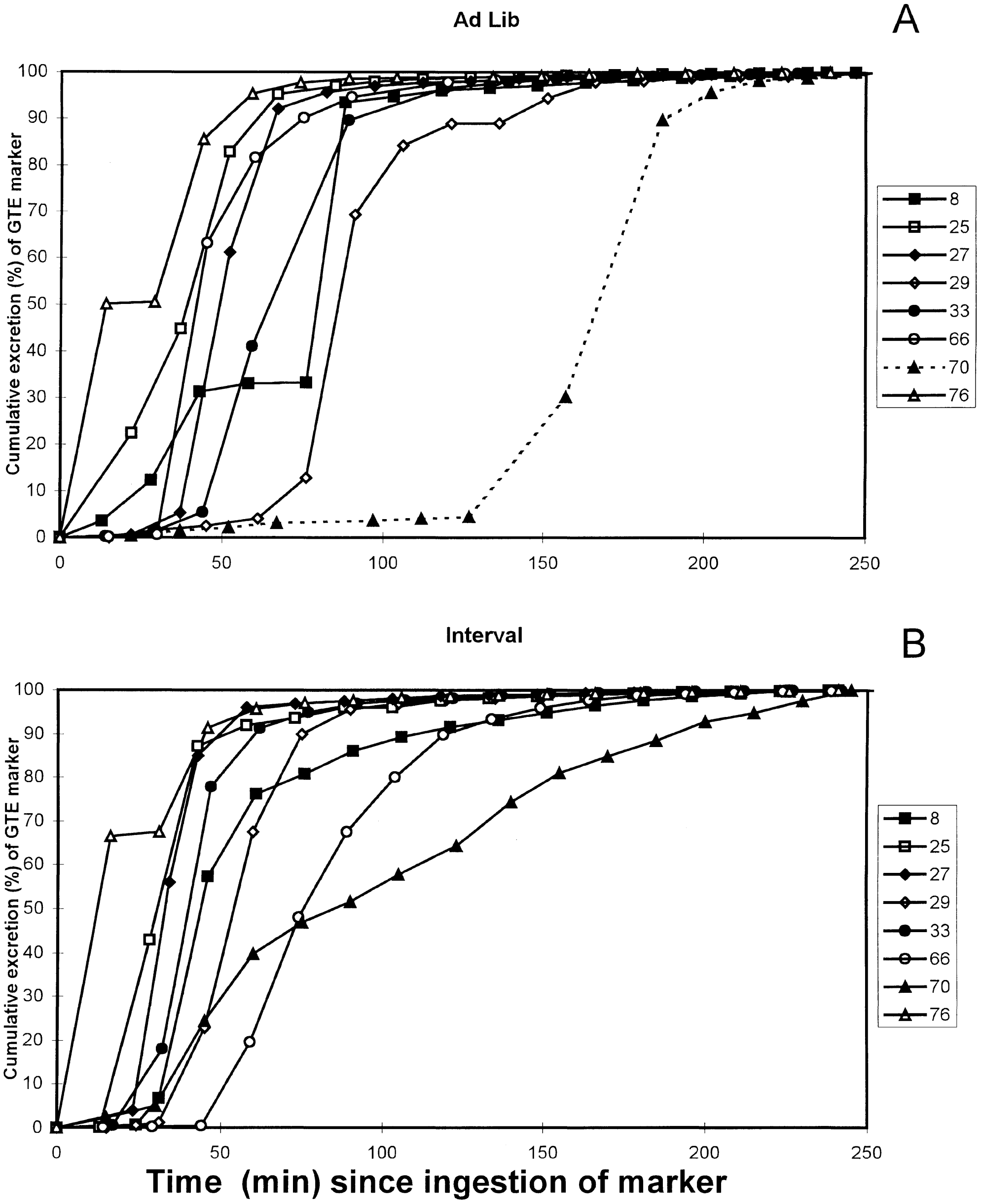

Fig. 1. Cumulative excretion of the inert lipid marker ^{3}H glycerol triether (GTE) as a function of time since the bird was gavaged with a solution containing the radiolabelled marker. Each figure shows the marker excretion pattern for the same seven treatment birds feeding either *ad libitum* always (A) or *ad libitum* only every other 2–3 h (B). Bird #70 on the Ad Lib feeding schedule was excluded from further analysis because he slept from ca. 20–100 min after gavaging and so he had an unusually protracted cumulative excretion curve

Table 3 Mouth-to-anus total mean retention time (TMRT), foregut mean retention time (FMRT), intestinal residence time (TT), and extraction efficiency of lipid in yellow-rumped warblers on two feeding schedules. Extraction efficiency (%) of a radiolabelled lipid, glycerol trioleate, was measured by the inert marker technique (Karasov et al. 1986). TMRT, FMRT, and TT were measured using output distributions of the inert lipid marker ^{3}H glycerol triether in excreta (see Methods)

Feeding Schedule[a]	TMRT (min)	FMRT(min)[b]	TT (min)[c]	Extraction Efficiency (%) of lipid
Treatment group:				
Ad lib	64.9 ± 7.9	35.9 ± 2.4	29.0 ± 10.3	92.9 ± 4.1
Interval	55.4 ± 7.1	45.6 ± 3.8	9.8 ± 10.8	93.5 ± 2.3
Statistical comparisons[d]:				
Ad lib vs. Interval	$F_{1,6}$ = 1.27 P = 0.30	$F_{1,6}$ = 8.55 P = 0.02	$F_{1,6}$ = 3.42 P = 0.11	$F_{1,6}$ = 0.02 P = 0.90

[a] see methods for definitions of each feeding schedule

[b] calculated as the inverse of the absolute values of the slopes in Fig. 2

[c] TT = TMRT–FMRT for each individual bird

[d] repeated measures ANOVA (N = 7)

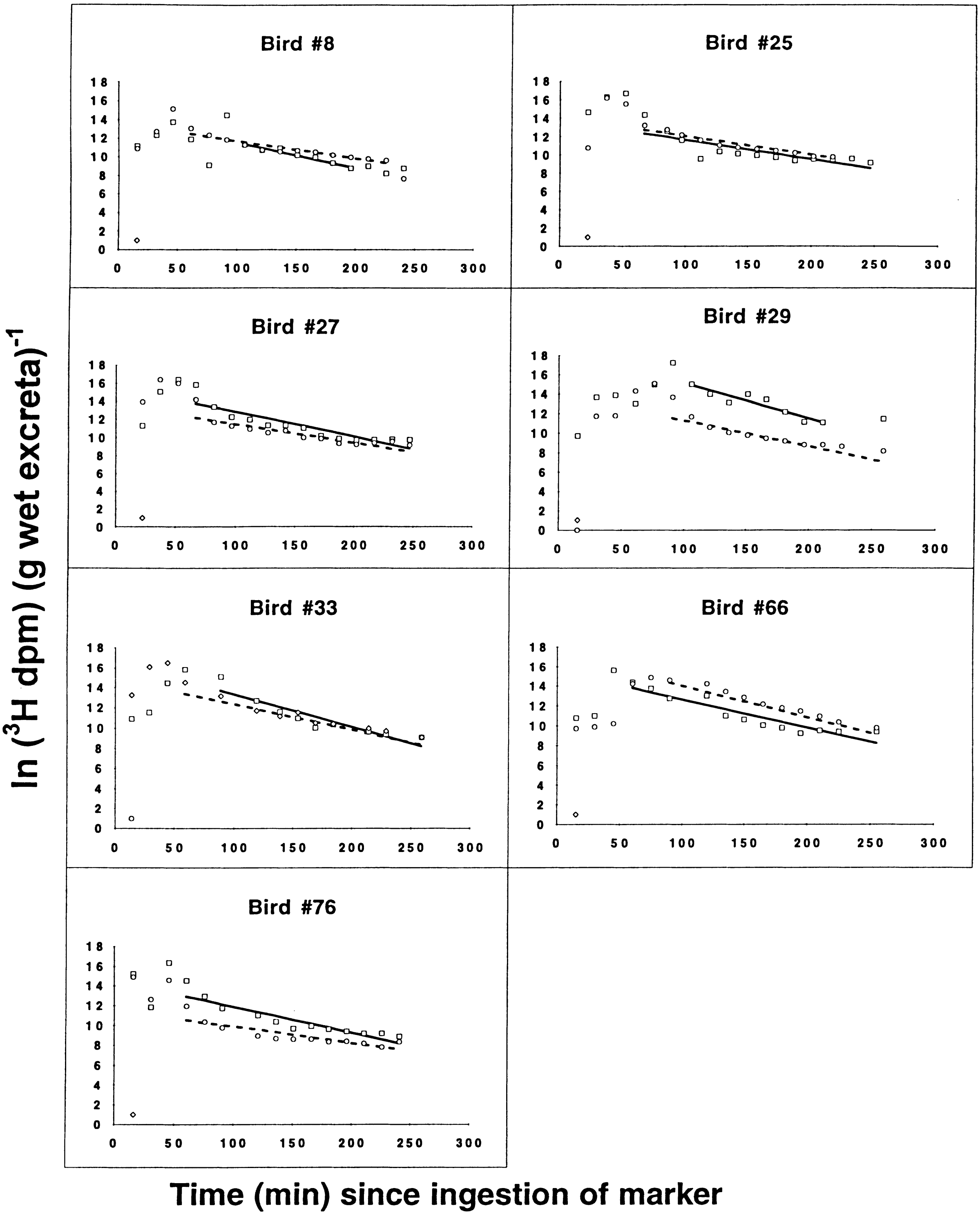

Fig. 2. Semilogarithmic plots of fecal marker concentration (^{3}H dpm per gram of excreta) versus time since ingestion of the inert lipid marker glycerol triether. Each figure shows the marker excretion pattern for an individual bird feeding on the Ad Lib (square symbols, solid line) or Interval feeding schedule (circles, dotted line). Lines were derived from fitting a linear regression model to values that were above background on the terminal portion of each curve

behavioral ecologists interested in modeling risk-sensitive foraging. After exploring these implications of our results, we then briefly discuss how our results permit quantification of the "spare capacity" (sensu Toloza et al. 1991) of the digestive system. The existence of significant spare capacity in any physiological system challenges the common assumption that the capacity of a physiological system is matched closely to the load on that system (Diamond 1991; Toloza et al. 1991; Karasov 1996).

Testing predictions from an optimal digestion model

The optimal digestion model has now been tested in a variety of circumstances. Effects of short-term changes in food quality on retention time and extraction efficiency have been studied using manipulations of sugar concentration in rainbow lorikeets (Karasov and Cork 1996), hummingbirds (Lopez-Calleja et al., in press), and cedar waxwings (Levey and Martinez del Rio, in press). Theoretically, the model can be tested by manipulating the rewards (e.g. by changing sugar concentration) or the costs of foraging. Our experiment is only the second to test the model by manipulating parameters like intermeal interval that directly affect the costs rather than the gains of foraging (also see McWilliams and Karasov, in press).

We tested the optimal digestion model by manipulating the time interval during which birds were provided with food. The predictions were that intestinal residence time and extraction efficiency would increase with longer intermeal intervals. Our manipulations of feeding schedule caused increases in feeding rate up to 50% compared to *ad libitum* conditions in treatment birds. When birds increased their feeding rates, however, their extraction efficiency of lipid remained constant and near maximum (90%). Likewise, retention time (TMRT or FMRT) did not increase over this range of food intake; in fact, there was some indication that intestinal residence time (TT) became shorter as food intake increased.

When our results are compared with those from other tests of the optimal digestion model, the following consistent patterns emerge: (1) extraction efficiency did not change when either sugar concentration or intermeal interval were manipulated; (2) when intermeal intervals were manipulated, TT did not change; (3) when sugar concentrations were manipulated, TT either did not change (Karasov and Cork 1996) or increased with increasing sugar concentration (Lopez-Calleja et al., in press; Levey and Martinez del Rio, in press). None of these results are consistent with the predictions of the optimal digestion model (Martinez del Rio and Karasov 1990).

Chemical reactor theory and guts

Tests of the optimal digestion model require estimating residence time of digesta in the intestine (Martinez del Rio and Karasov 1990). The method we used to estimate FMRT and TT assumes the gut can be modeled as a combination of two chemical reactors (a continuous stirred-tank reactor, the stomach, in series with a plug-flow reactor, the intestine (see Martinez del Rio et al. 1994 for complete descriptions)). The output distributions of inert markers from such chemical reactors have been described in detail by chemical engineers and so, to the extent that, guts function like such reactors, their results can be usefully applied to the transit of an inert marker through the digestive system (Penry and Jumars 1987; Martinez del Rio et al. 1994).

Modeling the intestine as a plug-flow reactor is undoubtedly an oversimplification for yellow-rumped warblers. In an ideal plug-flow reactor material flows continuously through a tubular vessel and there is little or no longitudinal mixing of material during transit (Martinez del Rio et al. 1994). In their studies of lipid digestion in yellow-rumped warblers, Place and Stiles (1992) found indirect evidence of retrograde movement of intestinal material back into the gizzard.

Retrograde movement of digesta would affect our estimates of retention time of digesta in the foregut and intestine. Our data indicate that the warbler's gut does not function as a simple combination of stirred-tank and plug-flow reactors. If the warbler's gut did function in this manner then FMRT subtracted from TMRT should equal residence time in the intestine (TT) (Levenspiel 1972; Martinez del Rio et al. 1994). We estimated TT as ca. 29 min for birds on the Ad Lib feeding schedule and ca. 9 min for birds on the Interval feeding schedule. However, we know that marker appeared in excreta from all our birds within 15 min of gavaging, suggesting that TTs were shorter than 15 min for all treatment conditions. Afik and Karasov (1995) estimated TT in yellow-rumped warblers as time of first appearance of marker in excreta. They estimated TTs of 10 min on average for warblers eating insect diets. Thus, it is likely that our estimates of TT, especially for the Ad Lib feeding schedule, were overestimates. In fact, the output distributions of inert markers from animals are often not as predicted assuming guts simply act as specific combinations of ideal chemical reactors (Martinez del Rio et al. 1994; Karasov and Cork 1996; McWilliams and Karasov, in press). Despite the limitations of the approach we used for estimating residence time of digesta in certain compartments of the digestive system, it is apparent that none of our estimates of residence time suggest an increase in retention time when birds were fed on the Interval feeding schedules, as predicted by the optimal digestion model.

Evaluating assumptions of the model

Post hoc interpretations of why the model failed to predict accurately the response of the birds must evaluate whether the assumptions of the optimal digestion model were satisfied. Below we evaluate the following assumptions of this model: (1) the currency (sensu Stephens and Krebs 1986) or optimization criterion was the maximization of net energy gain, (2) the absorption of the nutrient in question included a nonsaturable concentration-dependent process, and (3) the capacity of the intestine was constant during the experiment.

Our protocol was designed to increase the likelihood that the birds would be attempting to maximize their rate of energy gain. Treatment birds were exposed to increasing daylength in an attempt to induce migratory-state in these birds. Many other researchers have used the same manipulations of light to study other aspects of migratory behavior (e.g. foraging strategies (Moore and Simm 1985, 1986), nocturnal activity and orientation (reviewed by Able 1980) or physiology (e.g. body composition (King and Farner 1965; Blem 1990), food intake and digestive efficiency (reviewed by Berthold 1975)). By manipulating light levels during spring, we were able to produce much higher intake rates in experimental than control birds; thus, we produced a treatment group that was hyperphagic relative to control birds. Presumably, these hyperphagic birds were similar to other birds in migratory-state in that they foraged to maximize their rate of energy gain (Moore and Simm 1985).

The *a priori* predictions of the optimal digestion models depend mostly on whether the net energy gain curve is linear or decelerating toward a maximum (for a complete discussion see Martinez del Rio and Karasov 1990). We chose to test the model for triglyceride absorption because the diet of yellow-rumped warblers during spring often includes foods that contain much fat (Martin et al. 1951; Place and Stiles 1992; Afik and Karasov 1995). It is likely that the gain curve for a common dietary lipid like triglyceride decelerates towards a maximum because the rate-limiting step in lipid digestion and absorption is not the initial hydrolysis of lipid (Place and Stiles 1992) but rather the absorption of end-products of lipolysis, such as free fatty acids and glycerol, which is primarily by passive rather than carrier-mediated uptake (Shiau 1987). If the rate-limiting step is the passive absorption of end-products of lipolysis, then absorption rate will be fastest initially when luminal concentration is highest and then absorption rate will slow down as end-products of lipolysis are absorbed and luminal concentration declines. Thus, we assumed that the net energy gain curve for triglyceride was uniformly decelerating like that used for modeling sugar absorption (see Martinez del Rio and Karasov (1990) and Karasov and Cork (1996) for more discussion of this topic).

Finally, the optimal digestion model can be used to develop predictions about how both intestinal capacity and the rate of input into the intestine combine to affect retention time. However, we were interested in the short-term response of birds to changes in costs of foraging and so we made the simplifying assumption that intestinal capacity was constant as did Martinez del Rio and Karasov (1990). The feeding schedule we prescribed was carefully chosen to minimize any affect on gut morphology (and thus gut capacity). First, the 2-h intervals between meals were about twice the mean retention time (Table 2, Afik and Karasov 1995) so that most but not all food from the previous feeding period was digested and excreted before the birds were allowed to feed again. Second, the one-day acclimation period on a given feeding schedule was probably too short for substantial changes in gut morphology and capacity to occur by growth of tissue in response to the different feeding schedules (Karasov 1996). However, we cannot rule out that rapid adjustments in capacity could have occurred by adjustments in smooth muscle which is elastic.

Alternative models and explanations

We found that yellow-rumped warblers had consistently high digestive efficiency for lipid (ca. 90%) across all treatment conditions. In contrast, the optimal digestion model predicted that warblers would increase extraction efficiency with increased intermeal intervals and so maximize their net rate of energy gain. What if the warblers were not maximizing their rate of energy gain but were instead minimizing their feeding time? At least for a bird with relatively fixed energy requirements, feeding time is minimized when extraction efficiency is maximized (Karasov and Cork 1996). Thus, the yellow-rumped warbler's response is consistent with the goal of minimizing feeding time if we assume that 90% assimilation efficiency of lipid is maximal. The two other studies that have estimated assimilation efficiency of fatty acids in yellow-rumped warblers provide some support for this assumption. Afik and Karasov (1995) acclimated yellow-rumped warblers to diets with 5, 32, and 45% fat by dry wt and found the highest extraction efficiency of glycerol trioleate (83 ± 6%) on the diet with 45% fat. Place and Stiles (1992) report yellow-rumped warblers assimilated at most 90.1% of certain esterified 16-carbon saturated fatty acids.

Our results and those of Karasov and Cork (1996) are also consistent with a physiological model in which digesta flow is inhibited by increases in intraduodenal volume and by negative feedback from receptors in the proximate and medial small intestine that are stimulated by products of digestion of food (Duke 1982). Under this scenario, when warblers ate more of the same diet, the increased volume of digesta in the proximal small intestine caused inhibition of gastric motility and thus slow movement of digesta through the stomach. We found that when yellow-rumped warblers increased their food intake at least 50% they tended to have longer FMRT as predicted by this model. Presumably, there are limits to such a response. Theoretically, at some higher level of food intake, the stomach could not continue to slow digesta flow and either food intake would decrease so that FMRT would remain constant or food intake would increase causing a decrease in the FMRT. The specific predictions of such a physiological model depend on the particular step in the digestive process that is limiting food intake, and the degree to which a change in one step in the digestive process necessitates a change in another step (i.e., the level of spare capacity in each digestive process). We close with a brief discussion of how these two important concepts (digestive constraints and spare capacity) interrelate in the context of how birds respond to changes in food intake and foraging costs.

Digestive constraints, spare capacity, and risk-sensitive foraging

Theoretically, digestive constraints (e.g. slow rates of digestion inhibit short-term food intake) can directly affect daily foraging patterns in birds by forcing birds to spread their feeding more evenly through the day (Bednekoff and Houston 1994). Our direct measures of how feeding rate affects digestive efficiency and rate, however, suggest that the degree to which digestion constrains the animal is probably limited as long as increases in food intake are < 50% above *ad libitum* levels. Does this mean that models of risk-sensitive foraging can ignore digestive constraints? We think not. It is likely that the relative importance of digestive constraints at the whole-animal level depends on the time-scale (i.e., if acclimation has occurred) and the magnitude of spare volumetric or enzymatic capacity relative to the magnitude of change in foraging costs and food intake.

The importance of time-scale is evident from studies in which food intake is increased chronically rather than acutely. For example, Dykstra and Karasov (1992) increased food intake of house wrens by exercising the birds and decreasing temperature. After acclimating the wrens to these conditions for weeks, they found that, compared to unexercised wrens at room temperature, food intake of the cold-acclimated wrens had doubled yet there was no decrease in digestive efficiency and TMRT was unchanged. Most importantly, they deduced that digestive efficiency was maintained in high-intake wrens because the small intestine had increased in length allowing residence time in the intestine to increase while residence time in the stomach decreased. Doubling of food intake occurs commonly in birds preparing for and during migration (Berthold 1975; Blem 1980; Karasov 1996) and in birds at cold temperatures (Dawson et al. 1983). Presumably, if food intake doubled quickly (i.e., before compensatory changes in small intestine length occur) then residence time in the intestine would be shorter and extraction efficiency would decrease.

An implicit assumption in many physiological models is that the capacity of a given system is matched closely with the load on that system (Diamond 1991; Karasov 1996). For example, the optimal digestion model we tested assumes that changes in foraging costs or nutrient concentration in the diet will directly affect extraction efficiency unless compensatory changes occur in, for example, retention time. We found, however, that yellow-rumped warblers could increase their food intake about 50% without lengthening retention time and without any negative effects on digestive efficiency. Thus, we found no evidence for compensatory changes. Clearly, the digestive system of warblers has some spare capacity that enables it to maintain digestive performance across a range of food intakes without appreciable changes in digesta flow. One of the challenges for the future is delineating how much spare capacity the animal maintains and in what situations if any the level of spare capacity is modulated.

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