DIGESTIVE RESPONSES OF TEMPERATE BIRDS SWITCHED TO FRUIT OR INSECT DIETS

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ABSTRACT.—Diet switching between fruits and insects is common among many species of temperate birds. We took advantage of this behavior to examine phenotypic adaptations of birds to different diets. American Robins (*Turdus migratorius*) and European Starlings (*Sturnus vulgaris*) were presented with crickets or three species of wild fruits for 3- to 10-day feeding trials. During the course of these trials, we measured utilization efficiencies, nitrogen balance, consumption rates, changes in body mass, and feeding behavior. *Metabolizable energy coefficients* (energy ingested minus energy excreted is divided by energy ingested) increased over the course of the cricket feeding trial, indicating a lag in digestive responses and suggesting that digestive efficiency is at first compromised when a bird switches diet. Metabolizable energy intake on the cricket diet stayed constant, despite the changes in metabolizable energy coefficients (MEC). This suggests that birds regulated energy intake by balancing consumption rates against rising MECs. Fruit was consumed at higher rates than insects, yet birds did not eat enough fruits to meet energy and nitrogen requirements. Their inadequate consumption rate and subsequent weight loss may have resulted from intake limitation due to digestive constraints or secondary chemicals (toxins) in fruit pulp. MECs on fruit pulp were surprisingly low, considering that so much pulp mass was soluble in neutral detergent and hence potentially digestible. We suggest that these low utilization efficiencies are a result of rapid gut transit times. *Received 2 November 1988, accepted 7 June 1989.*

DIGESTIVE efficiency influences many aspects of an animal's life history. Consequently, animals are highly selective in food choice and display specialized methods of food processing (Karasov in press). Yet, the link between food type and gut processing efficiency remains poorly understood for most diets (Sibly 1981; Robbins 1983; Penry and Jumars 1987; Martínez del Rio et al. 1988, 1989). We examined digestive efficiency of wild-caught birds on two of the most common avian diets, fruit and insects.

Fruit and insects differ strikingly in nutritional value. In contrast to insects, fruits are typically low in protein, rich in simple carbohydrates, and high in bulk (White 1974; Foster 1978; Worthington 1983; Herrera 1984, 1987; Johnson et al. 1985; Moermond and Denslow 1985; Dinerstein 1986). Specialized frugivores and insectivores are likely to show pronounced differences in digestive physiology and morphology. A bird adapted to one diet will probably have digestive features that limit its efficiency on the other diet. The study of such adaptations and trade-offs provides a valid first step in understanding the relationship between an animal's diet and its gut processing, and how these, in turn, affect its ecology and behavior.

Digestive adaptations are often studied using a comparative approach. One problem, however, is the difficulty in finding similarly sized specialists on different food types within the same restricted taxon. To avoid this problem, we focused on phenotypic adaptations of birds that are primarily frugivorous in the autumn and insectivorous in the spring. Hence, we could compare frugivory and insectivory in individuals of the same species.

We chose two similarly sized species, American Robin (*Turdus migratorius*) and European Starling (*Sturnus vulgaris*), that differ in degree of frugivory and are in the same order. American Robins consume ca. 21% plant food (mostly fruits) in the spring and 81% in the autumn (*n* = 467; Martin et al. 1951). The remainder of their diet consists primarily of invertebrates. Starlings also show a large increase in fruit consumption from spring to autumn (7% in spring, 39% in autumn; *n* = 656; Martin et al. 1951), but they are less frugivorous than robins. The switch from an insect-based diet to one of fruit is rapid, occurring within 1–2 months in robins (Wheelwright 1986).

To test for phenotypic adaptations (i.e. changes in digestive functions) associated with

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TABLE 1. Nutritional properties ($\bar{x}$) of the three diets. Standard deviations are in parentheses.

Diet	Water (%)	Seeds[a] (%)	NDS[b] (%)	Nitrogen[a] (%)	Protein[a,c] (%)	Protein/ item (mg)	kJ/g	kJ/item	Ash[a] (%)
Crickets	72 (1)	—	57.5 (1.7)	10.2[d]	63.8	46.8 (6.0)	23.2 (0.1)	1.70 (0.22)	4.2 (0.1)
Fruits[e]									
Dogwood	76 (2)	54 (3)	81.2 (1.2)	1.22 (0.06)	7.6 (0.4)	3.1 (0.2)	21.5 (0.5)	0.88 (0.08)	3.8 (0.1)
Grape	81 (1)	44 (2)	68.1 (0.4)	1.02 (0.01)	6.4 (0)	4.5 (0.1)	17.6 (0.4)	1.25 (0.03)	3.8 (0.3)
Viburnum	74 (2)	52 (2)	91.5 (0.1)	0.68 (0.03)	4.2 (0.2)	0.9 (0.1)	22.2 (0.5)	0.49 (0.03)	3.7 (0.1)
Banana mash	85 (1)	—	85.0 (1.1)	2.22 (0.07)	13.9 (0.4)	—	17.3 (0.1)	—	4.1 (0.2)

[a] Percent dry mass.
[b] Percent dry mass soluble in neutral detergent (i.e. potentially digestible).
[c] Assumes a 6.25 conversion of nitrogen to crude protein (Maynard and Loosli 1969).
[d] From Karasov (1982).
[e] Nutritional data for pulp and skin only.

switching diets, we attempted to determine whether birds change their digestive functions rapidly to accommodate a new diet or whether they experience a lag time during which efficiency is compromised. We tried to identify physiological constraints on birds when they switched diets and to determine differences in digestive processing of fruit and insects. We discuss how these features help explain why switches to a fruit diet are not complete in most temperate birds.

METHODS

Ten robins and 5 starlings were caught near Madison, Wisconsin, in August–September 1986. They were housed indoors in separate cages (ca. 0.6 m³) at constant temperature (23 ± 1°C) and day-length (12 h). We maintained them on a synthetic ration ("banana mash") developed for fruit-eating birds (Denslow et al. 1987) and water; both water and mash were provided ad libitum. When on this diet, both species maintained a constant body mass equal to their capture mass.

We used the synthetic ration as a standard for measuring digestive responses of switches onto fruit and insect diets. Our justification for this standard is that birds in the wild do not switch abruptly between fruit and insects but rather go through a transition period in which they consume a mixed diet (Martin et al. 1951, Wheelwright 1986). For our transition periods, the synthetic ration served as an "intermediate" diet. Although the ration is fruit-based (⅔ of its dry mass is fruit) and nutritionally more similar to fruits than insects, it has approximately twice the protein content of fruits (Table 1). We assumed that the changes in digestive processing that occur over a longer time in the field when birds switch between radically different diets would be at least as great as the changes we might observe over a short period when birds were switched from a nutritionally intermediate diet.

To detect changes in food utilization efficiency after switches onto fruit or insect diets, we measured metabolizable energy coefficients (MEC) and assimilable mass coefficients (AMC). MECs were calculated as (energy ingested − energy excreted)/energy ingested. AMCs were calculated using the same formula, but dry mass was substituted for energy. Higher MECs and AMCs indicate more complete assimilation of ingested energy or dry matter, respectively. Because endogenous wastes are mixed with undigested material in the cloaca, these measures of utilization efficiency underestimate true MEC and AMC (Sibbald 1982, Karasov in press).

We followed changes in both coefficients on a daily basis. As a partial test of whether 1-day measurements gave an accurate estimate of utilization efficiencies, we ran a 3-day feeding trial on all birds on the banana mash ration. We then calculated AMCs and MECs on a daily basis and tested for significant variation among the days.

Feeding trials.—We ran feeding trials with fruit and insect diets. The fruit trial was run first, approximately one month after the birds were captured. They acclimated to captivity and maintained a stable body mass equal to their capture mass (for robins: capture mass = 78.4 ± 3.6 g, mass on first day of experimental trials = 77.8 ± 4.6 g; for starlings: capture mass = 75.2 ± 4.7 g, mass on first day of trial = 78.3 ± 5.4 g; P > 0.05, paired *t*-tests). At the end of the fruit trial, we put the birds back on the maintenance diet for 2 weeks and then started the cricket trial. Toward the end of the 2-week intertrial period, we monitored daily variation in AMC and MEC for 3 days to verify that the birds had reacclimated to the maintenance diet (see Results). At the start of the cricket trial, both species had regained the weight they had lost on the fruit trial and were back to capture weight.

The fruit diet consisted of gray dogwood (*Cornus racemosa*), toothed viburnum (*Viburnum dentatum*), and wild grape (*Vitis* sp.). These species were chosen because they were common and, based on pilot experiments, the birds preferred them to five other species

(*Sambucus, Rhamnus, Lonicera, Prunus*, and *Phytolacca*) that were easily available. To minimize intraspecific variation in fruit nutritional composition, we collected the fruits of each species from 2–5 neighboring plants during a 1-week period (October 2–9). The fruits were refrigerated in plastic bags. Before use, we removed stems and discarded any fruits that showed signs of decay. All three species were provided simultaneously in separate dishes. Because some fruits started to desiccate during the trials, we sprayed them with water as necessary.

We used 4-week-old (73.4 ± 9.4 mg dry wt) house crickets (*Acheta domestica*) as the insect diet. Because we could not easily retain live crickets in bird cages, we froze them prior to use. The birds quickly learned to eat thawed crickets, which were slightly darker than fresh ones. Both fruit and crickets were presented in petri plates, *ad libitum*.

We ran 10-day feeding trials for robins and starlings on the cricket diet and planned to conduct identical trials for birds on the fruit diet. After 3 days on fruits, however, the birds had lost 10–14% of their starting weight and five robins appeared sick (i.e. head under wing and feathers erected). To prevent further weight loss and possible death, we interrupted all trials for 4 days by providing the banana mash maintenance diet. We then completed the final 3 days of the trial for all the starlings and the five robins that had appeared most healthy at the end of the first 3 days.

On the 2 days before a new trial began, we placed a small number of either fruits or crickets in each cage. After 1–5 h, the birds ate these and learned to recognize them as food. Thus, when the experimental trials began, all birds quickly started to eat the new diet. No period of starvation accompanied the diet switches.

Daily dry matter consumption for birds on the cricket diet was calculated by subtracting the dry weight of uneaten crickets from the dry weight of crickets fed to the bird. The dry weight/wet weight conversion factor for fresh crickets was an average calculated from wet and dry weights of eight petri plates of crickets. Daily dry matter consumption of fruit pulp was measured by counting the number of defecated or regurgitated seeds of each species and multiplying it by a dry pulp/seed conversion factor, which was calculated from 50–100 fruits. This method was used because it agreed with, but was more precise than, a gravimetric determination of consumption.

Feces were collected from plastic sheets on cage floors during the initial and final 3 days of each feeding trial. We removed sheets from a given day on the morning of the following day, ca. 15 min after the lights had come on but before the birds had started to feed. In the fruit trials, we separated seeds from other fecal material and based all analyses on the non-seed portion of the sample. Despite thorough scraping, we were unable to remove all fecal material from the sheets. To estimate the proportion of feces/day

that was left, we sprayed 15 sheets with water and wiped them clean with towels of known weight. The towels were then dried to constant weight and their weight gain was divided by the weight of feces collected from the corresponding sheet. This proportion (0.05–0.10) was then used to correct collected fecal weight to true fecal weight.

To examine differences in feeding behavior on fruits and insects, we measured feeding-bout length and frequency by observing freely feeding robins and starlings for 2-h periods from behind a one-way mirror. A *feeding bout* was defined as a period of eating separated by at least 3 min from preceding or following feeding events. Almost all trials were completed between 0900–1200.

Nutritional analysis.—Fruit pulp, whole crickets, banana mash, and fecal samples were analyzed for total energy content, percentage of nitrogen, and the proportion of dry matter soluble in neutral detergent (i.e. neutral detergent solubles [NDS]). We used the latter measure to approximate the proportion of dry mass not refractory to chemical digestion. Energy content was measured on a Phillipson microbomb calorimeter (Gentry Instruments). Two or three replicates were run on each sample and coefficients of variation were generally <5%. Total nitrogen was determined by Kjeldahl extraction. Replicates were run until coefficients of variation were <4%. Because birds on the cricket diet were almost certainly in positive nitrogen balance (nitrogen content of the crickets was 5–10 times higher than banana mash or fruits), we did not analyze fecal samples from the cricket trial for nitrogen. We measured NDS as described in Goering and Van Soest (1970) with modifications proposed by Mould and Robbins (1981). During NDS analysis of fruit and banana mash samples, we treated the samples with a 2% amylase (SIGMA Chemicals) solution to ensure that starch would not impede filtration.

In comparisons of utilization efficiencies among the three diets, we used average AMCs and MECs calculated from the last three days of each trial. For robins on the fruit diet, we used the first 3 days' data, because there were no detectable changes in utilization efficiency (see below) and we had a larger sample size in the first half of the trial.

Statistical analyses.—We used paired *t*-tests or Mann-Whitney *U*-tests for all simple comparisons. Comparisons of utilization efficiency among the three diets by each bird species were made by one-way, repeated measures ANOVAs, which controlled for interindividual variation. All comparisons within each ANOVA were a priori. When >2 contrasts were made, alpha-levels were adjusted by Duncan's New Multiple-Range tests (Steel and Torrie 1980).

RESULTS

Nutritional content of diets and food preferences.—Crickets had the lowest proportion of

TABLE 2. Consumption and digestion parameters (averages and standard deviations) of robins and starlings on three diets. (n = 10 robins, 5 starlings). Matching letters (G–U) following values represent significant differences (P < 0.05, multiple range tests). Standard deviations are in parentheses.

Diet/bird	Consumed/ day (g dry)	Excreta/ day (g dry)	AMC[c]	kJ/day assimilated[d]	MEC	N balance[e] (mg/day)	Mass balance[f] (g)
Crickets[a]							
Robins	6.8 (1.3)	2.7 (0.6)	0.57 (0.03)G, O	111.4 (22.1)S, T	0.71 (0.03)J, K	—	1.9 (3.8)
Starlings	6.6 (1.1)	2.3 (0.3)	0.61 (0.02)I, O	112.6 (19.1)Q, R	0.73 (0.02)M	—	0.1 (1.7)
Fruits[b]							
Pulp and skin only							
Robins	7.0 (0.8)	3.0 (0.2)	0.57 (0.06)U	80.0 (18.9)T	0.55 (0.07)K	−14.9 (21.1)	−5.5 (2.1)
Starlings	5.2 (1.3)	2.2 (0.4)	0.56 (0.11)H	58.2 (24.7)R	0.55 (0.14)L, M	−39.2 (33.5)	−7.9 (5.0)
Entire fruit							
Robins	10.6 (1.2)	6.5 (0.4)	0.38 (0.04)				
Starlings	7.7 (2.0)	4.8 (1.0)	0.38 (0.08)				
Banana mash							
Robins	11.6 (2.0)	3.2 (0.5)	0.73 (0.02)U, G	154.3 (28.6)S	0.77 (0.02)J, N	75.6 (34.6)	−0.3 (1.5)
Starlings	14.9 (2.3)	4.5 (1.1)	0.70 (0.03)H, I	189.3 (27.7)Q	0.74 (0.03)L, M	104 (17.9)	2.4 (2.4)

[a] Data from last three days of trial (after acclimation).
[b] Data from first 3-day trial.
[c] Assimilable mass coefficient: 1 − (total consumption over 3 days divided by total defecation over 3 days).
[d] kJ consumed − kJ excreted.
[e] N consumed − N excreted.
[f] Weight changes on birds weighed with empty guts.

neutral detergent solubles, approximately half as much as the average proportion in the pulp of the three fruit species and one-third that of the banana mash (Table 1). The proportion (0.43) of cricket mass that was insoluble in neutral detergent (i.e. refractory to digestion) matched fairly closely the proportion (ca. 0.5) of cuticle in orthopterans (Bernays 1986). Despite this large proportion of refractory material in crickets relative to fruit pulp, fruit actually had the highest proportion of indigestible bulk because seeds constituted 44–52% dry weight of the fruits.

Ash content was generally lowest in fruits and was similar in crickets and in mash (Table 1). Caloric content was higher in crickets than in fruit pulp and mash, and it was slightly higher in fruit pulp than in mash (Table 1).

Daily dry matter consumption was highest for the mash diet and lowest for the cricket diet (Table 2). Birds on the fruit diet showed strong preferences among the three fruit species. These preferences differed among individuals and changed from day to day. The most notable change was for dogwood. On the first day of the trials, 10 of 15 birds preferred dogwood, but by the third day all were consuming more viburnum and grape than dogwood (Fig. 1).

Changes in digestive efficiency.—Mean gut retention times and AMCs from the mash trial demonstrated that one-day measurements of

AMC are appropriate for tracking changes in utilization efficiency. First, the time required to clear half a meal from the gut (i.e. median retention time) was generally <1 h (Karasov and Levey in press). This short retention time ensured that excreta collected on a given day corresponded to food ingested only on that day; cross-contamination between single day trials was negligible. Second, sufficient quantities of food were ingested and excreted to allow accurate and precise daily measurements. In particular, AMCs showed no daily variation (robins: F = 0.58, df = 2, 27, P = 0.57; starlings: F
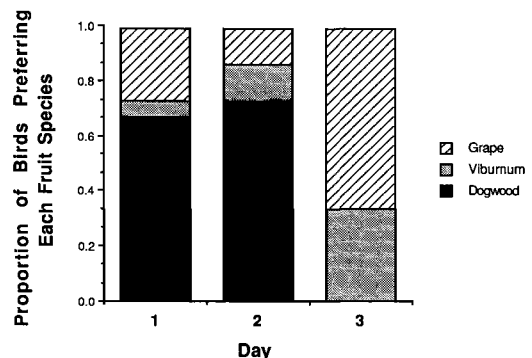

Fig. 1. Proportion of robins and starlings (n = 15) that showed a preference for each of the three fruit species over the first three days of the fruit trial. Preference was determined by dry mass consumed.

= 0.03, df = 2, 12, P = 0.97), and calculations of AMC based on one-day samples did not differ from those based on samples pooled over the entire trial (robins: paired t = 0.12, df = 9, P = 0.9; starlings: t = 0.01, df = 4, P = 1.0).

Average AMCs of both starlings and robins on the cricket diet increased 10–15% from the first three days of the trial to the last three days (paired t = 4.2, 3.2 [respectively]; df = 4, 9; P < 0.02) (Table 3). Average MECs for robins on the cricket diet showed an even greater (22%) increase over the same period (0.58 ± 0.03 vs. 0.71 ± 0.03; paired t = 8.4, df = 9, P < 0.001). Neither coefficient changed significantly from the first to the last three days of the fruit trial (paired t; P > 0.05). This trial, however, was discontinuous. During the first three days on fruits, average AMCs of starlings increased 8%, but the difference between day 1 and day 3 was not significant. Assimilable mass coefficients in robins on the fruit diet dropped significantly from day 1 to day 2 (0.61 ± 0.10 vs. 0.49 ± 0.13; paired t = 2.6, df = 9, P < 0.05) and on day 3 AMCs were approximately the same as on day 1 (day 3 = 0.62 ± 0.13).

Digestive efficiencies.—Comparing among diets, both robins and starlings displayed significant variation in assimilable mass coefficients (F = 44.4, df = 2, 18, P < 0.001; F = 7.2, df = 2, 8, P < 0.02, respectively; all ANOVAs are based on data calculated as in Table 2). For robins, AMCs were significantly higher on the mash diet than on either fruits or crickets (Multiple-range tests, P < 0.01; Table 2). Starlings displayed the same pattern (multiple-range tests, P < 0.01; Table 2). There was no difference (P > 0.05) in AMCs between crickets and fruits for either robins or starlings. Metabolizable energy coefficients also varied significantly among the three diets (robins: F = 51.5, df = 2, 18, P < 0.001; starlings: F = 12.0, df = 2, 8, P < 0.005). Robins had significantly higher MECs on the mash diet than on crickets and significantly higher on crickets than on fruits (multiple-range tests, P < 0.05; Table 2). MECs in starlings were significantly greater on both mash and crickets than on fruit (multiple-range tests, P < 0.01; Table 2) but there was no difference between the mash and cricket diets.

Robins had significantly higher MECs on the mash diet than did starlings (F = 4.9, df = 1, 13, P = 0.05; Table 2). On the cricket diet, robins had a lower AMC than starlings (F = 4.5, df = 1, 13, P = 0.05; Table 2), and on the fruit diet

TABLE 3. Changes in assimilable mass coefficients[a] (AMC) from the first to last three days of feeding trials ($\bar{x}$). Standard deviations are in parentheses. Sample sizes: robins, 10; starlings, 9.

| Diet/bird | AMC | | P[b] |
	First 3 days	Last 3 days	
Cricket			
Robins	0.52 (0.04)	0.57 (0.03)	<0.02
Starlings	0.53 (0.06)	0.61 (0.02)	<0.02
Fruit[c,d]			
Robins	0.57 (0.06)	0.59 (0.01)	NS
Starlings	0.56 (0.11)	0.63 (0.05)	NS

[a] 1 − (Total consumption over 3 days/Total defecation over 3 days).
[b] Paired t-tests.
[c] Trial interrupted.
[d] Seed mass not included in calculations.

there were no differences in either coefficient between the two species.

Energy balance.—Daily assimilation of energy was calculated by subtracting the total energy of excreta from that of consumed food. There were no detectable (P < 0.05) differences between robins and starlings in assimilated energy on any of the diets. However, both robins (F = 25.1, df = 2, 27) and starlings (F = 37.5, df = 2, 12) displayed significant differences in energy assimilation among the three diets (P < 0.001; Table 2). In both species, the amount of kJ/day assimilated was significantly greater on the mash ration than on crickets, and significantly greater on crickets than on fruit (multiple-range tests, P < 0.05).

Mass assimilation showed little daily variation on the cricket diet, despite the increase in digestive efficiency over the course of the trial. This suggests that the birds regulated energy intake by balancing consumption rates against assimilable mass coefficients. Indeed, daily consumption dropped as AMC increased (Fig. 2), so that total kJ assimilated stayed almost constant.

Robins lost 5.5 ± 2.1 g over the first three days of the fruit trial, and starlings lost 7.9 ± 5.0 g (Mann-Whitney U = 17, n = 15, P > 0.05; Table 2). Their weight loss was likely due to insufficient energy assimilation. The "average" 76-g bird (the mean weight of our robins and starlings) requires a minimum of ca. 97 kJ/day (Kendeigh 1970). Yet, robins had an average daily assimilation of only 80 kJ/day, and starlings 58 kJ/day (Table 2).

Nitrogen balance.—When feeding on fruit, total nitrogen of excreta was much higher than

A) Robins
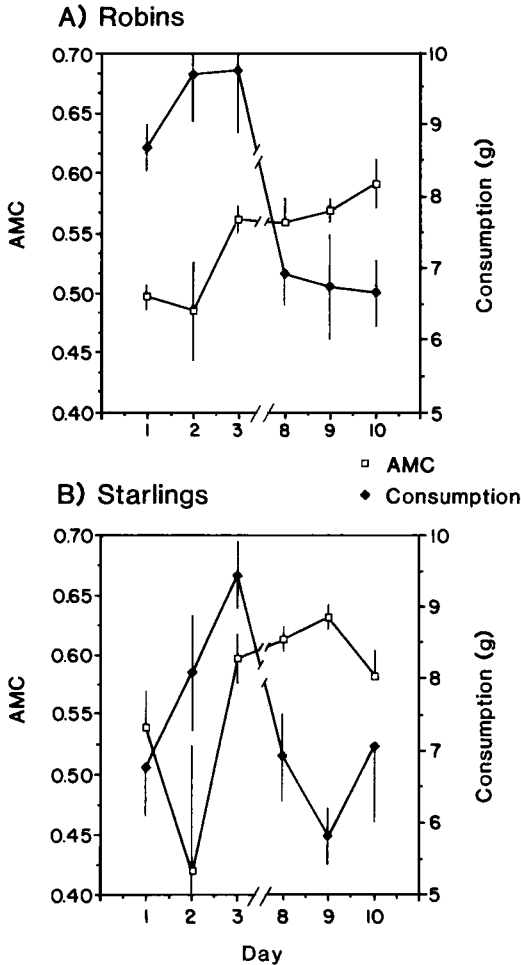

B) Starlings

□ AMC
♦ Consumption

Fig. 2. Daily assimilable mass coefficients (AMC) and consumption of crickets by robins and starlings on the first and last three days of a 10-day feeding trial.

that of ingesta; both robins and starlings were on a negative nitrogen budget (Table 2). Robins lost an average 15 mg/day of nitrogen and starlings lost 39 mg/day. In contrast, robins on the synthetic fruit-based mash (which was protein-fortified) gained an average 76 mg/day and starlings gained 104 mg/day (Table 2).

Feeding frequency.—Robins fed more frequently when eating fruits (median = 6.5 min between bouts) than when eating crickets (9.0 min) (Mann-Whitney $U = 456$, $n = 77$, $P < 0.002$). In addition, robin meal sizes were larger for fruits than for crickets (medians = 0.44 and 0.20 g/bout dry wt; Mann-Whitney $U = 440$, $n = 94$, $P < 0.001$). Starlings also showed a higher

feeding frequency on fruits than on insects (7.0 and 11.5 min/bout; Mann-Whitney $U = 74.5$, $n = 59$, $P < 0.001$).

DISCUSSION

Many temperate passerines change their diets from insects in the spring to fruits in the autumn (Martin et al. 1951, Berthold 1976, Wheelwright 1986). A shift in gut-processing accompanies the switch in diets (Table 2). The daily increases in efficiency after our robins and starlings switched from a fruit mash to a cricket ration demonstrate that these changes in gut-processing are not immediate. The lag time in response suggests a cost associated with diet switching: fewer than normal kJ/prey item are assimilated. Because we switched birds to fruit or insect diets from a nutritionally intermediate diet, this cost of reduced utilization efficiency may be greater in fruit-eating birds that switch directly to an insect diet. In short, the increase in metabolizable energy coefficient over time on the cricket diet suggests that birds cannot simultaneously process fruits and insects at peak efficiency; they require a period of acclimation to an insect diet.

The mechanism underlying the observed change in metabolizable energy coefficient remains unclear. Digestive efficiencies are determined by complex interactions of numerous variables (Sibly 1981, Robbins 1983, Demment and Van Soest 1985, Penry and Jumars 1987, Karasov in press). First, a change in gut morphology could have resulted in higher MECs (Tedman and Hall 1985, Jordano 1987). We found no evidence of change in gut length or surface area (Levey and Karasov unpubl. data). Second, the coefficient could have been affected by induced enzyme activity (Hulan and Bird 1972) or changes in microvilli structure (Okon 1977, Keegan and Mödinger 1979), neither of which we examined. Third, rates of amino acid and sugar absorption at the intestinal brush-border may depend upon diet and influence digestive efficiency (Karasov and Diamond 1987). However, we found no differences in in vitro glucose and proline uptake rates between robins on fruit and robins on insect diets (Levey and Karasov unpubl. data). Fourth, differences in passage rates of ingesta may have affected MECs (Demment and Van Soest 1985, Penry and Jumars 1987). Frugivores tend to have

shorter gut retention times than insectivores (Herrera 1984, Tedman and Hall 1985, Jordano 1987). We found that robins on the fruit diet had significantly shorter gut retention times than they did on the cricket diet (Levey and Karasov unpubl. data). Hence, the low MECs on the first days of the cricket trial may have been due to the birds processing crickets at the same rapid rate they had been processing the more easily digested fruit-based mash.

The reason digestive efficiency increased with time on the cricket diet but not on the fruit diet is unclear. Fruit trials lasted only three days, which may have been insufficient time for some digestive system responses. The time required for acclimation depends upon the type of response. Changes in gut morphology may take weeks (Miller 1975, Savory and Gentle 1976, Al-Joborae 1980) whereas activation of nutrient transport sites can occur within 24 h (Karasov and Diamond 1983). In general, however, acclimation is a positive function of gut passage time (Robbins 1983). Fruit, which passes quickly, should elicit relatively rapid responses in gut morphology and physiology.

We believe our three-day trials were sufficient time to detect changes in efficiency in response to the new diet of fruits. Yet, assimilable mass coefficients from the first day of trials did not differ from the third day. Assuming that enzymes and transport mechanisms are induced in 24–48 h, the lack of response suggests that induction of new enzymes or transport mechanisms had already occurred or lacked the proper stimulus, and that necessary morphological changes in gut structure were not complete, or both.

Alternatively, MECs may not have changed during the course of the fruit trials because the pretrial diet (banana mash) was fruit-based. Birds may have already acclimated to a fruit diet before the trials started. Furthermore, if there are endogenous seasonal adaptations to a fruit diet (Wheelwright 1988), our birds may have been preconditioned to a fruit diet when we captured them in the fall.

Diet and utilization efficiencies. —Because robins are generally more frugivorous than starlings, they might be expected to have higher utilization efficiencies than starlings on a fruit diet. Likewise, starlings may have adaptations that allow higher efficiencies than robins on an insect diet. Indeed, starlings had higher AMCs on crickets than did robins (Table 2). Utilization efficiencies on wild fruit are difficult to compare because they are confounded by the birds' negative energy balances (see below) and high variance due to individual birds eating different combinations of fruit species. Thus, we use the fruit-based synthetic ration as a basis for comparison. As expected, robins on the mash ration had higher MECs than did starlings (Table 2).

In general, differences in utilization efficiency between robins and starlings were small (0.03–0.04) and, although some are statistically significant, their ecological significance remains obscure. Most of the variation in digestive efficiencies was found among trials of the three diets rather than between the two bird species (Karasov in press).

Fruit pulp had much lower metabolizable energy coefficients than either crickets or mash (average MECs = 0.55 vs. 0.72 and 0.76, respectively). Given that nutrients in fruit are already in solution and easily absorbed (Foster 1978, Moermond and Denslow 1985, Worthington 1983, Baker and Baker 1986, Herbst 1986), the low utilization efficiencies of fruit pulp are puzzling. We do not believe that our metabolizable energy coefficient values for fruits are artifacts of experimental design or choice of species; they agree well with previously reported values (average = 0.63 ± 0.17, $n = 30$; data from Sorensen 1984, Worthington 1983, Studier et al. 1988). Neither do the fruit metabolizable energy coefficients appear low because the insect coefficients are inflated. The MECs for insects also agree with reported values (average = 0.69 ± 0.12, $n = 9$; data from Gibb 1957, Robel et al. 1979, Krebs and Avery 1984, Bryant and Bryant 1988).

That metabolizable energy coefficients of birds on the fruit diet are surprisingly low is clearly demonstrated by comparing them with a predicted coefficient based on nutritional characteristics of the fruits and on behavioral and physiological characteristics of the birds. We used a model proposed and tested by Karasov (in press) with data presented in our study (Tables 1 and 2) and in Karasov (in press). The model assumes that all nonrefractory components of a meal are digested and absorbed. Based on this model, both robins and starlings should display metabolizable energy coefficients on fruit of ca. 0.80 (because only ca. 20% of the energy is refractory)—well above the observed value of 0.55. In contrast, the model predicts MECs on crickets of 0.69 (assuming 50% diges-

tion of cuticle; Jeuniaux and Cornelius 1978), which agrees well with our observed values of 0.71 and 0.73.

A possible explanation for the low metabolizable energy coefficient of fruit pulp may be that our measurements underestimated the actual coefficient. Two biases probably contributed to an underestimate. First, our calculations were based on fecal samples that included endogenous sources of energy such as sloughed cells and secretions of the alimentary tract. Because we could not separate these energy sources from undigested pulp, they were treated as undigested. We corrected for these endogenous losses using the correction factor suggested by Guillaume and Summers (1970; see also Karasov in press). The resulting coefficients were only 0.03 higher than our original values. A second potential source of error in our measurement is the below-maintenance level of the birds' consumption of fruits. Their catabolism of body protein resulted in elevated excretion of energy-containing nitrogenous products (e.g. uric acid and urea), which we could not separate from undigested fruit pulp. We corrected MECs to nitrogen balance by subtracting 0.037 kJ/(mg nitrogen deficit) from fecal energy content (Sibbald 1981). This increased coefficients less than 0.01. We conclude that, despite the above biases in our original estimates, metabolizable energy coefficients of robins and starlings on a fruit diet are still surprisingly low. In fact, coefficients of most fruit-eating birds appear similarly low (Worthington 1983, Sorensen 1984, Johnson et al. 1985, Studier et al. 1988, Karasov in press).

We suggest that MECs of fruit-eating birds are low because of short food retention times. Digestive efficiency represents a trade-off between thoroughness of nutrient extraction and food passage rates (Milton 1981, Van Soest 1981, Penry and Jumars 1987, Karasov in press). Both robins and starlings defecated solid and liquid markers in fruit faster than they did the same markers in crickets (Levey and Karasov unpubl. data). These fast passage rates of fruits may allow a high consumption rate, but they probably compromise the intestine's ability to absorb nutrients.

Nitrogen and energy balances.—Neither robins nor starlings met their estimated daily energy requirements on the fruit diet, despite *ad libitum* supplies of three fruit species. On the cricket diet, however, they clearly regulated energy as-

similation by adjusting consumption to compensate for changing metabolizable energy. Likewise, birds on many diets show tight control over energy intake (Hill and Dansky 1954, Kendeigh et al. 1969, Fisher 1972). Many temperate birds on a fruit diet apparently lack this ability (Hazelton et al. 1984, Johnson et al. 1985, Borowicz 1988; but see Sorensen 1984).

In addition to the problem of insufficient energy assimilation, birds on the fruit diet were in nitrogen imbalance. This is not surprising because fruits are one of the poorest sources of dietary nitrogen (Mattson 1980, Milton and Dintzis 1981, Herrera 1987). On the other hand, some species can maintain a positive nitrogen balance when consuming fruits (Walsberg 1975, Worthington 1983, Studier et al. 1988). These birds are all highly frugivorous year-round. They may have unusually low nitrogen requirements (e.g. Smith and Green 1987) or high nitrogen extraction efficiencies.

We suggest that the nitrogen imbalance in our birds was a result of insufficient energy assimilation. Because the birds were out of energy balance, they catabolized their own tissues, which caused elevated excretion of nitrogen. In support of this explanation, note that all birds lost weight on the fruit diet and that nitrogen excretion rates (74 mg/day in robins, 77 mg/day in starlings) were well above the predicted rate of endogenous nitrogen loss (19 mg/day; Robbins 1983) for birds on nitrogen-limited rations. Also, Robbins (1981) predicted nitrogen equilibrium (i.e. the point at which intake and excretion are equal) at an intake of 0.43 g $N \cdot kg^{-0.75} \cdot day^{-1}$, or ca. 62 mg/day for a 76-g bird. Both our species had nitrogen intakes greater than this (69 mg/day in robins, 64 mg/day in starlings), yet they were still out of nitrogen balance. In short, our birds apparently consumed enough nitrogen to meet daily minimum requirements but lost excessive nitrogen due to their catabolism of body protein.

We offer two explanations as to why the birds did not increase their consumption of fruits to meet daily energy requirements. First, they may have been bulk-limited to a consumption rate that was too low to meet nutritional demands. Seeds accounted for an average of 50% of the fruits' mass (Table 1). Given this large amount of bulk and the relatively low nutrient content of fruit pulp, the birds must consume many fruits to meet nutritional requirements. For example, a robin would have to consume ca. 202

fruits to meet a minimum daily energy expenditure of 100 kJ (calculation assumes that MEC = 0.55, and that equal proportions of dogwood, viburnum, and grape are eaten). The observed consumption rate for robins was 12 fruits per hour, well below the rate needed to reach 202 fruits per day. Other authors have also suggested that fruit-eating birds may be consumption-rate limited (Sorensen 1984, Levey 1987, Borowicz 1988, but see Foster 1987). Furthermore, numerous reports of long periods of inactivity after feeding suggest that despite relatively rapid passage rates, gut-processing of fruits by small birds may nonetheless limit their consumption of more fruits (Salomonson and Balda 1977, Tye 1982, Pratt and Stiles 1983). Because so many fruits must be processed to meet nutritional demands, a processing rate that is quick in comparison with other foodstuffs may still not be fast enough to balance energy or nitrogen budgets.

Second, birds may not have eaten enough fruits to fulfill their nutritional requirements because of fruit toxins. Alkaloids, saponins, steroids, terpenoids, nonprotein amino acids, and a host of other toxins are common in wild fruits (even when fully ripe) and may affect fruit consumption (Herrera 1982, Sorensen 1983, Borowicz 1988; but see Foster 1977). Because each fruit species has a different suite of secondary compounds, birds may eat many different species over a short time period and avoid accumulation of any single compound to a toxic level. Indeed, both wild birds (Stiles and White 1986, Loiselle 1987, Jordano 1988) and captive birds thoroughly mixed the composition of fruits in their daily diets. In fact, all robins and starlings stopped feeding heavily on dogwood by the third day of the trial, even though it was rich in both energy and protein. In light of the birds' need for energy and protein, plus the overwhelming preference for dogwood on the first day of the trial, the decrease in dogwood consumption may be best explained by the accumulation and toxic effects of its secondary compounds.

Frugivory and digestive trade-offs.—Rapid gut processing is probably a major adaptation to frugivory because fruits are typically low in nutrient content but high in bulk, and birds have generally small gut volumes and high energetic demands (Sibly 1981, Moermond and Denslow 1985, Penry and Jumars 1987, Karasov and Levey in press). Indeed, frugivores commonly have short gut retention times, especially for seeds (Milton 1981, Herrera 1984, Sorensen 1984, Worthington 1983, Levey 1986, Jordano 1987). We suggest that a trade-off associated with rapid gut processing is a reduced utilization efficiency. Despite low metabolizable energy coefficients, net energy gain may be relatively high because fast passage rates allow high ingestion rates. High ingestion rates, in turn, are possible because fruit is easily found (due to colorful displays) and often abundant (Snow 1971, Willson and Thompson 1982).

Most fruit-eaters are probably constrained in their degree of frugivory by the consequences of how they process food. Because fruit supplies are highly seasonal (Thompson and Willson 1979; Foster 1982a, b; Terborgh 1986; Loiselle 1987; Levey and Wright in press), fruit-eaters must be able to vary their dependency on fruit to match patterns of fruit abundance. Their dietary switches to and from fruit (and the resulting changes in gut processing) are probably not only endogenous (Wheelwright 1988) but also induced.

We suggest that the inability of almost all temperate fruit-eating birds to switch to a diet of only fruits reflects constraints associated with how they process other types of food during periods of low fruit abundance. In particular, facultative frugivores must retain the ability to process both fruits and insects. It remains unclear, however, what digestive modifications limit a bird's ability to switch diets completely (Herrera 1984). At a very basic level, the extremely simple gut morphology that appears typical of "specialist" frugivores (*sensu* McKey 1975; Walsberg 1975, Worthington 1983, Wheelwright 1983, Moermond and Denslow 1985) may compromise their ability to assimilate insects. Likewise, a digestive system that retains the potential to process insects effectively is unlikely to meet the requirements imposed by a pure fruit diet (Herrera 1984). To understand the factors that limit a bird's ability to switch between fruits and insects, we first need to determine which requirements of a fruit diet (e.g. rapid passage rates, efficient handling of seeds, detoxification of fruit secondary compounds) are most important, how they influence digestive processing of other food items, and how quickly or completely they can be modified.

Changes in gut morphology and digestive processing take place when a bird switches from insects to fruits (Al-Dabbagh et al. 1987, this

study), but these changes are not of sufficient magnitude to enable most birds to shift to a diet of only fruit (Berthold 1976, Herrera 1984, Jordano 1988). It appears that the digestive requirements for maintaining long-term nutrient and energy balance on a diet of solely fruits are so restrictive that few species (if any) can facultatively modify their method of digestive processing to meet these requirements fully.

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