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Gut Passage of Insects by European Starlings and Comparison with Other Species

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Digestive processes influence a bird's net rate of energy gain and its utilization efficiency of food (Karasov 1990, Place and Stiles 1992). These factors, in turn, can influence feeding behavior and possibly constrain rates of growth and reproduction (Karasov et al. 1986, Tiebout 1989, Levey and Grajal 1991).

Retention time is a key feature of digestive processing, rarely studied in nondomesticated birds (Warner 1981). When reported, the data are often difficult to compare or interpret in an ecological context because animals were held under stressful conditions, fasted for an unnaturally long period of time, or fed a large dose of nonnutritive marker (e.g. barium suspensions). Even disregarding such problems, retention-time data are especially scarce for passerines eating insects; we know of only three published reports (Stevenson 1933, Dykstra and Karasov 1992, Levey and Karasov 1992).

Here we report retention times of crickets (*Acheta domestica*) in European Starlings (*Sturnus vulgaris*) feeding continuously under unstressful conditions. With these data and those from published studies we then address a fundamental question about gut processing: To what extent is retention time determined by diet, as opposed to vice versa? More specifically, is there an "ideal" retention time for an insectivore or frugivore and, if so, how fixed is it within a species? This issue is ecologically relevant since, if food processing is largely invariable, a bird may be unable to switch diets, or may be less effective using an alternative diet than a more specialized bird. The former result constrains niche width directly, and the latter may do so indirectly via competition.

We compare: (1) retention times in starlings on fruit and insect diets to determine if they can modulate retention time; and (2) mass-normalized retention

times in four passerine species on fruit and on insect diets. Our expectations were that retention time would be longer in starlings when on the insect diet than on the fruit diet, and that the more insectivorous species would have longer retention times than the more frugivorous species. Both predictions relate to the fact that insects have two to three times the digestible energy per unit wet mass as fruits (Levey and Karasov 1989). In poultry, and mammals generally, stomach emptying rate, gut motility and, hence, mouth-to-anus retention time are inversely related to luminal solute concentration as mediated by hormonal and neural negative feedback mechanisms (Duke 1989). This proximal mechanism can provide the basis for the second prediction as well, but there is a further ultimate explanation. An optimality model of digestion based on Sibly's model (1981), which maximizes the net rate of energy gain, predicts longer optimal retention time for animals eating energy-rich foodstuffs (Martínez del Rio and Karasov 1990).

Methods.—Five starlings were captured near Madison, Wisconsin in August 1986. They were held in separate cages (ca. 0.6 m³) under constant day length (12 h) and temperature (23° ± SD of 1°C) and fed a synthetic fruit diet of bananas and soy protein isolate (Denslow et al. 1987). Food and water were available *ad libitum*. After a short acclimation period, all individuals regained and maintained their body mass at time of capture (75 ± 5 g).

Retention times were measured by injecting crickets with 5–10 μl (5–10 μCi) of ^{3}H polyethylene glycol (PEG; mol. wt. = 4,000), a water-soluble marker. There is evidence that some PEG is absorbed in some birds (Karasov and Dykstra 1991), but its subsequent urinary excretion into the expelled cloacal excreta is rapid and does not seem to greatly influence measured retention times (D. Levey pers. obs.; based on comparison of PEG and ferrocyanide, which is not absorbed).

Birds were kept on a cricket diet for 10 days prior to the start of retention trials (for details, see Levey and Karasov 1989). On the morning of a trial, birds were fasted for no longer than 30 min and offered two PEG-injected crickets. Usually, they ingested at least one of them. If not, they were force fed. We then provided unlabeled crickets *ad libitum*.

Birds were watched from behind one-way mirrors. As they defecated onto plastic-backed paper toweling, we recorded the location and time of each defecation. After approximately 1 h, we replaced the toweling and continued as before for another hour. After that, we collected and pooled all defecations at the end of hourly periods up to 6 h.

Defecations were sprayed lightly with distilled water, scraped from the plastic backing, and placed into separate vials. Each sample was covered with water, refrigerated, and shaken periodically for at least 12 h. A pilot study demonstrated that PEG equilibrated in the water within 12 h. Aliquots (1.5 ml) of the samples were then mixed with Aquasol (New England Nuclear) and counted for decays per minute (dpms).

We calculated several retention-time parameters. Transit time was defined as the time at which excreta PEG dpms first rose dramatically (usually by at least two orders of magnitude). Mean retention time was calculated by multiplying the proportion of total ingested PEG in a defecation by the time of the defecation and summing these products across all defecations (Warner 1981). The defecation that contained the highest dpms of PEG defined the mode of each trial. The 50% clearance time was the time of the defecation at which cumulative PEG excretion exceeded 50%. When excreta from a time interval were pooled, we used the time at the end of the interval in calculations.

For comparison, we collected data from Levey and Karasov (1989, 1992), Levey and Grajal (1991), and Dykstra and Karasov (1992). These studies used experimental protocols almost identical to our study. However, we had to reanalyze some of the data to standardize slight differences in methodology or to calculate retention time parameters that were not included in the publications. All parameters reported here follow the above definitions. Excreta collections were made for 2 h in some studies and 20 h in others. Because mean retention times and 50% clearance times are influenced by long tails on curves of excretion versus time, we truncated curves with long tails at either 2 or 3 h, depending on when at least 90% of the PEG had been excreted. To control for mass-dependent differences in retention times, we divided all values by mass$^{0.25}$ (Karasov 1990).

We used isotonic regression to test the hypothesis that more frugivorous species have shorter gut retention times than more insectivorous species. Isotonic regression is a type of ANOVA designed to test ordered expectations (Gaines and Rice 1990). Our expected ranking of retention times was Cedar Waxwing (*Bombycilla cedrorum*) < American Robin (*Turdus migratorius*) < European Starling < House Wren (*Troglodytes aedon*). We used paired *t*-tests to determine whether retention time for fruit was shorter than for crickets in European Starlings.

Results and Discussion.—Starlings defecated practically all PEG in labeled crickets between 10 min and 2 h postingestion (Fig. 1). Transit time was 34 ± 16 min, mean retention time was 58 ± 9 min, the mode of PEG excretion was 54 ± 10 min, and the 50% clearance time was 54 ± 10 min (Table 1, where values are normalized to body mass). These values agree closely to those reported for starlings fed PEG-injected fruits (Karasov and Levey 1990). The lack of statistical difference between gut retention times on two different diets (Table 1) suggests that starlings are unable to modulate retention times.

This result contrasts with those from an identical study on American Robins in which retention-time

TABLE 1. Retention-time parameters ($\pm$SD) of passerine species fed fruit or insect diets. Data normalized by dividing by mass$^{0.25}$. Average body mass given below species names. Data on European Starlings eating crickets from this study; other data taken from Levey and Karasov (1989, 1992), Levey and Grajal (1991), and Dykstra and Karasov (1992). Note that robins are able to modulate retention times, whereas starlings are not.

	Retention times $(\text{min}/[\text{g}]^{0.25})$				
	Most frugivorous $\leftrightarrow$ Least frugivorous				
	Cedar Waxwings (34 g)	American Robin[a] (78 g)	European Starling[a] (75 g)	House Wren (11 g)	P[b]
	Insects				
n	—	10	5	9	
Transit time	—	19 ± 3	12 ± 5	8 ± 2	ns
Mean retention	—	22 ± 2	20 ± 3	33 ± 11	0.0007
Mode	—	22 ± 5	18 ± 5	29 ± 17	ns
50%	—	22 ± 4	18 ± 3	35 ± 16	0.003
	Fruit				
n	8	9	5	—	
Transit time	5 ± 0	11 ± 5	7 ± 3	—	0.02
Mean retention	13 ± 2	16 ± 2	18 ± 1	—	0.0001
Mode	10 ± 2	11 ± 3	16 ± 2	—	0.0003
50%	11 ± 2	12 ± 2	16 ± 2	—	0.0003

[a] In paired *t*-tests between matching passage-time parameters (e.g. transit time) of the two diets, $P < 0.001$ for all robin comparisons and $P > 0.2$ for all starling comparisons.
[b] Based on isotonic regression. Model assumes more highly frugivorous species have faster passage of digesta.

parameters decreased an average of 40% when birds were switched from an insect to fruit diet (Levey and Karasov 1992). Given that rapid gut passage apparently is an important adaptation to frugivory (Herrera 1984, Karasov and Levey 1990) and that it was the only feature of digestive processing that changed when robins switched diets, we were surprised not to find a similar change in starlings. Their inability to mod-

Fig. 1. Cumulative percentage of PEG excreted by five European Starlings fed cricket meals as function of time postingestion. Bars are standard errors.

ulate retention time may explain why they are less frugivorous than robins (Martin et al. 1951).

In fruit-retention-time trials, more frugivorous species clearly had shorter retention times than more insectivorous species ($P < 0.05$ for all variables; Table 1; no data for wrens). The ranking—Cedar Waxwings < American Robins < European Starlings—was opposite to the ranking of *in vitro* glucose uptake among these species. Waxwings have a higher uptake than robins, which have a higher uptake than starlings (Karasov and Levey 1990). Presumably, higher uptake rates help compensate for short retention times although, despite the higher rates, frugivorous species still have relatively low digestive efficiencies (Karasov and Levey 1990).

In insect-retention-time trials, the pattern was less clear. Robins, starlings and wrens did not differ significantly in their transit times or mode of PEG excretion ($P > 0.05$; Table 1). However, as predicted, mean retention times and 50% clearance times were less for the more frugivorous species ($P < 0.003$; Table 1; no data for waxwings).

In general, we found that the degree of frugivory and retention time are negatively associated. Within species, the more highly frugivorous robin was able to modulate retention time and the less frugivorous starling was not. Other digestive processes also are likely to differ within and among species (Karasov and Diamond 1988).

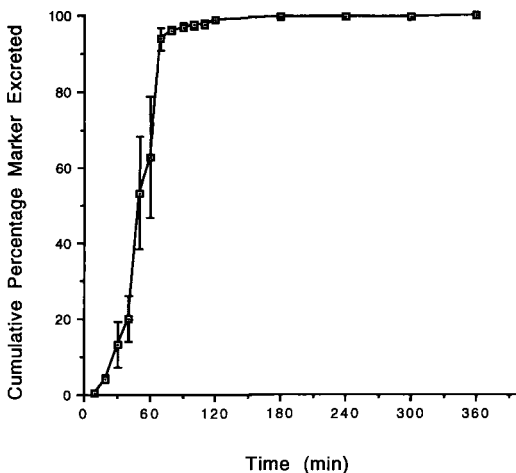Contrary to our expectation, European Starlings did not increase retention time when switched from a

nutritionally dilute food (fruits) to a nutritionally rich one (insects). Another passerine, the European Blackbird (*Turdus merula*), also appears to respond differently than expected. In this species, Sorensen (1984) found that passage time of pulp from fruit with the highest fat content was faster (not slower) than passage time of pulp from fruit with the lowest fat content.

The pattern that emerges from Table 1 suggests that, although some species can modulate retention time, a fast passage rate is to some extent an inherent feature of a frugivore's gut processing, regardless of what type of meal is being processed. This was essentially the conclusion of Herrera (1984), who measured transit times of frugivorous and insectivorous species at different times of the year when they majored on either fruit or insects. We stress, however, that this conclusion must remain tentative due to the small sample of passerine species ($n = 2$) tested experimentally for their ability to modulate.

The inability to modulate retention time may have important ecological consequences. For example, starlings and other frugivores unable to increase retention time on more nutrient-rich foods might extract less energy from insect foods than insectivores. Conversely, insectivores with fixed long retention times might be unable to process bulky fruits fast enough to stay in energy balance when feeding on them. Thus, retention time may have an important influence on food choice and diet breadth.

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