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Digestive Adjustments in Cedar Waxwings to High Feeding Rate

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ABSTRACT Birds may dramatically increase their food intake during migratory periods or during winter. We tested the hypotheses that when birds are hyperphagic, (a) their digesta retention time and extraction efficiency will not change compared with that of birds feeding at reduced rates, (b) their total capacity for breakdown and absorption of nutrients will increase, and (c) the mechanism responsible for the increase in total capacity will be an increase in amount of intestine rather than an increase in intestinal tissue-specific enzyme activity or nutrient transporter activity. We measured gut anatomy, retention time of digesta, enzyme hydrolysis rates, nutrient absorption rates, and digestive efficiency in individual cedar waxwings (*Bombycilla cedrorum*) acclimated to –20°C or +21°C. Compared with cedar waxwings held at +21°C, waxwings acclimated to –20°C more than tripled their daily food intake. Mass of digestive organs increased by 22–53%, but rates of enzyme activity and nutrient uptake per unit of small intestine did not change significantly. Retention time of digesta declined slightly, and there was a small decrease in digestive efficiency. As predicted, the main adjustment to increased energy requirements and food intake was an increase in gut length, mass, and volume which largely compensated for increased digesta flow at high intake rates. However, we detected a small reduction in retention time and digestive efficiency in waxwings with high intakes which suggests that these waxwings may be unable to further increase their gut size (i.e., that the increase in gut size was maximal). If adjustments involving gut size require weeks of acclimation time, migration patterns and the pace of migration in birds could be influenced by time required for preparation of the gut. *J. Exp. Zool. 283:394–407, 1999.*

Birds may dramatically increase their food intake to satisfy the high energy requirements of migration (Blem, '76, '90; Bairlein and Simons, '95; Berthold, '96) and to offset the higher thermoregulatory costs during exposure to cold temperatures (Dawson et al., '83; Karasov, '96). The energetic gains realized by a bird when it eats more depend on interactions between food intake rates and digestive efficiency. For example, if the absorptive surface of the gut or its capacity for absorption does not change when a bird eats more, then the increased flow of digesta may cause digestive efficiency to decline and thereby directly discount the potential energetic gains provided by hyperphagia.

The main digestive adjustment to increased food intake that has been described in birds is increased surface area and volume of the gut (Savory and Gentle, '76a,b; Savory, '86; Dykstra and Karasov, '92; Piersma et al., '93; Karasov, '96; Piersma and Lindstrom, '97). Few studies have addressed whether such changes in the gut compensate for the potentially negative effects of increased food intake on digestive efficiency (e.g., Savory, '86; Dykstra and Karasov, '92). Even fewer studies have examined the occurrence or significance of other possible digestive adjustments to increased food intake, such as increased activity of enzymes or nutrient absorptive mechanisms (Jacobs et al., '75; Dykstra and Karasov, '92). No study has simultaneously measured adjustments

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in gut anatomy, retention time of digesta, enzyme hydrolysis rates, nutrient absorption rates, and digestive efficiency in response to increased food intake (see Karasov, '96; Piersma and Lindstrom, '97 for recent reviews). Only by using such an integrative approach can we begin to understand important interactions between digestive adjustments or plasticity and their ecological consequences.

We use a simple integrative model of digestion (Karasov, '96) to generate some predictions about how digestive features might respond to increased food quantity:

$$\text{digestive efficiency} \propto \frac{\text{(digesta retention time)} * \text{(reaction rates)}}{\text{(volume of digesta)} * \text{(nutrient concentration)}}$$

This model suggests that digestive efficiency is positively influenced by longer retention time of digesta in the gut and higher reaction rates (including digestive enzyme hydrolysis rates and nutrient absorption rates). Alternatively, the model suggests that digestive efficiency is negatively influenced by increased volume of digesta (as would occur with increased food intake) or increased concentration of nutrient per unit volume of digesta (which is related to food quality). An implicit assumption in this model is that there is little spare capacity in these digestive features. For example, if diet quality increases so that concentration of nutrient increases, the model assumes that digestive efficiency will decline unless compensatory changes occur in digesta retention or reaction rates. Perhaps most important, the model shows explicitly how these digestive features may interact and influence digestive efficiency and thus provides a conceptual framework from which to evaluate digestive system function in an integrated fashion.

We can use this model to generate predictions about how the gut might respond when an animal increases its food intake. Without any compensatory changes in other features, when food intake increases then digesta flow increases, and retention time decreases [i.e., retention time $\propto$ volume of digesta (ml)/digesta flow (ml/min) (Karasov, '96)]. Consequently, increased food intake will result in decreased digestive efficiency if there is no modulation of digestive features. However, the increased flow of digesta might be compensated for in a number of ways that would maintain digestive efficiency: for example, if the gastrointestinal tract lengthens, then the retention time of ingested food particles may not change and digestive efficiency could remain constant. Alternatively, if the gut doesn't enlarge and retention time of digesta shortens, if enzyme hydrolysis rates and absorption rates increase then digestive efficiency could remain constant.

We predicted that cedar waxwings would adjust to high food intakes mainly by enlarging the gut rather than by increased tissue-specific reaction rates. Specifically, we tested the hypotheses that when waxwings are hyperphagic (a) their digesta retention time and extraction efficiency will not change compared with that of birds feeding at reduced rates, (b) their total capacity for breakdown and absorption of nutrients will increase, and (c) the mechanism responsible for both (a) and (b) will be an increase in amount of intestine rather than an increase in intestinal tissue-specific enzyme activity or nutrient transport activity. We simultaneously measured gut anatomy, retention time of digesta, enzyme hydrolysis and nutrient absorption rates, and digestive efficiency in cedar waxwings acclimated to –20°C or +21°C. Cold-acclimation is an ecologically relevant way to increase food intake in cedar waxwings because the waxwing is a common latitudinal migrant that spends the winter in northern regions of the United States (Bent, '50; American Ornithologists' Union, '83).

MATERIAL AND METHODS

Capture and maintenance of birds

Six of the 20 cedar waxwings used in this study were captured in Gainesville, Florida (29° 41′ N, 82° 16′ W) and sent to us on August 8, 1994. We captured the other 14 cedar waxwings on September 30 – October 1, 1994, in Madison, Wisconsin (43° 8′ N, 89° 20′ W) using mistnets. Birds were immediately weighed and banded and then housed individually in stainless-steel cages (60 × 45 × 33 cm) under an initially constant light cycle (12L: 12D, lights on at 700 hours) and temperature (21°C). All birds were acclimated to a banana-mash diet (Denslow et al., '87) that has been used successfully for maintaining cedar waxwings and other frugivorous passerines in good health in the laboratory (Levey and Karasov, '89; Martinez del Rio et al., '89; Karasov and Levey, '90).

Temperature and diet acclimation prior to the experiment

On October 10 we randomly assigned 11 birds to a cold-acclimated group and 9 birds to a control group. Birds captured in Florida and Wisconsin were evenly distributed between treatment

and control groups. All 20 birds continued on the same daily light schedule (12L:12D). For control birds, the ambient temperature was kept constant at 21°C. For cold-acclimated birds, the ambient temperature was gradually decreased over 30 d using the following schedule: from 21°C to 1°C over 10 d (–2°C d^{-1}), held constant at 1°C for 10 d, then from 1°C to –20°C over 10 d (–2°C d^{-1}).

On November 18, we acclimated all birds to a new semisynthetic diet (see McWilliams and Karasov, '98) that simulated a fruit diet in nutrient content (65% carbohydrate:13% protein:6% fat by dry mass). Cedar waxwings select fruits that contain relatively low lipid and high carbohydrate (Witmer, '96) as in the diet we formulated. The use of such a semisynthetic diet makes the composition of the diet less ambiguous than diets compounded from raw foodstuffs (see also Murphy and King, '82).

Feeding schedules and experimental design

Birds were always presented with fresh food and water each day at 0930–1030 hours. Each day birds were provided with excess food ensuring ad libitum feeding conditions. For birds at –20°C, a small hotplate was placed in each cage to keep the food soft and palatable. Food was placed in a glass petri dish set in a clay saucer that evenly distributed the heat from the hotplate. A wooden perch attached to each hotplate enabled birds to eat while avoiding direct contact with the hotplate or clay saucer. Once each day we supplied birds in the cold with hot tap water in a plastic petri dish. This water was used by the birds mainly for bathing. Water content of the food (75%) ensured adequate consumption of water in their diet.

On the pretest day, food was removed at 1730 hours to ensure that birds would start the test day with a small energy deficit. On the test day, food was provided ad libitum beginning at 0700 hr. Then, food intake, retention time, and extraction efficiency of 10 cold-acclimated and 8 room temperature-acclimated birds were measured during a 4–5 hr test period that began at 1330 hr when the bird ingested about 0.5 g of diet containing radiolabeled nutrient and marker (see below). Food intake on a dry matter basis was estimated by drying subsamples of food collected at the start and end of the test period. We measured food intake, retention time, and extraction efficiency in only 10 of 11 treatment birds and 8 of 9 control birds because we always tested two birds simultaneously in side-by-side special observation cages (see description later in this article), which required an even number of test birds. Cedar waxwings are quite social birds and appear to behave normally as long as they have visual contact with a conspecific.

Tests on all 18 birds were conducted between December 9, 1994, and January 5, 1995. All birds were tested twice: one trial was used to measure extraction efficiency of glucose, and the other trial was used to measure retention time of digesta. Test days were always separated by at least 1 and usually 2–3 d.

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 ['95] for full description). Most importantly, the cages were exactly the same as their regular cages except that the front door had one-way glass for observations and we placed a roll of plastic-coated paper (VWR Scientific Products, cat. no. 54110-527, S. Plainfield, NJ) 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 1 d before the test day. This one-day minimum acclimation period seemed adequate because food intake was similar on pretest and test days.

Retention time of digesta was measured using the inert marker [^{14}C] ferrocyanide (FeCN). Extraction efficiency of glucose was measured using the inert marker method (Karasov et al., '86). Separate trials were necessary for measuring retention time and extraction efficiency of glucose because in a companion study (McWilliams and Karasov, '98) we found that estimates of extraction efficiency based on tritiated nutrient underestimated actual extraction efficiency. For estimating extraction efficiency, we used [^{14}C(U) (uniformly labeled)] D-glucose (American Radiolabel Chemicals Inc., St. Louis, MO) and the inert marker polyethylene glycol ([1,2-3H] PEG (MW 4000), DuPont NEN Research Products, Wilmington, DE).

Radioisotopes were mixed into warm, unhardened food mash at a concentration of approximately 18.5 kBq of ^{14}C D-glucose and 74 kBq of ^{3}H PEG per gram of food mash for extraction efficiency trials and 18.5 kBq of ^{14}C FeCN per gram of food mash for retention time trials (for specific methods see McWilliams and Karasov, '98). The initially soupy mixture was continuously stirred as it cooled and hardened to ensure uniform labeling of food. When only extraction efficiency was measured in a trial,