Reprinted from:
Physiological and Ecological Adaptations to Feeding in Vertebrates
J. Matthias Starck and Tobias Wang (Editors)
Science Publishers 2005, Enfield, New Hampshire
ISBN 1-57808-246-3

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# Digestive Constraints in Mammalian and Avian Ecology

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**SYNOPSIS**

The difference between the rate of nutrient intake for maintenance and the maximum rate of digestion, termed spare digestive capacity, potentially limits energy allocation. Because the maximum digestion rate can be adjusted upward in relation to factors such as diet quality and quantity there are both immediate and long-term spare capacities. We review their quantitation and time course for change, which are both ecologically important. A critical design feature of most studies measuring immediate spare capacity is that they quickly challenge animals to increase rate of digestion through cold stimuli, forced activity, or reduction in feeding time. A rapid time course is important because within a few days adjustments occur in the digestive tract that increase digestive capacity, in which case immediate spare capacity is no longer measured. Technical reasons why biochemical measures of spare capacity may not necessarily establish limitation at the whole-animal level are discussed herein. The majority of species studied had quite modest immediate spare capacities (range 9–50%). But in the same species the long-term spare capacity was about 100-125% above routine rates of nutrient intake or digestion. In laboratory mice digestive capacity increased to match any demand put on it, but whether the gut sometimes ultimately limits the energy budget is unknown for most animals. We review examples in which digestive limits are apparently dictated by the volumetric capacity of the gut or the rates at which food is either mechanically or biochemically broken down, but we know of no examples of limiting absorption.

## DIGESTIVE CONSTRAINTS: SIGNIFICANCE AND GENERAL PRINCIPLES

Wild mammals and birds undergo a range of food intake from hyperphagia during low temperature acclimation or periods of production (e.g. lactation, migratory fattening), which may require an enlarged gut, to restricted feeding or fasting which may cause disuse atrophy (see examples below and in Chapters 8, 9, and 13 of this volume). Omnivorous species encounter different types of food on a daily and/or seasonal basis, and this may require biochemical adjustments for breaking down and absorbing different substrates (Karasov, 1996; Karasov and Hume, 1997). Our interpretation that the attendant changes in gastrointestinal (GI) tract structure and biochemistry are "adaptive" rests on our assumption that the GI tract digestive characteristics (e.g. size, enzymes, etc.) are matched to the prevailing diet composition and feeding rate, and that these characteristics do not provide a digestive capacity in great excess of what is necessary for the prevailing diet and feeding rate. The first part of this idea is very well supported by many studies that show a positive correlation between size and enzyme content of the GI tract and daily feeding rate, a positive correlation between enzyme levels and the diet concentration of the enzyme primary substrates, and a positive correlation between diet nutrient density and retention time of digesta in the gut (Karasov and Hume, 1997). The second part of the idea is more often asserted than actually demonstrated. We assume that when load is increased, the animal's feeding may be constrained until digestive capacity is increased via the aforementioned adjustments in digestive characteristics.

The idea of digestive limitation, besides operating as an important interpretive paradigm, could also be important if digestive processing limited energy flow or other ecological processes (e.g. diet selection). Wild animals do appear to have maximal sustained metabolic rates and if the limit is not imposed by food availability, three physiological hypotheses about the proximate factor(s) have been proposed (Karasov, 1986; Weiner, 1992; Hammond and Diamond, 1997). The central limitation hypothesis suggests that the bottleneck resides in physiological processes and systems, including the digestive system, that are involved in acquiring, processing, and distributing energy to energy-consuming organs such as muscle or mammary glands. The peripheral limitation hypothesis suggests that processes (such as thermoregulation, lactation, activity) within the energy-consuming organs each have their own metabolic ceilings and this determines the maximum sustained metabolic rate. Finally, the idea of "symmorphosis" proposes that capacities of several of these potentially limiting factors might be matched to each other and to natural loads (Taylor and Weibel, 1981; Weibel, 2000). One theme of interest here is that maximum sustained metabolic rate in many wild vertebrates may be determined by the capacity of their digestive system.

The concept of a digestive limitation can be traced back at least to the work of Max Kleiber (Kleiber, 1933, cited in Kleiber, 1961) on the maximal food capacity of domestic animals, and more recently updated by several authors (Kendeigh, 1949; West, 1960; Kirkwood, 1983; Karasov, 1986; Weiner, 1992). Most recently we have come to appreciate that digestion may represent a flexible limit because there is considerable evidence in birds (Karasov, 1996) and mammals (Karasov and Hume, 1997) that digestive features that may limit food processing are adjusted in relation to factors such as diet quality and quantity. Digestion rate for a particular food or substrate can be greatly increased through changes in digestive organ size, changes in the complement of enzymes and transport mechanisms for breaking down and absorbing food and substrate, and changes in alimentary tract muscular activity that affect the contact time between food or substrates and the gastrointestinal (GI) processes. The relative differences (or ratios) between either the current or the absolute maximal digestion rate and the current food intake rate are measures of an animal's "safety margin" (Diamond, 1991) or "reserve capacity" (Diamond and Hammond, 1992) for responding to changes in environmental conditions over different timescales. These concepts of GI flexibility and spare capacity are illustrated in Fig. 4.1. Two points deserve highlighting in Fig. 4.1: (1) at any given time an animal has some limited spare capacity (called "immediate spare capacity") but this decreases in extent as the GI system reaches its long-term capacity (Hammond et al., 1994); and (2) phenotypic flexibility of the GI organs is primarily responsible for an animal's ability to change food intake and diet (i.e. it represents most of the "long-term capacity"); however, such phenotypic flexibility requires acclimation time.

Explicit references in ecology to possible digestive constraints actually predate most of the works on digestive constraint. For example, C.S. Holling criticized early predator-prey models because they assumed a linear relationship between an individual predator's consumption rate of prey and the prey's density. He proposed instead a "functional response" whereby the consumption rate increased with prey density but reached a plateau value beyond which consumption would not increase (Holling, 1959). Though many ecologists today associate the plateau value with a handling time that defines maximal intake in Holling's "disc equation" or with an herbivore's maximum rate of cropping and chewing (Gross et al., 1993), some ecologists, even in Holling's time, have recognized that maximal digestion rate could also dictate the plateau value (Jeschke et al., 2002). For example, Mook (1963), observing clear satiation of wild bay-breasted warblers feeding on spruce budworms, modeled predation by including a functional response that included a digestive pause of two hours. Besides potentially limiting energy intake and thus growth, storage and reproductive rates, digestive limitations can be important in behavioral models of optimal diet, models of

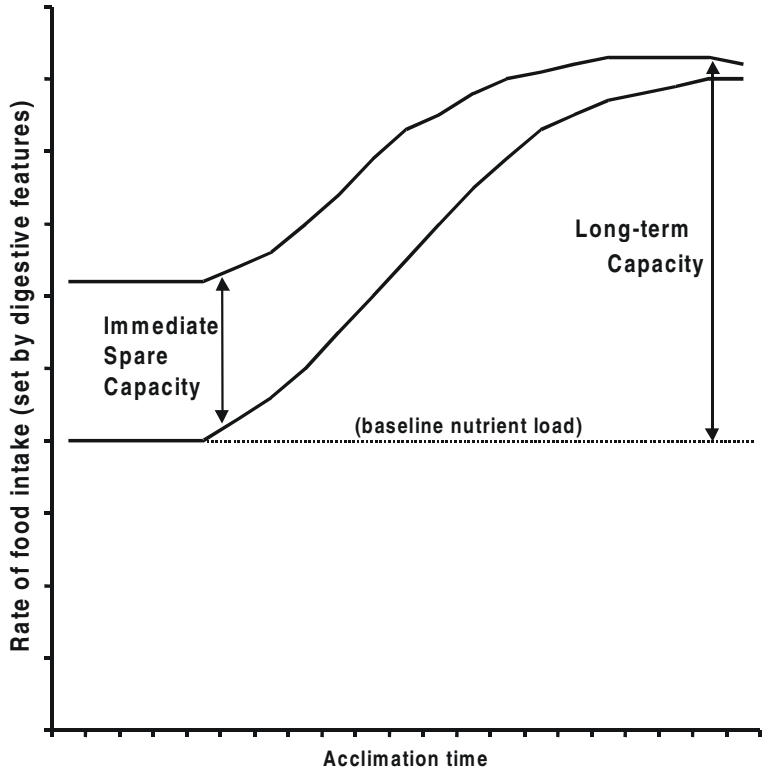


*Fig. 4.1.* Immediate spare capacity and long-term capacity (phenotypic flexibility plus immediate spare capacity) for a hypothetical animal exposed to increasing energy demands (e.g. during migration, during cold weather). The solid lower line represents the nutrient load from feeding. Its baseline corresponds to the animal's routine energy demands (e.g. not during migration or at thermoneutral temperatures). The solid upper line represents the capacity of the gut for processing that nutrient load. Capacity on the y-axis could be total digestion rate, volumetric intake, nutrient uptake capacity, rate of digestive enzyme activity or some other performance measure of the animal. The x-axis is time since the start of an increase in energy demand or change in diet quality.

At any given time, an animal can increase its food intake only within the limits set by the level of immediate spare capacity, which decreases as the animal approaches its long-term capacity. When energy and nutrient demands increase, and if the animal has been given time to fully acclimate to these elevated energy demands, then phenotypic flexibility in the digestive system of the animal enables increased energy intake (shown as the increase in solid lower line above the baseline nutrient load). These changes in digestive capacity are critically important in allowing animals to overcome the challenges associated with changing diet quality or quantity (adapted from Diamond, 1991; Diamond and Hammond, 1992).

territorial defense, daily foraging patterns, and optimal migration strategy (examples in Bednekoff and Houston, 1994; Karasov, 1996).

The easiest way to detect a digestion-limited animal is to directly measure food collection rate (or handling time) and digestion rate (or digestion time) and compare them, although there are some other methods as well (Jeschke et al., 2002). Thus, insectivorous house wrens *(Troglodytes aedon)* were found capable of collecting at least 21 grams dry mass arthropods/day (Dykstra and Karasov, 1993), three times as much as their maximal digestion rate (Dykstra and Karasov, 1992). Voles can consume herbage at a rate of 0.15 g $min^{-1}$, at least ten times faster than they can process it (Zynel and Wunder, 2002). Classic examples of digestive limitation are provided by some avian herbivores (Kenward and Sibly, 1977; McWilliams and Raveling, 2004) and by ruminant herbivores, for whom rate of intake may be limited by biting, chewing, and rumination, and not plant abundance (e.g. Spalinger et al., 1986; Spalinger et al., 1988). Similar kinds of arguments have been made for nectar-feeding hummingbirds (Diamond et al., 1986), and for bivalve- or crab-consuming birds (Zwarts and Dirksen, 1990; Kersten and Visser, 1996; Guillemette, 1994; Guillemette, 1998). Granivores ought to provide other examples of digestive limitation because they forage on a sometimes highly available food resource yet have a relatively long digestive processing time (Karasov, 1990), but to our knowledge no one has adduced an example to date. According to Jeschke et al. (2002), all animals for which measures of both digestion and handling time are available are digestion limited.

One goal here is to review the quantitation of digestive capacity. There have been far more estimates of long-term than immediate spare capacity and the two are sometimes not distinguished. Further, we think some current estimates of spare capacity are inaccurate and have illustrated how it can be more accurately estimated. While digestive limitation can have clear ecological significance, its mechanistic basis is rarely defined. The magnitude of the limit might be dictated by the volumetric capacity of the gut or the rates at which food are either mechanically or biochemically broken down or absorbed. Whichever feature(s) dictates the digestion limit, its time course for change is also rarely defined, though that too has important ecological implications. Without knowing such details, the quantitative integration of digestion with postabsorptive metabolism in the overall scheme of nutrient processing cannot be completely achieved in a fashion analogous to that achieved for respiratory and metabolic physiology (Weibel, 2000). To further this endeavor, and in light of their ecological significance, we therefore focus on these mechanistic details. We think that the magnitude of immediate and long-term spare capacity, and the time course over which digestive capacity can be increased, are the two keys to understanding the digestive challenges that animals face under a variety of interesting ecological situations.

## DEFINING THE LIMITS: MAGNITUDE OF OVERALL DIGESTIVE CAPACITY AND ITS MEASUREMENT IN FEEDING TRIALS

Immediate and long-term spare capacity can be estimated in balance trials in which maximum feeding and digestion rates are measured in animals highly motivated to feed, presumably at maximal levels. The spare capacity is the relative difference (or ratio) between the rates measured under those conditions and the rates measured under more routine or baseline conditions. The method is exemplified in Weiner's (1987) study of energetics of Djungarian hamsters. He took hamsters acclimated to room temperatures (22ºC) and switched them to cold conditions (-2ºC) either quickly or gradually over many days. In the cold, hamsters must eat more to balance higher heat loss or they will catabolize their body tissues to supply the extra energy. Hamsters switched quickly increased their feeding and digestion rate only 15% and lost body mass, whereas hamsters acclimated slowly increased their rates 92% and maintained body mass. Thus, hamsters switched quickly experienced an energy deficit and should have been motivated to eat more, but did not. Presumably, they did not have the spare digestive capacity to do so; their "immediate spare capacity" was only 15% above what they needed routinely for energy balance at 22ºC. Hamsters switched more gradually were able to increase their digestive capacity, but their 92% increase in response to cold acclimation was still less than their long-term spare capacity. Weiner (1987) found that hamsters at peak lactation could increase their digestion rate 116 % compared with nonreproductives, so this would be a closer estimate of their long-term spare capacity.

There have been many measurements of feeding and digestion rates in mammals and birds highly motivated to feed, presumably at near-maximal levels. Typically they involve animals acclimated to very low temperatures, ideally at their limit of thermal tolerance, high levels of forced activity, or hyperphagic animals during lactation, storing energy for migration and hibernation, or engaged in rapid growth. Some of these data have been

**Table 4.1.** Relationships between near maximum metabolizable energy intake ($ME_{max}$, kJ/d) and body mass ($m$ in g).

| Group | Energy demanding situation[1] | Allometric equation | Reference |
|---|---|---|---|
| Mammals and birds | C, L, G | $ME_{max} = 11.84\ m^{0.72}$ | (Kirkwood, 1983) |
| Mammals | L | $ME_{max} = 18.49\ m^{0.66}$ | (Weiner, 1992) |
| Birds | C | $ME_{max} = 16.42\ m^{0.66}$ | (Karasov, 1990) |
| Passerine birds | M | $ME_{max} = 16.09\ m^{0.70}$ | (Lindstrom and Kvist, 1995) |
| Shorebirds | M | $ME_{max} = 11.7\ m^{0.82}$ | (Kvist, 2001)[2] |

[1] Energy demanding situations: C = cold acclimation; L = lactation; G = growth; M = migratory fattening.

[2] Equation calculated by us.

summarized in allometric equations that express maximum metabolizable energy intake ($ME_{max}$) as a function of body mass (Table 4.1). As a general rule, $ME_{max}$ scales with body mass in a fashion similar to other metabolic rates (i.e. with mass$^{2/3-3/4}$; note though that none of the estimates control for phylogenetic association among the data) and is 4 – 7 times basal metabolic rate (Hammond and Diamond, 1997). The highest value we know of, measured in lactating mice exposed to low temperature, is 7.7 X resting metabolism (Johnson and Speakman, 2001). $ME_{max}$ can depend on the nature of the food. For example, shorebirds that must crush hard shellfish in their gizzards cannot sustain the very high rates they achieve when eating commercially prepared, soft trout food or mealworms (below). Also, Kvist and Lindstrom (2000) made an important point that the absolute amount of food digested per day is influenced not just by the hourly rate, but also the total hours available for feeding (also see McWilliams and Raveling, 2004).

The digestive adjustments of mammals and birds acclimated to high feeding rate almost always include increased gut size (though see Johnson and Speakman, 2001) and consequently increased amounts of digestive enzymes and nutrient transporters (Karasov and Hume, 1997; McWilliams and Karasov, 2001). Unfortunately, there is no published study for any vertebrate of both rapid and gradual adjustment of feeding and digestion to high energy demand that includes corresponding changes in gut size and biochemistry. The rapid-adjustment experiments, which have been least often performed, are perhaps most interesting because they reveal the immediate spare digestive capacity of the animal.

We designed a comprehensive study with white-throated sparrows *(Zonotrichia albicollis)* to determine their response to both rapid and gradual increase in energy demand in order to estimate the level of spare capacity and phenotypic flexibility in their digestive system in response to changes in feeding rate. The experiment involved manipulating ambient temperature, which caused changes in the metabolic rate of sparrows (i.e. increased metabolic rate with lower ambient temperature) and thus induced changes in their food intake to maintain their body temperature constant. By random assignment, sparrows were either held continuously at +21ºC, switched rapidly from +21ºC to –20ºC, or gradually acclimated to –20ºC over 50 days. We measured daily food intake and digestive efficiency of starch (the primary nutrient in their semisynthetic diet) in the three groups of sparrows. The prediction was that sparrows switched rapidly from warm to cold temperatures would maintain digestive efficiency constant only if some safety margin of nutrient absorption capacity over nutrient intake existed before the temperature switch.

White-throated sparrows at –20ºC required 83% more food than birds at +21ºC, as indicated by the comparison of feeding rates of acclimated sparrows in steady state at –20ºC and +21ºC (Fig. 4.2). When birds were switched rapidly from +21ºC to –20ºC they increased feeding rate only 45%, a level of

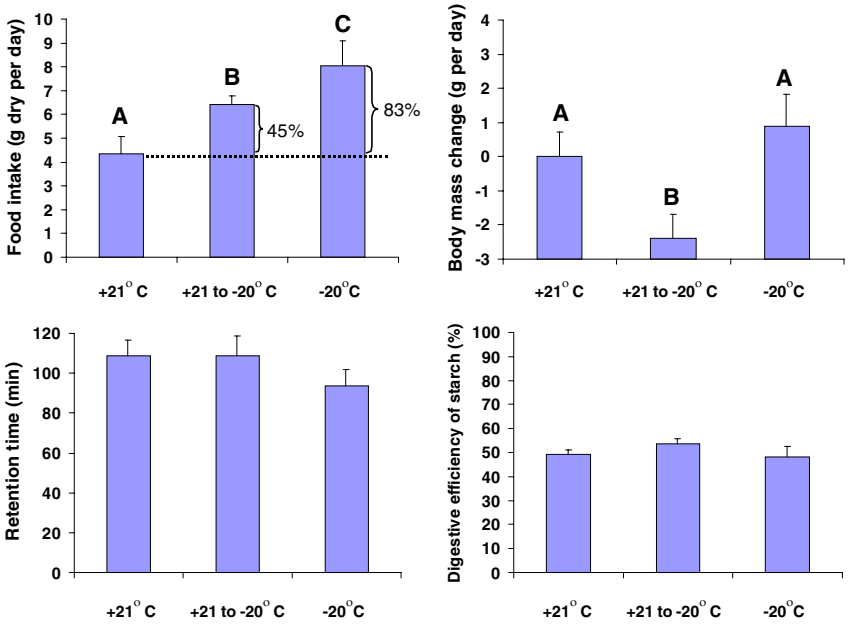


*Fig. 4.2.* Food intake, body mass change, retention time of digesta, and digestive efficiency of starch in white-throated sparrows that were either acclimated to +21°C or –20°C or switched immediately from +21°C to –20°C. Sparrows acclimated to –20°C ate more than sparrows acclimated at +21°C although both groups of sparrows maintained similar body mass. Sparrows in all three treatment groups had similar digestive efficiency and retention times. Thus, sparrows acclimated to +21°C have a limited spare capacity of about 45% as indicated by an increase in food intake of this magnitude for birds switched rapidly to colder temperatures. However, this limited increment in food intake did not suffice to satisfy the energy demands imposed by a rapid switch from +21°C to –20°C given these birds lost body mass. This indicates that phenotypic flexibility in digestive features is necessary for sparrows to achieve their long-term capacity.

food intake which was not sufficient to satisfy the extra energy demands, as evidenced by body mass loss (Fig. 4.2). Interestingly, birds in all three treatment groups had similar digestive efficiency and retention times (Fig. 4.2). Thus, sparrows have some spare capacity (of about 45%) but it did not suffice to satisfy the energy demands imposed by a rapid switch from +21°C to –20°C. If given enough time for acclimation to the cold, however, sparrows can satisfy the elevated energy demands associated with living in the cold, as evidenced by their ability to maintain body mass after 50 days of acclimation at –20°C.

The digestive adjustments to increased feeding rate that occurred during acclimation to the cold included an increase in size of small intestine (Fig. 4.3), large intestine, and liver but not gizzard and pancreas. We are currently completing analysis of digestive enzyme activity and nutrient uptake rates to determine whether adjustments in these digestive features are involved along with changes in gut size. Notice that the 57% increase in

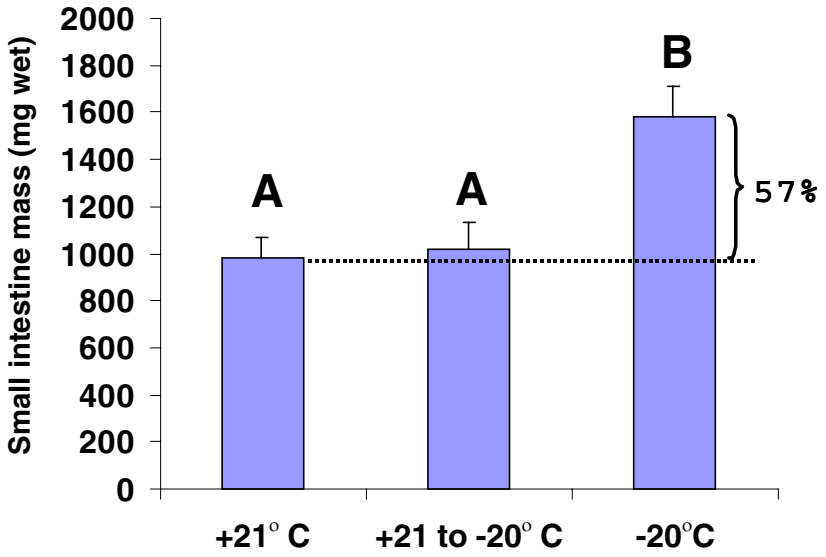


*Fig. 4.3.* Small intestine mass (g) of white-throated sparrows that were either acclimated to +21°C or –20°C or switched immediately from +21 C to –20°C. Sparrows acclimated to –20°C had larger small intestines than sparrows acclimated at +21°C, whereas sparrows switched immediately from +21°C to –20°C had similar small intestine mass as sparrows acclimated to +21°C. See text for a discussion of how these increases in gut size along with the results shown in Fig. 4.2 can be used to estimate the immediate spare capacity and long-term capacity of white-throated sparrows (depicted hypothetically in Fig. 4.1).

small intestine sufficed to accommodate the 83% higher feeding rate in birds acclimated at -20°C. This is apparent because mean retention time, efficiency digesting starch, and body mass did not decline significantly with cold acclimation (Fig. 4.2). If one considers that sparrows acclimated to +21°C had a spare capacity of 45% to start with, adding an increase in gut size of 57% to that can more than account for the 87% increased ability to process food. The two measures together imply that sparrows acclimated to -20°C probably still had some immediate spare capacity and therefore their long-term digestive capacity was higher than 87% above their digestion rate when held at +21°C. This makes sense because it is known that captive white-throated sparrows can tolerate temperatures down to -29°C when feeding rates are 2.26 (126%) times higher than at +21°C (Kontogiannis, 1968). Interestingly, white-throated sparrows engaged in forced activity could tolerate temperatures down to only -5°C but their digestion rates were similar to those of birds acclimated to -29°C, which is consistent with a central limitation set by nutrient processing rather than a peripheral limitation set by heat generation. Thus, the results from the experiment with white-throated sparrows, along with those of Kontogiannis (1968), conform nicely to the model presented in Fig. 4.1 and imply that immediate spare capacity is around 45%

but that after long term acclimation the long-term capacity is around 126% above "baseline".

Another method to estimate the immediate spare capacity is to measure intake/digestion rate during periods of restricted feeding. The approach is exemplified in the study by Winter (1998) on a single nocturnal nectarivorous bat *(Glossophaga longirostris,* 16.4 g), and other examples are provided below. Winter (1998) manipulated the ratio of day-to-night length and forced the bat to eat and digest relatively large amounts of sugar in relatively short amounts of time. He pointed out that after the first hour of feeding during which the gut becomes essentially filled, there is a steady-state period during which food intake can be no faster than the rate of processing, which includes both sugar (sucrose + glucose + fructose) digestion/absorption, postabsorptive processing, and excess water excretion. When feeding time was decreased after 7 d at 12 h/d to 2 h/d, the rate of glucose assimilation during the steady-state period of the night increased to a level 73% higher than during 12-h nights. But the bat feeding for just 2 h/d lost mass and so after 2 d it was switched to 4 h/d and then to 6 h/d feeding throughout which it maintained mass and continued to have an elevated hourly feeding rate as when given 2 h/d to feed. As the bat's energy budget was more and more stressed, it reduced its energy expenditures by reducing flight time. The results thus implied that when motivated to feed, the bat utilized its immediate spare digestive capacity to the maximum, which was apparently at least 73%. With the data it cannot be decided whether this is characteristic of the species (only one individual was studied), nor whether food intake was limited by sugar absorption capacity or water clearance capacity.

In a third method to infer immediate spare digestive capacity, which we term a hybrid method, results of feeding trials and in vitro assays are combined to yield estimates of spare capacity. A study on migratory yellow-rumped warblers *(Dendroica coronata)* can be used to illustrate the method (Lee et al., 2002). The birds were captured during migration and habituated to a diet of fruit mash and mealworms. Control birds were fed ad libitum but experimental birds were food restricted for 3 days by providing 44% of the ad libitum level of food. One purpose of the food restriction was to increase their motivation to feed maximally, and once they were again provided food ad libitum they increased their feeding and digestion rate by 18% compared with controls and the birds gained body mass. This suggests a spare digestive capacity of at least 18%, but other measures of digestive enzymes indicated that it was actually greater than this. The authors showed that the food restriction caused a 20% decline in intestine mass, declines of about 40% in intestinal enzymatic capacities (sucrase, maltase, and aminopeptidase activities were measured along the intestine), and pancreatic enyzme levels were not significantly affected (trypsin and chymotripsin) except for a 36% reduction in amylase. If the previously food-restricted birds could increase their digestion rate by 18% compared with controls while concomitantly

possessing around 40% less enzyme activity than controls, apparently the immediate spare capacity of the control birds must have been approximately 58% (= 18 + 40). There is some support for this estimate. McWilliams and Karasov (1998b) employed a time-limited intermittent feeding protocol and also found evidence of immediate spare digestive capacity in yellow-rumped warblers. In that study, yellow-rumped warblers were capable of increasing their food intake by 50% in a matter of hours with no change in digestive efficiency or mean retention time. With longer acclimation time warblers increase their feeding and digestion rates more than this during the migratory phase which can be induced by changes in light cycle. For example, warblers on long daylength (16L:8D) had hourly feeding/digestion rates 130% higher than warblers on short daylength (10L:14D; McWilliams and Karasov, 1998a).

We are aware of only seven balance studies that permit estimation of immediate spare digestive capacity in mammals and birds (Table 4.2). For now we have excluded a number of studies that estimated immediate spare capacity solely on the basis of biochemical measures (e.g. Buddington and Diamond, 1990, 1992; Toloza et al., 1991; Toloza and Diamond, 1992; Jackson and Diamond, 1995; Weiss et al., 1998) because they do not necessarily establish limitation at the whole-animal level (i.e. the chosen biochemical measure may have higher spare capacity compared with some other step of digestion) and because we have concerns (discussed below) about their accuracy. Of the balance trials, four were discussed above and the others will be considered shortly. The critical design feature of most of these studies is that they quickly challenged animals to increase rate of feeding and digestion, either through cold stimulus, forced activity, or reduction in feeding time. The last, hybrid method essentially inferred the immediate spare capacity by comparing digestive responses of control animals feeding at routine levels with experimental animals with reduced digestive tracts. Another method, never tried but which might be considered, is experimental ablation of the brain's food intake control center (ventromedial hypothalamus) which rapidly brings about hyperphagia. Whatever the method, a rapid time course is important because within a few days adjustments occur in the GI tract that increase the digestive capacity (discussed below), in which case immediate spare capacity is no longer measured. All the species studied had quite modest immediate spare capacities (range 9–50%), excluding the measurement on a single bat. This implies that in the wild sudden larger increases in energy needs due to increased activity or thermoregulatory costs cannot be immediately compensated by increased food intake even if food is abundant; instead, behavior patterns must be altered to save energy or energy stores must be recruited. But in the same species the long-term spare capacity, achieved partly through adjustments in the GI tract over the course of several days (below) is about 100–125% above routine rates of feeding/digestion (much higher in mice; Table 4.2).

**Table 4.2.** Immediate and long-term spare capacity estimated in balance trials in which maximum feeding and digestion rates were measured in animals highly motivated to feed, presumably at maximal levels. The critical design feature of most of these studies is that they quickly challenged animals to increase rate of feeding and digestion, either through cold challenge, forced activity, or reduction in feeding time.

| Species | Mass (g) | "Baseline" conditions | Immediate spare capacity | | Long-term spare capacity | | Ref.[a] |
|---|---|---|---|---|---|---|---|
| | | | Increase over baseline | Method of determination | Increase over baseline | Method of determination | |
| Djungarian hamster | 35 | Daily digestion rate at 22°C | 15% | Switched to -2°C | 116% | Peak lactation | 1 |
| *Mus musculus* | 26.4 | Daily digestion of lactating females at 21°C | 10% | Lactating females switched to 8°C | 30%[b]<br>488%[c] | Lactating females acclimated to 8 °C | 7 |
| White-throated sparrow | 24 | Daily digestion rate at 21°C | 45% | Switched to -20°C | 126% | Acclimated to -29 °C | 2 |
| *Glossophaga longirostris* | 16.4 | Hourly digestion rate for 12 h/d | 73%[d] | Reduced feeding time to 2 – 4 h/d | Not determined | | 3 |
| Prairie vole | 51 | Daily digestion rate at 23°C | 9% | Reduced feeding time and feeding trout duration | 95% | Cold acclimation, lactation | 4 |
| Yellow-rumped warbler | 11 | Daily digestion rate at 21°C | 50 – 58% | Hybrid estimate and reduced feeding time | 130% | Migratory mode induced by increasing daylength | 5 |
| Broad-tailed hummingbird | 3.3 | Daily digestion rate at 22°C | 20% | Measurement of sucrase and switched to 10°C | Not determined | | 6 |

[a]References: 1 Weiner (1987); 2 McWilliams and Karasov (2002); Kontogiannis (1968); 3 Winter (1998); 4 Zynel and Wunder (2002); 5 McWilliams and Karasov (1998a); Lee et al. (2002); 6 McWhorter and Martínez del Rio (2000); 7 Johnson and Speakman (2001)

[b]increase compared with lactating females at 21°C

[c]increase compared with nonreproductive females at 21°C

[d]only a single bat studied

## DEFINING MECHANISMS: DIGESTIVE FEATURES THAT MIGHT LIMIT OVERALL DIGESTIVE CAPACITY

The magnitude of the digestive limit might be dictated by the volumetric capacity of the gut or the rates at which food are either mechanically or biochemically broken down or absorbed. There are plausible examples of most of these.

### Limited Gastrointestinal Tract Volume as a Digestive Constraint

Zynel and Wunder (2002), employing a protocol of reduced feeding time (see above), described an apparent gut volume limitation in captive, nonreproductive herbivorous prairie voles *(Microtus ochrogaster).* They held the animals at 23ºC and fed the controls ad libitum and the experimentals either in a single 3-hour time block per day or in six half-hour time blocks spread every 4 h through the day (still 3 h total feeding time). Three hours of feeding was chosen for the experimental voles because this was more than enough time for them to ingest and chew their daily food requirement of 7.7 g $d^{-1}$. Voles in both the experimental groups rapidly filled their stomachs with up to 1.4 g dry food, the maximum stomach capacity determined in earlier studies. Voles fed in a single time block could not maintain body mass constant whereas voles fed in multiple time blocks could. In a single 3-h time block voles could apparently process at most 2 g if they continually "topped-off" as digesta moved from the stomach through the distal GI tract. In contrast, if voles filled their stomach with 1.4 g once every 4 h, which is apparently time enough to clear the stomach, they potentially could digest 8.4 g $d^{-1}$ (= 1.4 g x 24 h/4 h), which suggests an immediate spare capacity of 9% (8.4/7.7 = 1.09). Voles can increase their feeding and digestion rate much more than this when chronically acclimated to low temperature or during lactation. Their long-term spare capacity is about double the routine digestion rate of the controls in this study (Zynel and Wunder, 2002).

Though we have described this as an example of a volumetric constraint, perhaps it would be more accurate to say that the bottleneck might lie in the volumetric turnover in g/h, or rate of emptying in g/h of the stomach. This expression puts the bottleneck in the same units as the rate being limited (feeding rate in g/h). On the one hand the distinction seems moot if voles exhibit near instantaneous stomach filling time in relation to stomach emptying time, but on the other hand it begs the question of whether subsequent digestive processes (breakdown, absorption, etc.) are too slow to permit more rapid emptying of the stomach into the small intestine and thus signal the stomach by negative feedback. In any event, an important ecological interpretation of this putative bottleneck is framed in terms of time, i.e. that this bottleneck causes optimally spaced rest bouts between feeding and thus is the primary cause of the observed ultradian rhythm in voles (see discussion in Zynel and Wunder, 2002).

## Limited Rate of Mechanical Breakdown as a Digestive Constraint

Birds that consume and crush shellfish provide a compelling example of this kind of limitation. The limitation is suggested for red knots *(Calidris canutus)* by the fact that they achieve lower rates of $ME_{max}$ (by less than half) when consuming whole bivalves, whose shells they must crush and excrete via the cloaca, than when consuming the flesh alone which has been removed from shells (T. Piersma, pers. comm.). The increase in gizzard muscularity when knots are transited from soft food to whole bivalves (Piersma et al., 1993; Dekinga et al., 2001) is consistent with the idea that mechanical breakdown is an important limitation to overall digestion rate. The higher maximum rate on flesh perhaps reflects limits in digestive or postabsorptive biochemical processing of the primarily proteinaceous material.

Another example of an apparent bottleneck caused by limiting rate of mechanical breakdown might be rumen clearance in ruminants (Van Soest, 1994). The orifice between the rumenoreticulum and omasum functions like a particle size or density sieve so that particles do not escape the rumen until they are sufficiently reduced in size. Reduction is achieved partly through mechanical means (muscular activity of the rumen in conjunction with rumination and chewing) and partly through biochemical means (fermentation rate). Intake of additional food must be matched to the rate of clearance from the rumen.

There are other interesting cases of possible limitation by mechanical breakdown that beg to be studied. As mentioned above, among birds granivores have relatively long digesta processing times but the possibility of this being a mechanical digestion limitation has not been systematically explored. Insectivores have been little studied, but Hanski (1984) reported that apparent digestive pauses became more evident when shrews were fed heavily chitinized beetles than when fed lightly chitinized insect pupae. It seems reasonable to apply the same research approach to these situations as described above for red knots: present the same food either intact or mechanically preprocessed under conditions that motivate the animals to feed maximally.

## Limited Rate of Biochemical Breakdown as a Digestive Constraint

McWhorter and Martínez del Rio (2000) proposed that food intake by migratory broad-tailed hummingbirds *(Selasphorus platycercus)* is limited by rates of hydrolysis. These birds digest mainly sucrose and so sucrase activity in the intestine's brush border was measured in vitro. The in vitro measurement was made with homogenates of tissues collected along the length of the intestine under conditions that saturate the enzyme(s) so that the maximal reaction velocity ($V_{max}$) could be integrated along the length to yield a total hydrolytic capacity. This capacity was about 120% higher than the

observed rates of sucrose intake and digestion, implying that the immediate spare capacity was quite high. But, as the authors pointed out, the common procedure of using the $V_{max}$ over the entire intestinal length is physiologically unrealistic because the sucrose concentration progressively lowers as the digesta flows distally along the gut during digestion. Using a more sophisticated model of the gut as a plug-flow chemical reactor, Jumars and Martínez del Rio (1999) calculated a lower digestive capacity that was only 15–35% higher than observed rates of sucrose intake/digestion. They considered this to be the more accurate estimate of the immediate spare digestive capacity of the broad-tailed hummingbird. Support for their argument came in trials in which they rapidly exposed the hummingbirds to low temperature. The birds did not (could not?) increase their intake but instead reduced their expenditure by utilizing torpor. In a similar kind of experiment rufous hummingbirds (*Selasphorus rufus*, 3.2 g) switched suddenly to low temperature did not (could not?) sufficiently increase their intake and lost body mass (Gass et al., 1999).

The study by McWhorter and Martínez del Rio (2000) underscored some important considerations in estimating digestive capacity by extrapolation from measures of maximum enzymatic breakdown rate in vitro. First, the method assumes that hydrolysis rates measured in vitro correspond to actual rates in vivo. This may apply best for digestion of sucrose for which hydrolysis depends only on an enzyme bound to the intestine's brush border that is easily measured. Second, for most foods, besides sucrose-rich nectars, there are multiple substrates (e.g. starch, protein, fat) whose digestion is much more complex involving gastric and/or pancreatic enzymes that act in addition to multiple intestinal brush border enzymes. This complexity far exceeds our current abilities to model the overall process. Third, the hydrolysis rate is concentration dependent over some substrate range. Though most other studies estimating hydrolytic capacity (e.g. Hammond et al., 1994; Weiss et al., 1998; Martínez del Rio et al., 2001) have assumed constant saturating substrate concentrations, the newer, more physiologically realistic approach by McWhorter and Martínez del Rio (2000) showed that the aforesaid studies surely overestimated the hydrolytic capacity.

## Limited Rate of Nutrient Absorption as a Digestive Constraint

We know of no published study that provides strong evidence of nutrient absorption acting as a digestive bottleneck. Earlier studies that stimulated much interest in digestive bottlenecks (Karasov et al., 1986; Diamond et al., 1986) may be used to illustrate the problem. The intestinal glucose uptake capacity of rufous hummingbirds (*Selasphorus rufous*, 3.2 g) was estimated to be 87.7 μmol $h^{-1}$ based on in-vitro measurement. How does this compare with actual intake? A 3-g hummingbird held at room temperature digested 1.5 – 2 g sucrose $d^{-1}$ (McWhorter and Martínez del Rio, 2000) or 4.4

– 5.8 mmol/$d^{-1}$. Assuming that all this was digested in 16 h and that half was glucose, the bird's actual glucose absorption rate was thus at least 138 μmol $h^{-1}$, 56% higher than the maximal uptake capacity in vitro! In some other studies when the in vitro measurement of D-glucose absorption was less than what animals actually achieved, the authors argued that glucose that was not absorbed by the intestine was later fermented in the hind gut. But this kind of explanation cannot apply to a hummingbird (no hind gut). The simplest explanation is that the in vitro measurement underestimated actual glucose absorption rate. There is valid concern that in other studies a similar underestimation occurred but was overlooked by invoking cecal fermentation.

Consider some of the problems that plague estimates of nutrient absorption capacity, which can easily lead to either over- or underestimation. Overestimation of absorption rate, as for hydrolysis rate, is possibly caused by improper assumptions about lumenal nutrient concentrations. For example, when Toloza and Diamond (1992) estimated the immediate spare absorptive capacity of adult laboratory rats they found that mediated glucose absorption was 130% higher than daily glucose intake rate when they assumed lumenal concentration was 50 mM, but only 20% higher when they assumed the lower actual determinations of lumenal glucose concentration because absorption rate is much lower at low concentration (Fig. 4.4). Several factors can lead to underestimation of absorption rate. It is possible that absorption rates measured in vitro are less than the rates in vivo because isolated tissue may become damaged and lead to underestimation of active transport rates (Starck et al., 2000). Also, measures of absorption with isolated intestinal tissue apparently fail to incorporate processes that may function in the intact animal such as trafficking of additional glucose transporters (GLUT 2) to the brush border stimulated by the presence of lumenal sugar (Kellett and Helliwell, 2000), and an important passive absorption pathway that seems very important, at least in birds (Karasov and Cork, 1994; Caviedes-Vidal and Karasov, 1996; Chediack et al., 2001) and probably in mammals (Pappenheimer, 1998; Fig. 4.4). Other kinds of absorption measures in vivo in anesthetized animals may be suspect because the anesthesia can influence the rates of absorption (Uhing and Kimura, 1995). Weber and Ehrlein (1998) arguably misestimated spare capacity by overlooking the very real physiological constraint that animals do not excrete a large amount of unabsorbed solute (see Mc Whorter and Martínez del Rio 2000), and by assuming that the apparent maximum absorption rate at their test concentration would represent the maximum absorption rate at higher test concentrations.

Estimation of whole-animal glucose absorptive capacity by in vitro methodology has rarely been validated and in one of the earlier studies applying it, Toloza and Diamond (1992) pointed out that the calculation, which has numerous approximations, should be considered meaningful to an order of magnitude. Setting aside the issue of quantitative accuracy, we

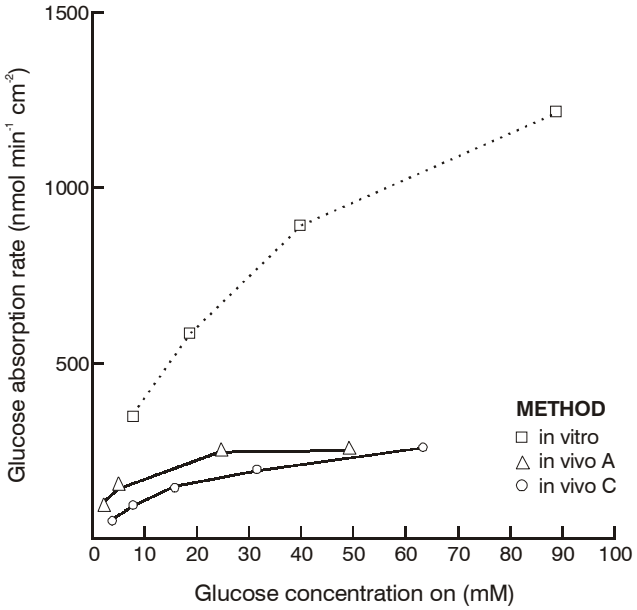


***Fig. 4.4.*** Estimation of nutrient absorption capacity depends on method used and concentration assumed. This is illustrated in the comparison of measures in jejunum of adult laboratory rats. Many studies have applied the everted sleeve method (Karasov and Diamond, 1983) which was used by Debnam et al., (1988) to measure mediated D-glucose uptake ("in-vitro", open triangles, solid line). These researchers also measured mediated D-glucose absorption in perfused jejunum of anesthetized rats ("in-vivo A", open circles, dashed line). At low concentrations the rate is lower than in the in-vitro preparation because of unstirred layer effects, but maximal mediated uptake (plateau values) is fairly similar. Both measures, as well as the single highest reported maximal mediated in-vitro uptake in rats (431 nmol $min^{-1}$ $cm^{-2}$; Toloza and Diamond, 1992) are lower than absorption rates measured in chronically perfused, unanesthetized adult rats (Ugolev et al., 1986), interpreted by Pappenheimer, 1998) ("in vivo C", open squares, dotted line). This latter measurement may include the effect of recruitment of additional glucose transporters (GLUT 2) that have lower affinity than the brush border glucose transporter (SGLT 1) (Kellett and Helliwell, 2000) and includes passive absorption, typically neglected in calculations of absorption capacity but which becomes especially important as concentration increases.

do think that in vitro measures are very useful for indicating qualitative changes in digestive capacity. Furthermore, when in vitro biochemical measures are made in conjunction with other whole-animal measures, perhaps they can lead to useful hybrid estimates of immediate spare capacity, as described above.

## HOW QUICKLY DOES DIGESTIVE CAPACITY INCREASE?

In the wild when energy needs suddenly increase, the digestive system could act as a bottleneck over some short term even if it eventually adjusts to permit

a higher rate of energy flow. The period of time over which this digestive constraint operates is dictated by the time it takes to increase digestive organ size or tissue-specific levels of digestive enzymes and nutrient absorption mechanisms. Relying on a rather limited number of studies, we can assemble a picture of the time course of digestive adjustment starting with turnover time of intestinal enzymes and epithelial cells and proceeding through rates of change of entire tissues to whole-animal feeding responses. The picture that emerges is that biochemical changes may occur faster than structural changes and changes may occur faster in small than in large animals.

Starting with the most basic level, birds and mammals switched from carbohydrate-free diet to high carbohydrate diet could at least double the specific activity of their carbohydrate-digesting enzymes and/or nutrient transporter within 1–2 days of the diet switch (Karasov and Hume, 1997). An important mechanism is the replacement of intestinal cells with new cells possessing more copies of particular digestive enzymes (Karasov and Hume, 1997). In birds the rate of cell proliferation, indexed by the length of the S-phase (phase of DNA replication, measured by labeling in vivo) was measured in two different-sized species during growth (Starck, 1996). This rate did not differ markedly by age or species and so given a rather invariant S-phase (average 6 hours), the intestinal turnover time of small birds (replacement time of intestinal cells) was 2–3 days compared with 8–12 days in larger birds (Starck, 1996). Among the six mammal species studied by Smith et al. (1984), however, there was no marked body-size dependent variation in enterocyte life span and, as in birds, enterocyte turnover rate was independent of age in mice (Ferraris and Vinakota, 1995). In laboratory rats, which have a one-day enterocyte turnover (Karasov and Diamond, 1987), following a fast the villi returned to their normal length within a day after initiation of feeding (Buts et al., 1990; Hodin et al., 1994). The first responses of the atrophied gut of starved rats to initiation of feeding occurred as early as two hours after the first meal, when genes such as *c-fos* and *c-jun*, which represent the mitogenic response in many types of tissues, were first expressed in intestinal crypt cells (Hodin et al., 1994).

Several studies, especially in birds, have monitored progressive changes in organ sizes following diet switches using destructive or nondestructive sampling methods. Fasted blackcaps (*Sylvia atricopilla*) that had reduced intestinal mass grew back their small intestine in two days or less once they were provided with food ad libitum (Karasov et al., 2004). Red knots switched from soft food to hard shellfish increased gizzard mass 147% within 6 days (Dekinga et al., 2001). Japanese quail switched to high fiber diet increased gizzard mass 110% within 6 days, but significant increases were already apparent 1 day after the diet switch (Starck, 1999a). Reversible changes in gut length in response to changes in diet composition have been reported to occur within 3–4 weeks in grouse and quail (Moss and Parkinson, 1972;

Savory and Gentle, 1976a, b) and ducks (Miller, 1975), with significant responses within 5 days in ducks (Drobney, 1984; Kehoe et al., 1988).

Whole-animal feeding trials gave a similar picture of the time course for adjustment. American robins (*Turdus migratorius*) and European starlings (*Sturnis vulgaris*) switched from fruit to insect diets progressively increased digestive efficiency within three days of the diet switch (Levey and Karasov, 1989). Fasted blackcaps and thrush nightingales that had been food restricted, progressively increased their digestion rates to a maximum over the course of 3 days after returning to ad libitum feeding (Karasov and Pinshow, 2000; Kvist and Lindstrom, 2000). Red knots delayed accepting a new shellfish diet for at least 2 days when switched from soft food (Piersma et al., 1993; Dekinga et al., 2001).

In summary, the response of the digestive system to changes in diet composition and feeding rate seems rapid. Even for structural measures (e.g. gizzard or intestine mass) that may respond more slowly than biochemical measures, statistically significant changes of a magnitude of 20–40% are apparent in most species within 1–2 days of a change in diet (Starck, 1999b). But systematic studies within and across species of correlated rates of change in digestive biochemistry and structure in response to whole-animal dietary adjustment are generally lacking.

## Long-term Digestive Capacity–How High can it Go?

If birds are given adequate time to acclimate, then increases of at least two times in food intake and digestion rate are possible (Karasov, 1996). Doubling food intake occurs commonly in birds preparing for migration (Berthold, 1975; Blem, 1980; Karasov, 1996) and in birds at cold temperatures (Dawson et al., 1983; Karasov, 1990; Dykstra and Karasov, 1992; McWilliams et al., 1999). Many mammals exhibit increases of similar magnitude (e.g. Tables 4.1 and 4.2) but some truly extraordinary increases have been recorded in laboratory mice (Hammond et al., 1994). For example, nonreproductive Swiss-Webster female mice doubled their intake/digestion rate when switched from 23 to 5°C and could still increase it 3.3 times more at peak lactation with very large litters. The net long-term digestive capacity was thus about 6.7 times the rate under routine conditions. The relative increase was similarly high, 5.9 times, in the MF1 strain of *Mus musculus* (Johnson and Speakman, 2001). Are mice exceptional in this regard because of selection for high reproductive rate? In domesticated birds an important digestive change obtained as a result of artificial selection for more rapid growth was an increase in the relative size of the digestive organs (Lilja et al., 1985; Jackson and Diamond, 1996) which presumably permits relatively high digestion rates.

As mentioned above, the digestive adjustments of mammals and birds to long-term acclimation to high feeding rate almost always include increased gut size and consequently increased amounts of digestive enzymes and

nutrient transporters (Karasov and Hume, 1997). Interestingly, the processing time of each meal, measured as mouth-to-cloaca total mean retention time (MRT; an index of turnover), and digestive efficiency do not change markedly (Dykstra and Karasov, 1992; McWilliams et al., 1999; Fig. 4.2). Probably, feedback mechanisms in the digestive tract ensure that the rate food enters the intestine from the stomach and travels distally along the intestine does not exceed the rate at which it is broken down and absorbed. What permits higher food intake (inflow) even though turnover time is held fairly constant, is the larger volumetric capacity (Karasov, 1996). The primary instance in which MRT is altered is when food richness is altered, in which case MRT changes in a corresponding fashion with the result that movement of digesta is matched to breakdown and absorption rates and digestive efficiency is maintained (Karasov, 1996). Thus, for these cases in which the intestine's rate of breakdown and absorption is limiting, if the feeding rate or food richness is to increase, then the biochemical features (enzyme levels, nutrient absorption rates) must be increased through an increase in activity per unit tissue or an increase in total amount of tissue. Both kinds of adjustments occur in mammals (Weiss et al., 1998) and birds (McWilliams and Karasov, 2001). This kind of integrated analysis of how the gut functions and adjusts has not been performed for the types of feeders whose intake is possibly limited by the rate of physical breakdown of the food (e.g. feeders on bivalves and crabs; see below).

Whether the digestive capacity can be increased to match any demand put on it or whether the gut sometimes ultimately limits the energy budget is not known for most animals. The issue has been thoroughly studied in laboratory mice challenged during cold acclimation, lactation, and a combination of these factors (Hammond et al., 1994; Johnson and Speakman, 2001). With each increasing energetic challenge Swiss-Webster mice increased gastrointestinal mass and hydrolytic and absorptive capacity and, for the highest load of lactation in the cold, the energy budget limit was not set by the digestive system but more likely by lactational performance (Hammond et al., 1996). For the MF1 strain Johnson and Speakman (2001) doubted that even lactational performance was a limit, at least during a female's first lactation. They speculated that in that strain females may limit themselves during their first reproduction perhaps to maximize lifetime reproduction.

How can we test whether the gut limits the energy budget for an animal in the field? The method used so far has been to measure the long-term limit in laboratory studies and compare it with the field energy budget. Studies on house wrens (Dykstra and Karasov, 1992, 1993) and yellow-eyed Juncos (*Junco phaeonotus)* (Weathers and Sullivan, 1989), for example, rejected the hypothesis that rate of digestion might limit brood size proximally because parental energy expenditure, measured with doubly labeled water, was below the longer term digestive capacity.

Should we generalize from these results with laboratory mice and two passerine species and conclude that for all mammals and birds that digestive capacity can be increased to match any demand put on it and will not be limiting in the ecological setting? This would be premature we think. As described above, there are interesting plausible examples of digestive bottlenecks involving animals eating foods quite different from the formulated laboratory chow fed to mice. There are other energy intensive points in the life cycle, such as growth (Karasov and Wright, 2002) and migration, during which digestion may prove to be the limiting factor in the energy budget. Also, there may be situations in which the immediate spare digestive capacity may be ecologically important even if over the longer term digestive capacity increases and the long-term capacity is not limiting. For example, a gut-limitation hypothesis for many migratory birds suggests that the initially slow rate of mass gain at stopover sites occurs because birds lose digestive tract tissue and hence function during fasting, and rebuilding of the gut takes time and resources and itself restricts the supply of energy and nutrients from food (McWilliams and Karasov, 2001). For birds that fly, the size of the digestive tract is likely ultimately limited by mass balance requirements for flight (i.e. big guts can't fly; Piersma and Gill, 1998).

## FUTURE DIRECTIONS

(1) The idea of a digestive constraint is most plausible when food collection rate and digestion rate are both measured and the former is higher than the latter. Granivores are good candidates for such digestive limitation but to our knowledge no one has yet provided an example.

(2) There is no published study for any vertebrate of both rapid and gradual adjustment of feeding and digestion to high energy demand that includes corresponding changes in gut size and biochemistry.

(3) Rapid-adjustment experiments, rarely performed (only seven studies that we know of), are perhaps most interesting because they reveal the immediate spare digestive capacity of the animal.

(4) Granivores and insectivores eating heavily chitinized prey, provide interesting cases of possible digestive limitation by mechanical breakdown and beg to be studied.

(5) Estimation of whole-animal hydrolytic and absorptive capacity by in–vitro methodology has rarely been validated which undercuts their application for quantitative estimation of spare digestive capacity.

(6) More integrative studies are needed that simultaneously measure adjustments in gut anatomy, retention time of digesta, enzyme hydrolysis

rates, nutrient absorption rates, and digestive efficiency in response to changes in food quantity and quality.

(7) Our understanding of the time course of digestive adjustment starting with turnover time of intestinal enzymes and epithelial cells and proceeding through rates of change of entire tissues to whole-animal feeding responses is based on very few studies.

(8) Can wild species or much larger species achieve the increases in long-term digestive capacity achieved by small rodents such as laboratory mice (6.7 times the digestion rate under routine conditions)?

(9) Do laboratory mice reflect the norm or are they exceptional in their ability to match digestive capacity to any demand put on it?

(10) More integrative studies are needed that compare immediate and long-term digestive capacity with rates of energy flow in free-living animals at energy intensive points in their life cycle. Are there other ways to test the hypothesis that digestion proximally limits energy budgets in the field?

### *Acknowledgments*

Supported by N.S.F. (IBN-9723793, IBN-0216709 to W.H.K. and IBN-9984920 to S.R.M.).

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