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Migration Takes Guts

Digestive Physiology of Migratory Birds and Its Ecological Significance

PHENOTYPIC FLEXIBILITY IN THE digestive system of migratory birds is critically important in allowing birds to successfully overcome the physiological challenges of migration. However, phenotypic flexibility in the digestive system of birds has limits that can influence the pace of migration. For example, partial atrophy of the gut after one to two days without feeding limits utilization of ingested food energy and nutrients and thereby slows the pace of migration. Lack of certain digestive enzymes can directly limit diet choice and utilization of foods that require such enzymes for digestion. Regular switching of diets also may reduce utilization of ingested food energy and nutrients of a given diet. Finally, maximal food intake of migratory birds may ultimately be limited by associated increases in gut size that negatively affect flight performance. Determining when rates of digestion constrain diet choice or re-fattening rates in migratory birds requires understanding the magnitude of spare volumetric or biochemical capacity relative to the magnitude of change in food quantity or quality. We discuss an approach for studying the importance of spare capacity in limiting performance of migratory birds and review the few such studies that have been conducted on migratory songbirds. We conclude that digestive constraints are likely to influence the pace of migration in birds when birds must refuel after one to two days without feeding, when birds lack certain digestive enzymes, when birds regularly switch diets, and when birds are hyperphagic and must also fly.

INTRODUCTION

Birds during migration are like Olympic marathon athletes in that to be successful they must satisfy the physiological demands associated with formidable feats of athletic endurance. Just as exercised muscles increase in size in well-trained human athletes, flight muscles increase in size and capacity when birds migrate (Marsh 1984; Driedzic et al. 1993; Bishop et al. 1996). More recent studies demonstrate that lean mass (including flight muscles) of birds is quite dynamic over even short time scales (e.g., hours and days) and that birds store and use both lean and fat mass during migration (Piersma 1990; Piersma and Jukema 1990; Lindstrom and Piersma 1993; Bauchinger and Biebach 2001). The increase in muscle capacity in migratory birds is necessary to satisfy the physiological demands of long-distance flight (reviewed in Butler and Bishop 2000). Furthermore, these changes in muscle size and capacity are reversible for both birds and mammals as demonstrated by the seasonal hypertrophy and atrophy of pectoralis and cardiac muscle in migratory birds (e.g., Gaunt et al. 1990; Jehl 1997).

Although these changes in skeletal muscle are relatively obvious in birds (and mammals), there are also coincident changes in internal, vital organs that are less apparent but just as important. For example, digestive organs such as the small intestine, gizzard, and liver increase in size and capacity with increased food intake and energy demands such as those associated with exercise (McWilliams and Karasov 2001). The increase in digestive organ capacity converts more food energy into usable metabolic energy to fuel the increased energetic costs of exercising enlarged skeletal muscle. These same energy-supplying organs are some of the most metabolically active and energetically expensive organs in vertebrates (Martin and Fuhrman 1955; Alexander 1999), and this may explain why they atrophy when energy demands are reduced (e.g., once migration is complete [Piersma 2002]).

The fundamental issue addressed by these examples is that the capacity of many physiological systems, including that of the digestive system, is matched to the prevailing demand but can be modulated in response to changes in demand (Diamond and Hammond 1992; Hammond and Diamond 1997). In other words, as demands on the physiological system increase or decrease there is a coincident increase or decrease in the capacity of key organs. Rapid reversible changes in physiological systems such as the digestive system provide examples of flexible norms of reaction (Stearns 1989; Travis 1994) or phenotypic flexibility in that they enable individuals to respond flexibly to changes in the environment (Piersma and Lindstrom 1997; Piersma 2002; Piersma and Drent 2003). Phenotypic flexibility in physiological traits may itself be a critical component of the adaptive repertoire of animals that may influence diet diversity, niche width, feeding rate, and thus the acquisition of energy and essential nutrients (Karasov 1996; Kersten and Visser 1996; Pigliucci 1996; McWilliams et al. 1997; Piersma and Lindstrom 1997; Piersma 2002).

A related fundamental issue is that at any given time the key organs of a physiological system are not exactly matched to the prevailing demand, but instead they provide some limited excess capacity (Diamond and Hammond 1992; Diamond 1998). This "spare capacity" is measured as the excess in capacity of the system over the load on the system (Toloza et al. 1991). The level of spare capacity is ecologically important because it defines the limits of short-term response in animals. For the digestive system in particular, the amount of spare capacity determines, for example, how much an animal can change its feeding rate or diet before digestive efficiency is reduced (Toloza et al. 1991). Because changes in feeding rate and diet are common in migratory birds, understanding the extent of spare capacity in their digestive systems provides insights into when digestion may constrain diet choice and feeding rate.

These concepts of phenotypic flexibility and spare capacity are illustrated in fig. 6.1, using the digestive system of migratory birds as a model physiological system. Two points are worth highlighting in fig.6.1: (1) at any given time, a migratory bird has some limited spare capacity (called "immediate spare capacity"), but this decreases in extent as the digestive system reaches its ultimate capacity; and (2) phenotypic flexibility of the digestive organs is primarily re-

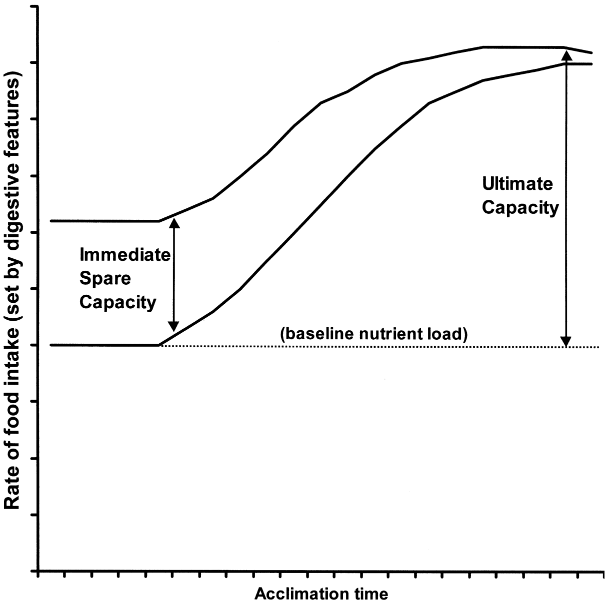

Fig. 6.1. Immediate spare capacity and ultimate capacity (phenotypic flexibility plus immediate spare capacity) for a hypothetical bird exposed to increasing energy demands (e.g., during migration or during cold weather). The solid lower line represents the nutrient load from feeding. Its baseline corresponds to the bird'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 volumetric intake rate (as shown), nutrient uptake capacity, rate of digestive enzyme activity, or some other performance measure of the bird. The *x*-axis is time since the start of an increase in energy demand or change in diet quality. When energy demands are near maximum and the bird has been given time to fully acclimate to these elevated energy demands, then phenotypic flexibility in the digestive system of the bird enables increased energy intake.

sponsible for a bird's ability to change food intake and diet (i.e., it represents the majority of the "ultimate capacity"); however, such phenotypic flexibility requires acclimation time.

A central theme of this chapter is that birds during migration face considerable nutritional challenges and that phenotypic flexibility and spare capacity of their digestive system play key roles in how they respond to these challenges. We focus here on the digestive system of migratory birds because recent research has shown that: (1) features of the gut (e.g., size, nutrient uptake rates, digestive enzyme activity) are modulated in response to changes in the quality and quantity of the diet (see McWilliams and Karasov 2001 and Piersma 2002); and (2) these digestive adjustments are likely important for permitting the high feeding rate of migratory birds and conceivably could constrain the rate of energy intake and the diets of birds during migration (Piersma 2002). Because there are other recent, comprehensive reviews of phenotypic flexibility in the digestive systems of birds and mammals (Karasov 1996; Piersma and Lindstrom 1997; Starck 1999b; McWilliams and Karasov 2001; Karasov and McWilliams 2004), we concentrate in this chapter on providing examples of this phenomenon and its ecological importance for migratory passerine birds generally, and particularly in Old and New World warblers when possible. In the next section, we use the phenomenon of hyperphagia in migratory birds to illustrate how spare capacity of the digestive system can be measured and to demonstrate the importance of phenotypic flexibility in digestive organs for migratory birds.

PREPARING FOR MIGRATION

In preparation for migration, birds increase their food intake (i.e., become hyperphagic) and store the energy and nutrient reserves necessary to fuel the costs of subsequent migratory flight(s) (Alerstam and Lindstrom 1990; Blem 1990; Biebach 1996). What changes in the digestive system might facilitate hyperphagia in migratory birds? Studies of free-living migratory birds (mostly geese and ducks) have reported significantly larger gut size during migratory periods compared with nonmigratory periods (reviewed in Starck 1999b and in McWilliams and Karasov 2001). However, results from such studies of wild birds are not definitive evidence for increases in gut size with elevated food intake because most wild birds change their diets during migratory periods, and this also affects their digestive system (see section below).

Direct evidence for modulation of digestive features in response to changes in food intake comes from work with captive birds. Studies of passerine birds report increased surface area and volume of the gut with long-term increases in food intake (Dykstra and Karasov 1992; Karasov 1996; Piersma and Lindstrom 1997; McWilliams et al. 1999). Only Dykstra and Karasov (1992) and McWilliams et al. (1999), however, have simultaneously measured adjustments in gut anatomy, retention time of digesta, digestive biochemistry (i.e., enzyme hydrolysis rates and/or nutrient absorption rates), and digestive efficiency in response to increased food intake. They found that the rate of digestive enzyme activity and nutrient uptake per unit of small intestine in House Wrens (*Troglodytes aedon*) and Cedar Waxwings (*Bombycilla cedrorum*) did not change with fourfold higher food intake. Instead, the main digestive adjustment to increased food intake was an increase in gut length, mass, and volume, which largely compensated for increased digesta flow at high intake rates so that digestive efficiency remained constant as food intake increased.

If changes in food intake occur faster than the time scale required for digestive adjustment, rather than gradually and slowly, then increased food intake may have quite different effects on digestive performance. We know little about how short-term changes in food intake affect digestive performance in wild birds. When their food was taken away for 2- to 3-h intervals throughout the day, Cedar Waxwings and Yellow-rumped Warblers (*Dendroica coronata*) increased their short-term (hourly) food intake 25 and 50%, respectively, compared with ad libitum conditions (McWilliams and Karasov 1998a, 1998b). These short-term increases in food intake did not result in changes in digestive efficiency or retention time, suggesting some spare digestive capacity when food intake increases by as much as 50%.

We designed a comprehensive study with White-throated Sparrows (*Zonotrichia albicollis*) to determine their response to both rapid and gradual increases in energy demand so that we could estimate the level of spare capacity and phenotypic flexibility in their digestive systems in response to changes in feeding rate. The experiment involved manipulating ambient temperature, which causes changes in the metabolic rate of sparrows (i.e., increased metabolic rate with lower ambient temperature) and thus induces changes in their food intake as they maintain a constant body temperature. By random assignment, sparrows were either held continuously at +21°C, switched rapidly from +21° to –20°C, or gradually acclimated to –20°C over 50 days. For all sparrows in these three treatment groups, we measured daily food intake, digestive efficiency and retention time of starch (the primary nutrient in their semisynthetic diet), ingesta-free mass of the digestive tract (gizzard, small intestine, large intestine), and mass of the liver and pancreas (see McWilliams et al. 1999 for specific methods). The primary prediction was that sparrows switched rapidly from warm to cold temperatures would maintain constant digestive efficiency only if some safety margin of nutrient absorption capacity over nutrient intake existed before the temperature switch.

White-throated Sparrows at –20°C required 83% more food than birds at +21°C, as indicated by their greater feeding rates while maintaining body mass (fig. 6.2). When birds were switched rapidly from +21° to –20°C they increased feeding rate only 45% and lost body mass (fig. 6.2). Interestingly, birds in all three treatment groups had similar digestive efficiency and retention times (fig. 6.2), as measured using a

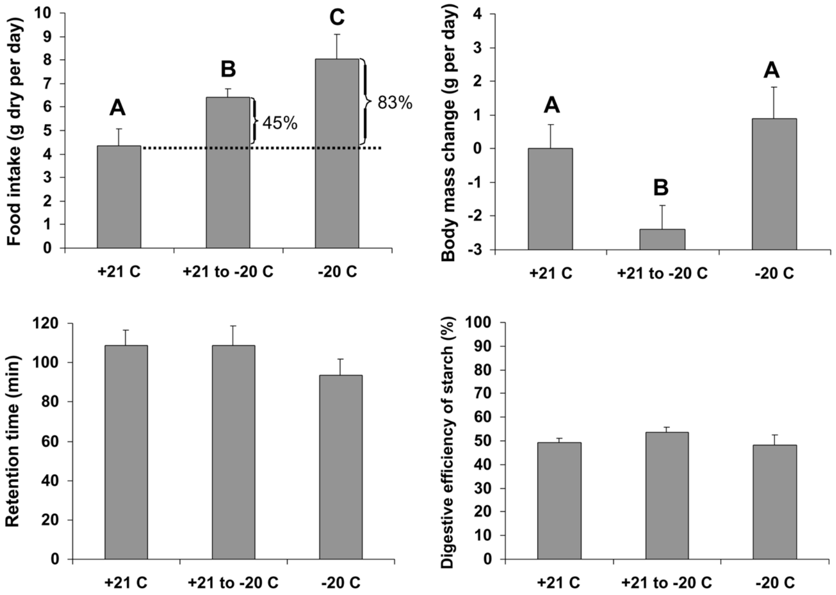

Fig. 6.2. Food intake, body mass change, retention time of digesta, and digestive efficiency of White-throated Sparrows (*Zonotrichia albicollis*) that were either acclimated to +21° or –20°C or switched immediately from +21° to –20°C. Sparrows acclimated to +21°C have a limited spare capacity of about 45% as indicated by an increase in food intake of this magnitude for birds switched rapidly to colder temperatures. These results and those in fig. 6.3 suggest that phenotypic flexibility in digestive features is necessary for sparrows to achieve their ultimate capacity.

radiolabeled inert marker and starch (see McWilliams et al. 1999 for specific methods). Thus, sparrows have some spare capacity (of about 45%) but this was not enough to satisfy the energy demands imposed by a rapid switch from +21° 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 mass of small intestine (fig. 6.3), large intestine, and liver but not gizzard and pancreas. We are currently completing analyses of digestive enzyme activity and nutrient uptake rates to determine if adjustments in these digestive features are involved along with changes in gut size. Note that the 57% increase in small intestine was enough 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. 6.2). 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 83% increased ability to process food. The two measures together imply that sparrows acclimated to –20°C probably still had some spare capacity, perhaps 22% (calculated from the ratio [45 + 57]/83). This makes sense, because it is known that captive White-throated Sparrows can tolerate temperatures down to –29°C, where feeding rates are 2.26 (126%) times higher than at +21°C (Kontogiannis 1968). Thus, the results from the experiment with White-throated Sparrows, along with those by Kontogiannis (1968), conform nicely to the model presented in fig. 6.1 and imply that immediate spare capacity is around 45% but that after long-term acclimation the ultimate capacity is around 126% above "baseline."

Given the lack of change in rates of digestive enzyme activity and nutrient uptake per unit of small intestine in House Wrens and Cedar Waxwings exposed to lowered ambient temperature (Dykstra and Karasov 1992; McWilliams et al. 1999), we suspect that the primary digestive adjustment in White-throated Sparrows (as well as most other passerine birds) to increased food intake is an increase in gut length, mass, and volume. Theoretically, there must be some limit to an animal's ability to enhance gut size, increase food intake, and sustain elevated metabolic rates (see, e.g., Ricklefs 1996, Hammond and Diamond 1997, and Piersma 2002 for recent reviews). For migratory birds that must fly, gut size increases with energy expenditure, but the increase in gut

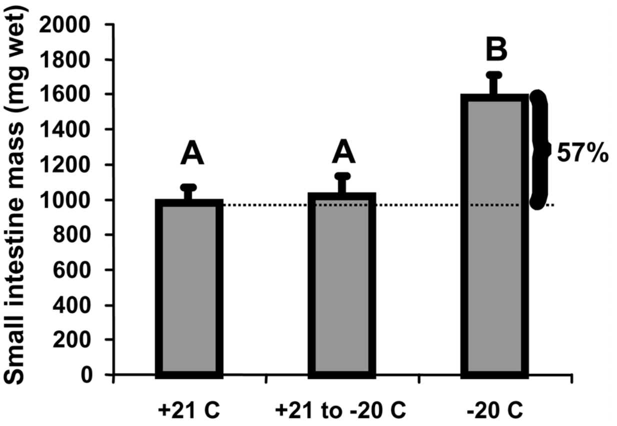

Fig. 6.3. Small intestine mass (mg) of White-throated Sparrows (*Zonotrichia albicollis*) that were either acclimated to +21° or –20°C or switched immediately from +21° to 20°C. See the text for a discussion of how these increases in gut size along with the results shown in Fig. 6.2 can be used to estimate the immediate spare capacity and ultimate capacity of White-throated Sparrows (depicted hypothetically in fig. 6.1 and actually in fig. 6.7).

size may be limited by other physiological and morphological constraints associated with flying.

ATROPHY OF BIRD GUTS DURING MIGRATION

For most migratory songbirds, migration itself involves many flights interspersed with layovers at "stopover" sites where energy and nutrient reserves are rebuilt. Thus, birds during migration alternate between periods of high feeding rate at migratory stopover sites and periods without feeding as they travel between stopover sites. These intervals without food may be relatively short (e.g., less than 8 h) for birds migrating short distances at a given time, or they may last for days for birds migrating over oceans or other large ecological barriers (e.g., deserts, mountains).

Ecological field studies of passerine birds have revealed that recovery of body condition after arrival at stopover sites is typically slow for 1 to 2 days and then much more rapid despite apparently abundant food resources (Davis 1962; Nisbet et al. 1963; Muller and Berger 1966; Langslow 1976; Rappole and Warner 1976; Biebach et al. 1986; Moore and Kerlinger 1987; Hume and Biebach 1996; Gannes 1999). Although ecological conditions influence the rate of recovery (Rappole and Warner 1976; Moore and Kerlinger 1987; Hansson and Pettersson 1989; Kuenzi et al. 1991), birds exhibit the two-step recovery after fasting even when provided food ad libitum in the laboratory (Ketterson and King 1977; Klaassen and Biebach 1994; Hume and Biebach 1996; Gannes 1999; Karasov and Pinshow 2000).

Physiological mechanisms to explain the initially slow recovery of body mass after arrival at a stopover site are largely unexplored (Berthold 1996; Biebach 1996). The gut-limitation hypothesis (see McWilliams and Karasov 2001 for alternative hypotheses) suggests that the initially slow rate of mass gain at stopover sites occurs because birds lose digestive tract tissue and hence digestive function during fasting, and rebuilding of the gut takes time and resources and itself restricts the supply of energy and nutrients from food. Shorebirds studied by Piersma (Piersma 1998, 2002; Piersma and Gill 1998) had reduced digestive organs just before migratory departure, presumably to reduce the energetic costs of carrying larger guts during migratory flight. Other studies of shorebirds as well as passerine birds documented reductions in digestive organs during migratory flights (Biebach 1998; Battley et al. 2000, 2001). Migrant Blackcap Warblers (*Sylvia atricapilla*) at a desert oasis stopover site had reduced digestive organs that increased in size when they were provided food ad libitum (Karasov and Pinshow 1998), and Yellow-rumped Warblers killed by colliding into a radio tower in central Wisconsin during their nocturnal migration had small intestines that were smaller than captive birds (fig. 6.4) (D. A. Afik, pers. comm.).

What are the consequences for migratory birds of having smaller guts after a migratory flight? The effect of reduced digestive organs on food intake and digestive efficiency has been studied in wild-caught Garden Warblers (*Sylvia borin*), Blackcap Warblers, Thrush Nightingale (*Luscinia luscinia*), Yellow-rumped Warblers, and White-throated Sparrows (Klaassen and Biebach 1994; Hume and Biebach 1996; Klaassen et al. 1997; Karasov and Pinshow 2000; Lee et al. 2002; Pierce and McWilliams 2004), and may differ depending on whether gut size was reduced by fasting or food restriction (i.e., reduced feeding). When digestive organs were reduced by fasting, digestible dry matter intake of Blackcap (fig. 6.4) and Garden Warblers were also reduced even though the birds were provided ad libitum food after the fast. In contrast, when Blackcap (fig. 6.4) and Yellow-rumped Warblers were food restricted (ca. 50% of ad libitum daily intake), digestive organs such as the small intestine were reduced by 20% but food intake and digestive

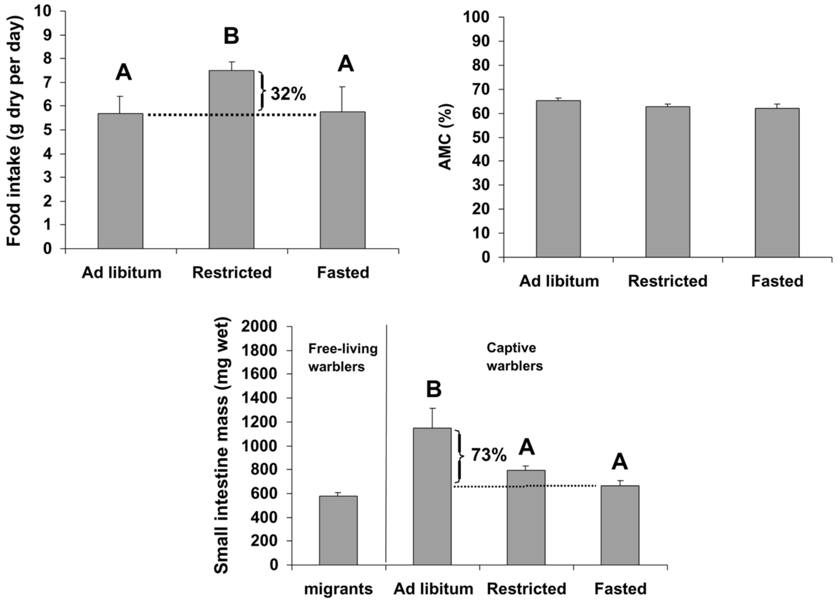

Fig. 6.4. Food intake, apparent metabolizability coefficient (AMC), and small intestine mass of Blackcap Warblers (*Sylvia atricapilla*) on the day the birds were returned to ad libitum feeding after being fasted for 2 days ("fasted"; $n = 7$), fed ad libitum ($n = 6$) or fed for 3 days at 45% ad libitum ("restricted"; $n = 6$). Small intestines of blackcaps were reduced by fasting and food restriction although blackcaps caught just after completing a migration had even smaller intestines ("migrants" [from Karasov and Pinshow 1998]). However, digestible food intake, the product of intake and digestive efficiency, was lower in fasted blackcaps than in food-restricted blackcaps.

efficiency did not change relative to unrestricted birds. Only one published study of a species of wild bird has investigated the effects of fasting or food restriction on biochemical aspects of digestion (Lee et al. 2002). Food restriction reduced digestive enzyme hydrolysis rates by 37–48% in Yellow-rumped Warblers (depending on the type of enzyme [fig. 6.5]).

These studies of captive songbirds demonstrate that reductions in digestive organs occur in both fasted and food-restricted migratory birds, but the reductions in organs of digestion seem to limit refueling rates only in fasted birds. This would suggest that digestion is most likely to constrain refueling rates in long-distance migrants or in other migrants that go without feeding for at least a day at a time. In fact, short-distance migrants, which rarely face extended periods without food, may exhibit phenotypic flexibility in their digestive system like that observed in long-distance migrants, but the spare capacity of their digestive system may usually allow these birds to avoid digestive constraints. For example, Lee et al. (2002) showed that food-restricted warblers had a spare biochemical capacity of at least 37–48% as indicated by their ability to maintain constant food intake and digestive efficiency despite a reduction in digestive organ size and enzyme hydrolysis rates. However, refueling rates of short-distance migrants such as Yellow-rumped Warblers may still be constrained by digestion if their spare capacity is depleted. For example, the free-living Yellow-rumped Warblers that were killed at night by colliding with the radio tower had guts that were more atrophied even than fasted warblers in captivity. If these free-living warblers had survived migration that night, they probably would have had to rebuild their guts before resuming high feeding rates and efficient digestion.

BIRDS SWITCH THEIR DIETS DURING MIGRATION

Migratory birds often switch their diets seasonally. For example, many insectivorous songbirds switch to feeding primarily on fruits during migration (Evans 1966; Herrera 1984; Izhaki and Safriel 1989; Bairlein 1990, 1991; Bairlein and Gwinner 1994; Biebach 1996; Parrish 1997, 2000). In addition, birds on migration may frequently switch their diet because of changes in food availability. For example, migrating birds may one day encounter preferred fruits that are ubiquitous, whereas the next day they may encounter few fruits but insects are ubiquitous. In general, dramatic changes in dietary substrate, for example, from protein- and fat-rich insects to carbohydrate-rich fruits, offer significant physiological challenges for birds (Afik et al. 1995; Afik and Karasov 1995; Karasov 1996; Levey and Martinez del Rio 2001; McWilliams and Karasov 2001). Whether such dietary changes are constrained or facilitated by digestive processes is a central issue in foraging ecology and digestive physiology (Karasov 1990, 1996).

Digestive efficiency for a particular diet eaten by a bird depends in part on the nutrient composition of the diet (Karasov 1990). For example, birds digest nectar almost completely (>95%), and they can assimilate most (ca. 75%) of the energy in seeds, whole vertebrates, insects, and fruits, but birds digest plant foliage relatively poorly (<50%). Similar relative differences in digestive efficiency were observed intraspecifically in omnivorous Yellow-rumped Warblers acclimated to seed, insect, and fruit diets (Afik and Karasov 1995). However, Yellow-rumped Warblers switched from low-fat to high-fat diets and American Robins (*Turdus migratorius*) and European Starlings (*Sturnus vulgaris*) switched

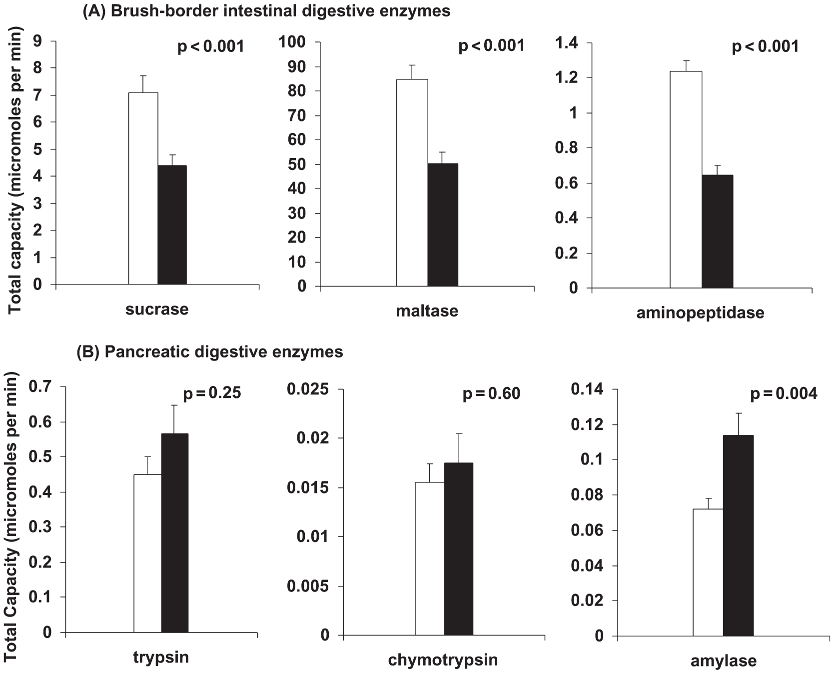

Fig. 6.5. Activity rates of key intestinal (A) and pancreatic (B) digestive enzymes in Yellow-rumped Warblers (*Dendroica coronata*) fed ad libitum (white bars) or fed at 45% ad libitum ("restricted"; black bars) (Lee et al. 2002). Enzyme hydrolysis rates ("total capacity" in micromoles per min) were calculated for the entire small intestine and pancreas given measured mass-specific hydrolysis rates and the mass of the digestive organs. Despite the 37–48% reductions in activity rates of intestinal digestive enzymes and reductions of ca. 20% in small intestine mass, food intake and digestive efficiency were similar in food-restricted and ad libitum fed birds on the day after the birds were returned to ad libitum feeding (see Lee et al. 2002). Thus, these warblers have some spare digestive capacity to compensate for the reductions in gut size and enzyme hydrolysis rates.

from fruit to insect diets had reduced digestive efficiency the day after a diet switch and achieved diet-specific efficiency levels only after 2 to 3 days (Levey and Karasov 1989; Afik and Karasov 1995 [fig. 6.6]). Thus, a migratory bird that switches its diet more frequently than every few days will likely digest a given diet less efficiently than a bird that does not switch diets.

This reduction in digestive efficiency associated with frequent diet switching occurs in part because it takes days for complete modulation of gut size, digestive enzymes, and nutrient uptake transporters (Biviano et al. 1993; Afik et al. 1995; Karasov and Hume 1997; Levey et al. 1999). For example, changes in gut size have been reported in many birds in relation to seasonal changes in diet composition (Pendergast and Boag 1973; Moss 1974, 1983; Ankney 1977; Dubowy 1985; Al-Dabbagh et al. 1987; Walsberg and Thompson 1990; Moorman et al. 1992; Piersma et al. 1993). Such changes in digestive organ size may occur within 1 or 2 days, and certainly within a week, as indicated by measurements of organ size change over time, the rate of cell proliferation, and turnover time of intestine (Piersma et al. 1999; Starck 1999a, 1999b; Dekinga et al. 2001). However, these estimates are based largely on studies of nonpasserine birds (e.g., shorebirds, ducks, quail, and chickens) and only a few notable recent studies of passerine birds (reviewed in Starck 1999b).

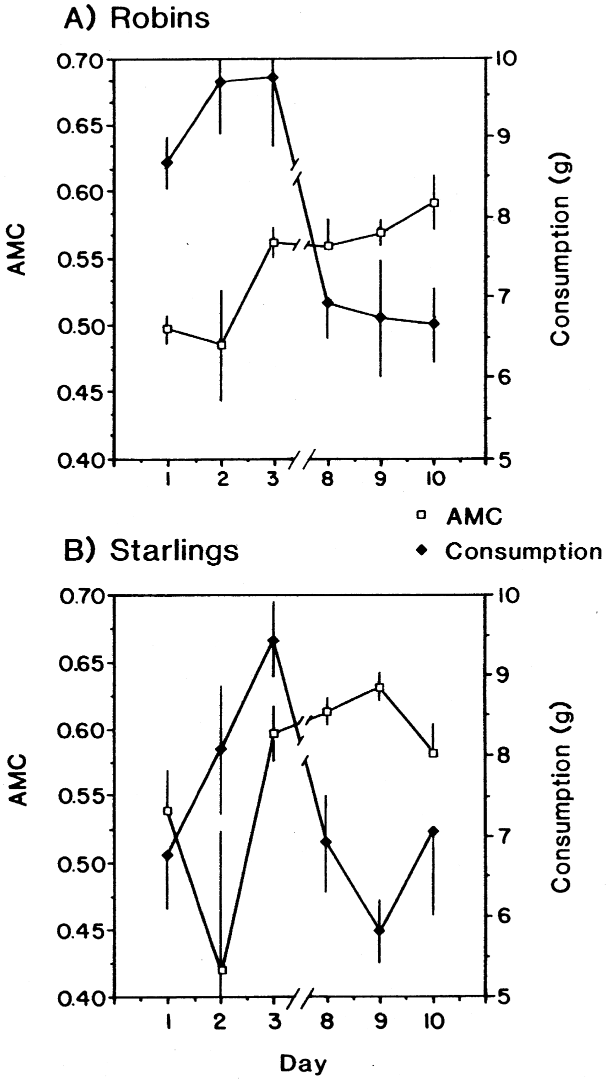

Fig. 6.6. Consumption (g) and apparent metabolizability coefficient (AMC) of crickets (*Acheta domestica*) eaten by American Robins (*Turdus migratorius*) and European Starlings (*Sturnus vulgaris*) as a function of time since switching the birds from a fruit mash diet (Denslow et al. 1987) to crickets. AMC reached diet-specific efficiency levels only after 3 days of feeding on crickets. Figure from Levey and Karasov (1989) with permission of The American Ornithologists' Union and Allen Press, Inc.

Moreover, it is not always true that after a diet switch the initially reduced digestive efficiency improves and eventually reaches levels similar to those in birds regularly eating that diet. Digestive features of some birds are relatively fixed and essentially define the bird's diet. For example, passerine birds in the Sturnidae-Muscicapidae taxon lack sucrase and behaviorally avoid diets with sucrose (Martinez del Rio 1990). Similarly, all vertebrates lack cellulase, the enzyme that can digest plant cellulose. Accordingly, the majority of birds species (97%) do not eat plant leaves or stems, and the few bird species that primarily eat leaves are relatively large birds that use fermentation by indigenous gut microbes to digest cellulose (McWilliams 1999). In the remainder of this section, we discuss digestive constraints associated with switching between certain types of diets.

Among vertebrates in general, nutrient absorption rates and activity of digestive enzymes correlate with the amount of dietary substrate (e.g., protein-digesting enzymes increase with their respective dietary protein substrate, carbohydrate-digesting enzymes increase with their respective dietary carbohydrate substrate [Ferraris and Diamond 1989; Stevens and Hume 1995; Karasov and Hume 1997]). Although there are relatively few studies of digestive enzymes in wild birds, comparisons of bird species with different feeding habits (e.g., insectivores, frugivores, granivores) have generally supported this general pattern (e.g., Afik et al. 1995; Witmer and Martinez del Rio 2001).

In contrast, intraspecific studies of modulation of digestive enzymes and nutrient uptake rate in response to changes in diet composition have not consistently found that enzyme activity or uptake rate changes in proportion to the amount of dietary substrate. For example, activity of digestive enzymes in Pine Warblers (*Dendroica pinus*) changes in proportion to dietary substrate (Levey et al. 1999), but the few other wild passerine birds studied to date exhibit somewhat different patterns of modulation in digestive enzymes. Specifically, wild birds fed diets with higher carbohydrate concentrations did not increase their digestive disaccharidases, whereas birds fed diets with higher protein concentrations increased their aminopeptidase-N activity (Afik and Karasov 1995; Martinez del Rio et al. 1995; Sabat et al. 1998; Caviedes-Vidal et al. 2000). Similarly, none of the four species of omnivorous birds studied to date showed modulation of mediated glucose transport activity, and amino acid uptake increased with dietary protein in only two of the four species studied (Caviedes-Vidal and Karasov 1996; Karasov 1996; Afik et al. 1997a; Chediack et al. 2003). The absence of modulation of mediated glucose transport in birds may occur because birds rely less on active transport for absorption of glucose and more on passive absorption of glucose (Karasov and Cork 1994; Levey and Cipollini 1996; Afik et al. 1997b).

The pattern of modulation of digestive peptidases but not disaccharidases holds across bird species that are dietary generalists and specialists (Sabat et al. 1998), although more comparative studies are needed to determine if dietary flexibility is generally unrelated to this type of digestive plasticity (e.g., see Levey et al. 1999). The lack of modulation of carbohydrate-digesting enzymes suggests that birds switching from insects (mostly protein and fat with little carbohydrate) to fruits (mostly carbohydrate or fat with little protein) may digest the carbohydrates in fruits less efficiently than fruit specialists. Although there are few studies of digestive enzymes in wild frugivorous birds, available evidence provides some support for this hypothesis. For example, omnivorous Pine Warblers up-regulated carbohydrase activity when switched to fruit diets, yet they could not maintain body mass on pure fruit diets and they had relatively low rates of carbohydrase activity compared with the predominantly frugivorous Cedar Waxwing (Levey et al. 1999; Witmer and Martinez del Rio 2001). In contrast, omnivorous Yellow-rumped Warblers did not modulate carbohydrase activity in response to changes in diet (Afik et al. 1995), yet they could maintain body mass on pure fruit diets and their carbohydrase activity was much higher than that of Pine Warblers (Levey et al. 1999) but it was still lower than in Cedar Waxwings (Witmer and Martinez del Rio 2001). Clearly, more research is needed before general patterns of digestive constraints and diet breadth are revealed.

THE PACE OF MIGRATION IN RELATION TO THE PACE OF DIGESTIVE CHANGE

If energy and nutrient demands cannot be satisfied because of inadequate rates of digestion or capacities of the digestive system, then digestive features can constrain choice of diet and food intake. For most birds, the maximum size of the digestive tract is likely limited by constraints associated with flying. For birds that lack certain digestive enzymes, digestive features clearly constrain diet choice. Determining when rates of digestion constrain diet choice or re-fattening rates in migratory birds requires understanding the magnitude of spare volumetric or biochemical capacity relative to the magnitude of change in food quantity or quality.

Studies of short-term changes in food intake suggest that digestion does not appreciably constrain the animal as long as increases in food intake are less than 50% above ad libitum levels (McWilliams and Karasov 1998a, 1998b). Doubling of 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; Dykstra and Karasov 1992; McWilliams et al. 1999). Recent studies have shown that increases in food intake of two- to fourfold are possible without measurable effects on digestive efficiency as long as birds have had sufficient time to acclimate (see "Preparing for Migration" above and fig. 6.7). Presumably, if a fourfold increase in food intake occurred before compensatory changes in these digestive features (i.e., over less than 3 days), then digestive efficiency would decrease.

Whereas the primary digestive adjustment to changes in food quantity is change in the amount of gut and not in the absorption rate of tissue-specific enzymes or nutrients, changes in diet quality cause a suite of digestive adjustments including modulation of digestive enzymes and nutrient uptake rates, as well as gut size (Karasov 1996; Starck 1999a; Dekinga et al. 2001; McWilliams and Karasov 2001). The few studies of short-term changes in food quality suggest that certain changes in diet are possible without measurable effects on digestive efficiency as long as birds have had sufficient time to acclimate (see "Birds Switch Their Diets during Migration" above). However, certain changes in diet (e.g., insects to leaves) are impossible for most birds because of constraints associated with digestion.

How long does it take for the digestive system to become acclimated to such changes in food intake and diet quality? Fasted songbirds (e.g., Blackcaps s and White-throated Sparrows) progressively increased their absorption rates to a maximum over 3 days (Karasov and Pinshow 2000). Intestinal turnover time is 2 to 3 days for small birds compared

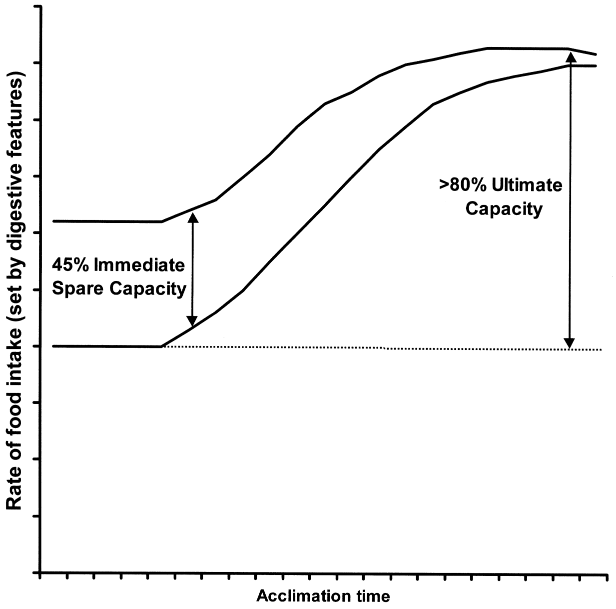

Fig. 6.7. Immediate spare capacity and ultimate capacity (phenotypic flexibility plus immediate spare capacity) for White-throated Sparrows (*Zonotrichia albicollis*) exposed to increasing energy demands associated with cold ambient temperatures. White-throated Sparrows acclimated for at least 50 days at –20°C required 83% more food than birds acclimated at +21°C. When birds were switched rapidly from 21° to –20°C they increased feeding rate only 45% and this was not sufficient to satisfy the extra energy demands given that these birds lost body mass. We estimated that sparrows acclimated to –20°C probably still had some spare excess capacity, perhaps 22% (see text).

to 8 to 12 days for larger birds (Starck 1999b). Activity of digestive enzymes and nutrient transporters increased within 2 days (Karasov and Hume 1997). Digestive organs of birds increased in size within 1 to 6 days after switching diet or increasing food intake (Dekinga et al. 2001; McWilliams and Karasov 2001). Thus, digestive adjustments in response to certain changes in diet quantity and quality appear to require at least a few days and perhaps as much as a week or more, depending on the type of digestive adjustment (see fig. 6.7). For an actively migrating bird, this pace of digestive change may be too slow and so digestive constraints may directly retard the pace of bird migration.

CONCLUSIONS AND FUTURE DIRECTIONS

If the biological cost associated with maintaining large guts were minimal or the consumable resources used by migratory birds were relatively constant, then migratory birds would likely maintain a relatively constant and enlarged digestive system with significant excess capacity. However, phenotypic flexibility in the digestive system of migratory birds is pervasive and we have shown here that birds maintain significant but limited spare capacity. For migratory birds, phenotypic flexibility and spare capacity in the digestive system have likely evolved both to reduce the biological costs associated with maintaining large guts and to solve the difficult physiological problems associated with a changing environment.

In general, maintaining large guts is costly, in part because digestive organs are some of the most metabolically active tissues in vertebrates. Quantitative measurements of the costs associated with maintaining extensive spare capacity and phenotypic flexibility in the digestive system of migratory birds have not yet been attempted. These costs would include not only the energetic and nutritional costs of maintaining more gut than immediately necessary, but also the trade-offs associated with using the finite space within the animal for digestive organs and tissues instead of other necessary physiological systems (Diamond 1998). For migratory birds in particular, carrying the extra mass of enlarged digestive organs imposes an additional energetic cost during flight. Thus, although empirical data are lacking, the biological costs associated with maintaining large guts are likely to be significant for migratory birds.

Phenotypic flexibility and spare capacity are adaptive for animals that live in a changing environment. Certainly, the migratory habit of some birds has evolved to take advantage of seasonal environments that are quite dynamic over time. We have argued that most migratory birds change both what they eat and the amount they eat as a normal part of migration; thus, food resources used by migratory birds are dynamic and, in this sense, too, migratory birds live in a changing environment. What remains to be determined is whether phenotypic flexibility and spare capacity are greater in migratory birds than in nonmigratory birds.

Theoretically, animals in highly variable environments or those that are mobile and so encounter quite different environments during their annual cycle (e.g., migratory birds) are more likely to have evolved phenotypic flexibility. We have provided examples of how phenotypic flexibility and spare capacity of the digestive system are critically important to the success of migratory birds. However, there is little evidence that these features of the digestive system are unique to migratory birds. This is, in part, because too few studies have focused on this aspect of birds as a group. No study has compared the extent of phenotypic flexibility and spare capacity in migratory and nonmigratory birds with appropriate controls for phylogeny. We caution that such a study would have to be carefully planned. Some migratory birds (e.g., albatrosses) travel great distances as they track the same food resource(s), for example, so their food resources are relatively unchanging despite their extensive travels. As well, relatively sedentary birds that live in northern latitudes, such as Ruffed Grouse (*Bonasa umbellus*), must successfully overcome dramatic seasonal changes in their environment. Thus, migration alone is unlikely to select for phenotypic flexibility in the digestive system of birds.

Migratory birds that vary in the extent to which they change diets and the amount they eat would be the most useful subjects for comparative studies of phenotypic flexibility and spare capacity. We predict that phenotypic flexibility in the digestive system will be most extensive in migratory birds that regularly switch their diet or that dramatically alter their food intake as a regular part of their migration. Studies cited here provide examples of how to measure phenotypic flexibility and spare capacity of the digestive system in birds. What remains to be discovered is how the flexibility and capacity of the avian digestive system vary across taxa and how they are related to the phylogeny, ecology, and life history of birds.

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