

Review

Phenotypic flexibility in digestive system structure and function in migratory birds and its ecological significance

Scott R. McWilliams^{a,*}, William H. Karasov^b

^a*Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881, USA*

^b*Department of Wildlife Ecology, University of Wisconsin, Madison, WI 53706, USA*

Received 1 April 2000; received in revised form 31 August 2000; accepted 4 October 2000

Abstract

Birds during migration must satisfy the high energy and nutrient demands associated with repeated, intensive flight while often experiencing unpredictable variation in food supply and food quality. Solutions to such different challenges may often be physiologically incompatible. For example, increased food intake and gut size are primarily responsible for satisfying the high energy and nutrient demands associated with migration in birds. However, short-term fasting or food restriction during flight may cause partial atrophy of the gut that may limit utilization of ingested food energy and nutrients. We review the evidence available on the effects of long- and short-term changes in food quality and quantity on digestive performance in migratory birds, and the importance of digestive constraints in limiting the tempo of migration in birds. Another important physiological consequence of feeding in birds is the effect of diet on body composition dynamics during migration. Recent evidence suggests that birds utilize and replenish both protein and fat reserves during migration, and diet quality influences the rate of replenishment of both these reserves. We conclude that diet and phenotypic flexibility in both body composition and the digestive system of migratory birds are important in allowing birds to successfully overcome the often-conflicting physiological challenges of migration. © 2001 Elsevier Science Inc. All rights reserved.

Keywords: Body composition; Digestive system; Fasting; Food intake; Food quality; Migratory birds; Phenotypic flexibility

1. Introduction

Birds face many physiological challenges during migration, especially in terms of feeding and digestion. In preparation for migration, birds increase their food intake (i.e. become hyperphagic) and store the energy and nutrient reserves neces-

sary to fuel the costs of subsequent migratory flight(s) (Alerstram and Lindstrom, 1990; Blem, 1990; Biebach, 1996). For most temperate zone breeding 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. < 8 h) for birds

* Corresponding author. Tel.: +1-401-874-7531; fax: +1-401-874-4561.

E-mail address: srmcwilliams@uri.edu (S.R. McWilliams).

migrating short distances at a given time or the intervals without food may last for days for birds migrating over oceans or other large ecological barriers (e.g. deserts, mountains). Herein we review how hyperphagia and short-term fasting affect digestive structure and function in migratory birds, and how they may influence the tempo of their migration.

Migratory birds often switch their diets seasonally. For example, many waterfowl switch from high carbohydrate foods (e.g. seeds) to high protein foods (e.g. aquatic insects, new plant tissue) when preparing for breeding (Krapu and Reinecke, 1992). Also, 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). This dietary switch from insects to fruits may conserve energy because fruits that are abundant are less energetically expensive to obtain compared to insects. Fruits may be nutritionally adequate if only fat reserves must be replenished. However, fruits may be inadequate if birds must replenish both fat and protein reserves during migration because, in general, fruits contain relatively little protein (Biebach, 1996). Dramatic changes in dietary substrate from, for example, protein-rich insects to carbohydrate-rich fruits, offer significant physiological challenges for birds (Afik and Karasov, 1995; Karasov, 1996). Herein we review how changes in diet quality affect digestive structure and function in migratory birds, and how it may influence the tempo of their migration.

2. Phenotypic plasticity and flexibility in physiological systems

Physiological adaptation can be deduced from comparative interspecific analyses of traits (e.g. organ size and function, nutrient transport rates and metabolic rate) with appropriate control for phylogeny. Accordingly, a central theme of evolutionary physiology involves conducting comparative studies of physiological traits in vertebrate taxa with different life styles (Feder et al., 1987; Wainwright and Reilly, 1994). However, many such physiological traits exhibit considerable variability in ecological time both within and among individuals which may make it difficult to detect important adapted patterns. The form of pheno-

typic variation that involves a single genotype producing different phenotypes in response to variation in some environmental variable is called 'phenotypic plasticity' (Travis, 1994; Piersma and Lindstrom, 1997). Rapid reversible changes in body composition, organ size, and digestive processes provide examples of flexible norms of reaction (Stearns, 1989; Travis, 1994) or 'phenotypic flexibility' in that they may represent flexible responses to changes in the environment (Piersma and Lindstrom, 1997). Such 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).

Understanding the patterns and consequences of phenotypic plasticity and flexibility has important implications for animal ecology. Defining these implications requires mechanistically linking the study of the trait in its various forms with some ecologically relevant performance criteria (Arnold, 1983; Wainwright and Reilly, 1994). Ecomorphologists have established a tradition of such studies although their usual focus is on comparing the average response of many individuals, thus viewing variation in response or phenotypic plasticity as a nuisance to be avoided or at least for which control must be exercised. One of the central themes in this paper is that both body composition and digestive features of migratory songbirds are modulated in response to environmental change and this phenotypic flexibility has important ecological consequences for birds during migration.

3. Food intake and digestive performance

The energetic gains that are realized by a bird when it eats more depend on interactions between food intake rates and digestive efficiency (Karasov, 1996). In the absence of extensive spare digestive capacity, if the absorptive surface of the gut or its capacity for absorption does not change when a bird eats more, then the increased flow of digesta may cause digestive efficiency to decline and thereby directly discount the potential energetic gains provided by hyperphagia. Alternatively, if gut size increases with food intake, then

digestive efficiency may not change when a bird eats more. If tissue-specific digestive enzyme rate or nutrient transport activity increases with food intake (with no change in gut size), then digestive efficiency may also not change when a bird eats more. Below we discuss the effects of long-term and short-term increases in feeding rates on digestive performance in birds.

3.1. Effects of long-term increases in food intake on digestive performance

Many studies of birds report increased surface area and volume of the gut with long-term increases in food intake (Savory and Gentle, 1976a,b; Savory, 1986; Dykstra and Karasov, 1992; Piersma et al., 1993; Karasov, 1996; Piersma and Lindstrom, 1997; McWilliams et al., 1999) (Table 1). However, only a few of these studies have addressed whether such changes in the gut compensate for the potentially negative effects of increased food intake on digestive efficiency (e.g. Savory, 1986; Dykstra and Karasov, 1992) (Table 1). Dykstra and Karasov (1992) and McWilliams et al. (1999) provide the only studies to date in birds that 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 rate of digestive enzyme activity and nutrient uptake per unit of small intestine

did not change with four-fold higher food intake. Instead, the main digestive adjustment to increased food intake was an increase in gut length, mass, and volume that largely compensated for increased digesta flow at high intake rates.

Digestive efficiency in some birds has been reported to increase with increasing intake (Owen, 1970; Stalmaster and Gessaman, 1982; Dykstra and Karasov, 1992) whereas in other birds, digestive efficiency has been reported to not change (El-Wailly, 1966; Hamilton, 1985) or decline with increasing intake (West, 1968; Moss and Parkinson, 1972). Bairlein (Bairlein, 1985; Bairlein and Simons, 1995) suggested that increased digestive efficiency during hyperphagia is a key mechanism by which premigratory fattening is achieved in birds, although his conclusion was based on measurements of apparent and not true digestibility (Karasov, 1996). More recent studies of migratory birds report a slight increase (Hume and Biebach, 1996) or no change in digestive efficiency associated with increases in food intake during migratory periods or during cold temperatures (McWilliams et al., 1999; Karasov and Pinshow, 2000). Based on current evidence, hyperphagia is the main mechanism by which energy assimilation is increased and fattening achieved in migratory birds.

In summary, birds primarily adjust amount of gut rather than tissue-specific enzyme or nutrient absorption rates with long-term increases in food intake. The increase in gut size allows digestive

Table 1
Phenotypic flexibility in digestive features and digestive performance in response to changes in food intake in migratory birds^a

Digestive character	Effect of short-term increase in food intake	Effect of long-term increase in food intake
<i>Digestive feature:</i>		
Gut size	No change	Increase
Specific enzyme activity ^b		
Disaccharidases	(Not measured)	No change
Aminopeptidase-N	(Not measured)	No change
Specific uptake rate ^b		
Glucose	(Not measured)	No change
Amino acids	(Not measured)	No change
<i>Digestive performance:</i>		
Digestive efficiency	No change	No change or increase
Retention time	No change	No change

^aSee text for references.

^bPer unit mass or length of gut.

efficiency to remain constant as food intake increases. Theoretically, there must be some limit to an animal's ability to enhance digestive features, increase food intake, and sustain elevated metabolic rates (see Ricklefs, 1996 and Hammond and Diamond, 1997 for recent reviews). For migratory birds that must fly, gut size increases with energy expenditure but the increase in gut size may be limited by other physiological constraints associated with flying.

3.2. Effects of short-term increases in food intake on digestive performance

Birds may often experience short-term changes in food quantity that occur faster than the time scale required for changes in gut morphology. For example, birds during migration may one day encounter preferred fruits or insects that are ubiquitous, allowing relatively constant food intake, whereas the next day their preferred foods may be patchily distributed and require much travel time between patches. In such situations, a bird's pattern of food intake may differ from day to day. If changes in food intake occur faster than the time scale required for digestive adjustment, then increased food intake may have quite different effects on digestive performance compared to when longer acclimation times occur.

We know little about how short-term changes in food intake affect digestive performance in wild birds. Theoretical optimality models make explicit predictions about how an animal's digestive parameters should respond to short-term changes in time or energy costs associated with procuring food (Penry and Jumars, 1986, 1987; Martinez del Rio and Karasov, 1990; Martinez del Rio et al., 1994). If animals maximize the net rate of energy gain, then the model predicts that when costs of food acquisition are increased, food should be held longer in the intestine and thus nutrients in the food will be more thoroughly digested despite higher food intake. Importantly, if retention time and extraction efficiency are modulated as predicted by the model, then determining the profitability (e.g. energetic gain divided by the energetic costs) of a given food type is complicated because digestive efficiency is not fixed but is instead conditional on the costs of acquiring the food.

Only two studies have empirically tested the model's predictions regarding the effect of short-

term changes in food intake on digestive performance (McWilliams and Karasov, 1998a,b). In both tests of the model, gut volume or size was assumed constant because the changes in food intake occurred within a day. Adding 2–3 h intervals when the birds received no food caused both Cedar Waxwings (*Bombycilla cedrorum*) and Yellow-rumped Warblers (*Dendroica coronata*) to increase their food intake 25 and 50%, respectively, compared to ad libitum conditions. However, contrary to the predictions of the model, digestive efficiency and retention time remained constant as food intake and costs of feeding increased (Table 1). These results suggest that birds may minimize feeding time by maximizing their extraction efficiency rather than maximizing their net rate of energy gain by reducing extraction efficiency in favor of eating more.

In summary, short-term increases in food intake did not result in changes in digestive efficiency or retention time, as predicted by optimal digestion models. Modulation of food intake and digesta mixing may be the primary ways high, constant extraction efficiency is maintained during short-term changes in food intake. The ability of birds to maintain high digestive efficiency with no change in retention time suggests some spare digestive capacity when food intake increases by as much as 50%. In general, animals at a given level of energy intake maintain some spare digestive capacity as evidenced by an ability to rapidly increase food intake without loss of digestive efficiency (Diamond, 1991). As energy requirements and thus food intake increase, however, the level of spare capacity at least in small mammals declines even after sufficient acclimation time (Toloza et al., 1991).

4. Diet quality and digestive performance

If digestive features such as gut size and rates of enzyme hydrolysis and absorption are relatively fixed, then digestive processes will largely determine diet. Species lacking particular digestive enzyme(s) provide clear examples of how digestive features directly constrain diet flexibility. Passerine birds in the Sturnidae-Muscicapidae taxon lack sucrase and behaviorally avoid diets with sucrose (Martinez del Rio, 1990). Although cellulose is the most abundant compound in the biosphere, no vertebrate produces cellulase

(Karasov and Hume, 1997). Accordingly, the majority of birds species (97%) do not eat leaves or stems of terrestrial plants, 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).

If digestive features are modulated in response to changes in diet, then diet can determine digestive performance to some extent. We focus the remainder of this section on those situations in which temporal changes in diet quality affect digestive performance in birds. Time-scale of the change in diet relative to the digestive adjustment is important, so we divide the following discussion into long-term and short-term effects of diet change on digestive performance.

4.1. Effects of long-term changes in food quality on digestive performance

As discussed above, the primary digestive adjustment to long-term changes in food quantity is changes in amount of gut and not in tissue-specific enzyme or nutrient absorption rate. In contrast, long-term changes in diet quality cause a suite of digestive adjustments including modulation of digestive enzymes, nutrient uptake rates, as well as gut size (Karasov, 1996). Consequently, we discuss the effects of long-term changes in food quality separately for each of these digestive features.

Activity of digestive enzymes in vertebrates, including pancreatic proteases, amylase and lipase as well as intestinal aminopeptidase, sucrase and maltase, generally change in proportion to the amount of dietary substrate (i.e. protein-digesting enzymes increase with their respective dietary protein substrate, carbohydrate-digesting enzymes increase with their respective dietary carbohydrate substrate) (Stevens and Hume, 1995; Karasov and Hume, 1997). Although this generalization holds for poultry (see Karasov, 1996 for review), the few wild 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) (Table 2). This 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.

Studies of absorption rate of dietary nutrients in the intestine of vertebrates provide strong evidence for adaptive modulation of digestive fea-

Table 2

Phenotypic flexibility in digestive features and digestive performance in response to changes in food quality in migratory birds^a

Digestive character	Effect of short-term increase in food quality	Effect of long-term increase in food quality
<i>Digestive feature:</i>		
Gut size	No change	Decrease
Specific enzyme activity ^b		
Disaccharidases	(Not measured)	No change
Aminopeptidase-N	(Not measured)	Increase ^c
Specific uptake rate ^b		
Glucose	(Not measured)	No change
Amino acids	(Not measured)	Increase ^c or no change
<i>Digestive performance:</i>		
Digestive efficiency	No change	Change ^d
Retention time	Increase or no change	Change ^d
Food intake	Decrease or no change	Change ^d

^a See text for references.

^b Per unit mass or length of gut.

^c Change in food quality involved increasing dietary protein.

^d Direction of change depends on nutrient composition of diets.

tures in response to diet change (Ferraris and Diamond, 1989; Karasov and Hume, 1997). However, birds do not conform to some patterns of modulation of nutrient uptake rates that are evident in other vertebrates. For example, none of the four species of omnivorous birds studied to date showed modulation of mediated glucose transport activity as measured using the everted sleeve technique (reviewed by Karasov, 1996) (Table 2). However, the recent demonstration that this method causes tissue damage in some species (Starck et al., 2000) underscores the need for additional careful testing in more avian species. Amino acid uptake increased with dietary protein in only two of the four species (Caviedes-Vidal and Karasov, 1996; Karasov, 1996a; Afik et al., 1997a). 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). Whether passive glucose absorption is modulated in birds is not known.

Phenotypic flexibility in gut size has been reported in many birds in relation to seasonal changes in diet composition (Pendergast and Boag, 1973; Moss, 1974; Ankney, 1977; Moss, 1983; Dubowy, 1985; Al-Dabbagh et al., 1987; Walsberg and Thompson, 1990; Moorman et al., 1992; Piersma et al., 1993). Diet quality may affect gut size by directly influencing food intake. Since food intake generally increases with dilution of dietary energy, animals acclimated to poorer quality diets with lower energy density will increase food intake and thus have larger gut volume or mass (Miller, 1975; Savory and Gentle, 1976a,b; Kehoe et al., 1988; Starck and Kloss, 1995).

Alternatively, diet quality may directly affect retention time of digesta and digestive efficiency independent of changes in food intake (Table 2). Mean retention time of digesta is longest for granivorous birds, shorter for insectivorous birds, and shortest for frugivorous birds (Castro et al., 1989; Karasov, 1990; Levey and Karasov, 1994). 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 can assimilate most (approx. 75%) of the energy in seeds, whole vertebrates, insects, and

fruits. Similar relative differences in retention time of digesta and digestive efficiency were observed intra-specifically in Yellow-rumped Warblers habituated to seed, insect, and fruit diets (Afik and Karasov, 1995).

4.2. Effects of short-term changes in food quality on digestive performance

Birds may often experience short-term changes in food quality that occur faster than the time scale required for changes in digestive features. For example, birds during migration may one day encounter preferred fruits that are ubiquitous, whereas the next day they may encounter few fruits, but insects are ubiquitous. In such situations, diet of a bird may differ from day to day. Changes in food quality may occur faster than the time scale required for biochemical or morphological adjustment.

We know little about how short-term changes in food quality affect digestive performance in wild birds. If animals maximize the net rate of energy gain, then optimality models predict that when food quality increases, intestinal residence time of digesta will decrease and thus nutrients in the food will be less thoroughly digested (Penry and Jumars, 1986, 1987; Martinez del Rio and Karasov, 1990; Martinez del Rio et al., 1994). In short, the model predicts that animals will expel some of the digesta prior to complete absorption (and so decrease digestive efficiency) and refill the gut with higher concentration food (and so decrease mean retention time).

Only three studies have empirically tested the model's predictions regarding the effect of short-term changes in food quality on digestive performance (Karasov and Cork, 1996; Lopez-Calleja et al., 1997; Levey and Martinez del Rio, 1999). In all tests of the model, manipulations of food quality involved rapid changes in dietary sugar concentration. Contrary to the predictions of the model, digestive efficiency did not change with sugar concentration, and retention time either did not change (Karasov and Cork, 1996) or increased with increasing sugar concentration (Lopez-Calleja et al., 1997; Levey and Martinez del Rio, 1999) (Table 2). Modulation of retention time in the latter two studies occurred rapidly, within a few hours of the diet switch. None of these results were consistent with the predictions of the optimal digestion model. These results suggest that

birds may minimize feeding time by maximizing their extraction efficiency during short-term changes in food quality (and quantity—see above).

During short-term increases in food quality, high digestive efficiency may be maintained by negative feedback from intestinal receptors that detect high nutrient concentrations in digesta and so slow digesta flow. Such control mechanisms are known to occur in mammals (Spiller et al., 1984) but have not yet been verified in birds (Karasov and Hume, 1997).

5. Time-scale of digestive adjustments and changes in spare capacity

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, 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 the degree to which digestion constrains the animal is probably limited as long as increases in food intake are <50% above ad libitum levels (McWilliams and Karasov, 1998a,b). If birds are given adequate time to acclimate, then increases in food intake of two–four-fold are possible without measurable effects on digestive efficiency. 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). Presumably, if a four-fold increase in food intake occurred before compensatory changes in gut size, then digestive efficiency would decrease.

Unfortunately, we know little about the time required for digestive adjustments. Reversible changes in gut length in response to changes in diet composition have been reported to occur within three to four weeks in grouse and quail (Moss and Parkinson, 1972; Savory and Gentle,

1976a,b) and ducks (Miller, 1975; Drobney, 1984; Kehoe et al., 1988). Turnover time of intestinal epithelium in adult Japanese quail (*Coturnix coturnix japonica*) was 9–17 days depending on the region of the intestine (Starck, 1996) and may be as fast as a few hours or days in very young birds (Imondi and Bird, 1966; Lilja, 1987; Starck, 1999). Based on this evidence, daily changes in food quantity are likely faster than the time scale required for changes in gut size in at least adult birds.

The few studies of short-term changes in food quality suggest that at least a few days are necessary for adjustments in activity of digestive enzymes. Yellow-rumped warblers switched from low fat to high fat diets (Afik et al., 1995), and American Robins (*Turdus migratorius*) and European Starlings (*Sturnis vulgaris*) switched from fruit to insect diets (Levey and Karasov, 1989), all progressively increased digestive efficiency within days of the diet switch. The increased digestive efficiency in the warblers was not apparent within the first 2 h after the diet switch (Afik et al., 1995). Thus, digestive adjustments in response to these types of changes in diet quality appear more rapid than digestive responses to changes in diet quantity, although this conclusion is based on relatively few studies. In the following two sections, we discuss how the time-scale of digestive adjustments may influence the tempo of migration in birds.

6. Effects of short-term fasting on body composition and digestive performance

Seasonal changes in body composition of small migratory passerine birds are common and critically important for fueling their migration (Blem, 1976, 1980, 1990). Passerine birds increase their fat loads considerably during migratory periods (fat loads are 24% on average, 70% maximum) compared to pre-migratory periods (when fat loads are <5% on average) (Blem, 1980; Alerstram and Lindstrom, 1990). The increase in body mass in birds during migration has been commonly assumed to be composed of fat and no protein (Connell et al., 1960; Odum et al., 1964, 1965; Blem, 1980, 1990). More recent studies of non-passerine and passerine birds, however, suggest that the reserves in birds may be composed of appreciable amounts of protein as well as fat

(van der Meer and Piersma, 1994; Piersma and Lindstrom, 1997; Karasov and Pinshow, 1998).

Studies of non-passerine birds suggest the following hypothesis regarding prioritized use of body components during food deprivation: a progression from use of glycogen, then lipid, then protein to fuel metabolic needs in fasted birds. Recent theoretical treatments of body composition dynamics in migratory birds in general assume this prioritized use of body components (van der Meer and Piersma, 1994). Glycogen stores are limited in birds (Blem, 1976), and if these decline enough during food deprivation, lipids are used for fuel (Ramenofsky, 1990). The timescale for depletion of glycogen stores is on the order of hours (Farner et al., 1961). The timescale for depletion of lipid stores is on the order of many days, although it can be quite variable because lipid depots vary on a daily and seasonal basis and increase with body size (Blem, 1976, 1990). If food deprivation is prolonged, gluconeogenesis is enhanced by amino acid metabolism and is stimulated by increased glucocorticoid secretion (Biebach et al., 1986). Thus, a progression from use of glycogen then lipid then protein is apparent in fasted non-passerine birds (LeMaho et al., 1981; Groscolas, 1986; Cherel et al., 1988; LeMaho et al., 1991; Lindgard et al., 1992). Reduction in flight muscle or in the ability of the digestive system to supply energy and nutrients for flight could directly limit migratory performance (Piersma et al., 1999). Alternatively, reduced gut size may be an adaptive strategy associated with migration because of the benefits of reduced wing loading (Piersma and Lindstrom, 1997).

For birds other than penguins, domestic geese, galliformes (e.g. grouse and chickens), and shorebirds, very little is known about the dynamics of body composition and use of fat and protein reserves during episodic undernutrition (Murphy, 1996), like that experienced by some passerines during migration. This pattern of prioritized use of body components in fasted non-passerine birds may not apply to migratory songbirds. Many of the non-passerine species studied to date regularly go through long periods without eating during the breeding season as a normal part of their life history, and their fat and protein reserves enable fasting for months. In contrast, periods of food deprivation are shorter in duration for passerine birds (rarely as long as one week) and

are associated mainly with the migration period (Berthold, 1975; Biebach, 1996). Two recent studies of small passerine birds suggest simultaneous rather than sequential use of fat and protein stores during food deprivation (Swain, 1992; Karasov and Pinshow, 1998).

Ecological field studies of passerine birds have revealed that recovery of body condition after arrival at stopover sites is typically slow for one to two 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 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 initial mass loss after arrival at a stopover site are largely unexplored (Berthold, 1996; Biebach, 1996), but two hypotheses have some support. The nutrient-limitation hypothesis suggests that the initially slow rate of mass gain occurs because birds utilize protein reserves during migration, and recovery of these protein reserves must occur first, and is slow. Only after recovery of protein reserves can lipid reserves be repleted and, once initiated, this recovery of lipid reserves is faster. This hypothesis is supported by studies of migrating hummingbirds (Carpenter et al., 1983), domestic geese (LeMaho et al., 1981; McLandress and Raveling, 1981; Cherel et al., 1988), shorebirds (van der Meer and Piersma, 1994), and a few passerine birds (Kendall et al. 1973; Jones and Ward, 1976; Marsh, 1983, 1984; Selman and Houston, 1996).

Alternatively, the gut-limitation hypothesis 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. This hypothesis is supported by studies that show reduced gut size after fasting in mammals and chickens (reviewed by

Karasov, 1988) and by a few studies on migratory songbirds that show food intake and gut function are reduced after fasting (e.g. Ketterson and King, 1977; Klaassen and Biebach, 1994; Hume and Biebach, 1996; Klaassen et al., 1997; Karasov and Pinshow, 2000).

These hypotheses may not be mutually exclusive if protein in the gastrointestinal tract is used as a primary source of reserve protein (Piersma et al., 1993; Piersma and Lindstrom, 1997; Piersma, 1998). Karasov and Pinshow (1998) provide the only quantitative support for this idea in a migratory songbird. They showed that a disproportionate amount (44%) of protein lost during fasting in Blackcaps (*Sylvia atricapilla*) occurred as loss of small intestine, stomach, and liver tissue. Although Blackcaps lost gut and liver mass during fasting, it is unclear whether this available protein was used as a nutrient reserve or whether it was simply lost through disuse and excretion.

7. Conclusions

Birds during migration adjust their food intake and often eat foods that vary appreciably in nutrient composition and hence quality. These changes in food intake and food quality are associated with changes in digestive features (e.g. gut size, nutrient uptake rates and hydrolytic activity of digestive enzymes) and digestive performance (e.g. digestive efficiency and retention time of nutrients). In addition, short-term fasting may cause atrophy of the gut that then may limit utilization of ingested food energy and nutrients. The results relevant to birds during migration can be summarized as follows: (a) mass of the small intestine and gizzard increase with food intake as occurs during the migratory period (McWilliams and Karasov, 1998a,b; McWilliams et al., 1999), (b) increase in food intake is not associated with significant changes in mass-specific activity of digestive enzymes or nutrient uptake rates (McWilliams and Karasov, 1998a,b; McWilliams et al., 1999), (c) change in diet from insects to fruits, as occurs in many small migratory birds during migration (Blem, 1976; Herrera, 1984; Izhaki and Safriel, 1989; Bairlein, 1990; Parrish, 1997), can involve substantial changes in digestive organ size and mass-specific activity of digestive enzymes or nutrient uptake rates (e.g. Afik and Karasov,

1995), and (d) digestive organ size and function may be compromised by food deprivation (Hume and Biebach, 1996; Karasov and Pinshow, 1998, 2000), as may occur during overnight or long-distance migration over ecological barriers.

In summary, phenotypic flexibility in the digestive system of migratory birds is critically important in allowing birds to successfully overcome the conflicting physiological challenges of migration. However, phenotypic flexibility in the digestive system of birds has limits and this can influence the tempo of migration in birds. For example, partial atrophy of the gut, after 1–2 days without feeding, limits utilization of ingested food energy and nutrients and thereby slows the pace of migration in birds. If birds lack certain digestive enzymes, then this directly limits diet choice and utilization of foods that require such enzymes for digestion. If birds regularly switch diets, then this 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. Such limits on food intake and utilization of ingested food energy and nutrients may slow the pace of migration in birds, especially if food resources and foraging time are limited. In short, digestive constraints are likely to influence the tempo of migration in birds when birds must refuel after 1–2 days without feeding, when birds lack certain digestive enzymes, when birds regularly switch diets, and when birds are hyperphagic and must also fly.

8. Future directions

8.1. Integrative studies of digestive performance

Predicting the effect of changes in food quality and quantity on digestive performance in migratory birds requires understanding interactions between digestive adjustments and their ecological consequences. Most of our understanding to date is based on separate experiments in which food quality or quantity is manipulated and its effects on digestive performance assessed using only one or a few digestive features (e.g. gut size). More integrative studies are needed that simultaneously measure adjustments in gut anatomy, re-

tention time of digesta, enzyme hydrolysis rates, nutrient absorption rates, and digestive efficiency in response to changes in food quantity and quality.

8.2. Modulation of digestive enzymes and nutrient transporters

Evidence to date on modulation of digestive enzymes and nutrient transport rates in birds suggest important differences between birds and other vertebrates. However, this evidence is restricted to a few species representing only a few taxonomic groups. More comparative studies are needed that focus on factors that influence modulation of digestive enzymes and nutrient transport rates in birds. Studies of passive vs. active absorption of glucose in birds, and their modulation, would be especially important.

8.3. Time-scale of digestive adjustments

The time-scale required for digestive adjustments to changes in food intake and quality is poorly understood. A key issue is whether digestive adjustments occur because of changes in food intake and quality during migration or whether they occur in anticipation of migration (e.g. Piersma, 1998).

8.4. Spare capacity and digestive constraints

One of the challenges of the future is delineating how much spare capacity the animal maintains and in what situations if any the level of spare capacity is modulated. Studies in mammals suggest that the level of spare capacity declines as energy demands approach maximum sustainable levels (Toloza et al., 1991; Hammond and Diamond, 1997). Tests of the hypothesis using migratory birds would be especially enlightening because their response is likely different than mammals that do not fly.

8.5. Dynamics of body composition in small migratory birds

Understanding the dynamics of body composition in small migratory songbirds has fundamental and practical importance. The dynamics of body composition influences nutrient requirements which then interacts with resource avail-

ability to determine length of stopover at sites along the migration route, the pace of migration, and ultimately the success and survival of individuals. For example, if fat and protein are utilized during migration, then estimates of flight distances will be overestimated and dehydration problems more acute than if all mass loss were composed of fat (Klaassen, 1996; Klaassen and Lindstrom, 1996). If significant loss of protein occurs during migration then it becomes essential to determine the source of this reserve protein in the body, and the dietary source(s) for replacing it.

Of the few studies reporting utilization of fat and protein reserves in migratory passerines, most use regressions of fat mass and body mass from birds sampled during migration to quantify protein reserves (e.g. Evans, 1969; Fry et al., 1972; Marsh, 1984). Unfortunately, this method has a poor theoretical rationale and methodological shortcomings (Lindstrom and Piersma, 1993; van der Meer and Piersma, 1994). The fundamental problem with such an approach is that changes in body composition across individuals in a population rarely provides accurate estimates of body composition changes within individuals (van der Meer and Piersma, 1994). The solution to this problem is to repeatedly measure the protein and fat content of individual birds using non-destructive techniques (e.g. Karasov and Pinshow, 1998). Further development of non-invasive techniques such as total body electrical conductivity (TOBEC), isotope dilution, and other non-destructive techniques (reviewed by Piersma and Klaassen, 1999) is required before these important issues can be addressed.

8.6. Exercise physiology of migratory birds

The ecological circumstances that have prompted much of the work on migratory birds discussed in this review are relevant to actively migrating birds. However, almost all the experiments conducted to date have used either cold-acclimation, increased light levels, or diet manipulations to explore the effects of food quantity and quality on digestive physiology and have ignored the effect of actually flying (but see recent work of Klaassen, Lindstrom, and associates (Lindstrom et al., 1999; Klaassen et al., 2000; Kvist and Lindstrom, 2000; Lindstrom et al., 2000). Phenotypic flexibility in the digestive system and

body composition of actively flying birds may be different than that of non-flying birds that are forced to switch diets or are hyperphagic because of cold-acclimation or increased light levels.

Acknowledgements

Supported by N.S.F. (IBN 9318675 and IBN-9723793 to W.H.K. and IBN-9984920 to S.R.M.).

References

- Afik, D., Caviedes-Vidal, E., Martinez del Rio, C., Karasov, W.H., 1995. Dietary modulation of intestinal hydrolytic enzymes in yellow-rumped warblers. *Am. J. Physiol.* 269, R413–R420.
- Afik, D., Darken, B.W., Karasov, W.H., 1997a. Is diet shifting facilitated by modulation of intestinal nutrient uptake? Test of an adaptational hypothesis in Yellow-rumped Warblers. *Physiol. Zool.* 70, 213–221.
- Afik, D., McWilliams, S.R., Karasov, W.H., 1997b. Test for passive absorption of glucose in the yellow-rumped warbler and its ecological implications. *Physiol. Zool.* 70, 370–377.
- Afik, D., Karasov, W.H., 1995. The trade-offs between digestion rate and efficiency in warblers and their ecological implications. *Ecology* 76, 2247–2257.
- Al-Dabbagh, K.Y., Jiad, J.H., Waheed, I.N., 1987. The influence of diet on the intestine length of the white-cheeked bulbul. *Ornis Scand.* 18, 150–152.
- Alerstram, T., Lindstrom, A., 1990. Optimal bird migration: the relative importance of time, energy and safety. In: Gwinner, E. (Ed.), *Bird Migration: Physiology and Ecophysiology*. Springer-Verlag, Berlin, pp. 331–351.
- Ankney, C.D., 1977. Feeding and digestive organ size in breeding lesser snow geese. *Auk* 94, 275–282.
- Arnold, S.J., 1983. Morphology, performance and fitness. *Am. Zool.* 23, 347–361.
- Bairlein, F., 1985. Efficiency of food utilization during fat deposition in the long-distance migratory garden warbler, *Sylvia borin*. *Oecologia* 68, 118–125.
- Bairlein, F., 1990. Nutrition and food selection in migratory birds. In: Gwinner, E. (Ed.), *Bird Migration: Physiology and Ecophysiology*. Springer-Verlag, Berlin, pp. 198–213.
- Bairlein, F., 1991. Nutritional adaptations to fat deposition in the long-distance migratory Garden Warbler (*Sylvia borin*). *Proceedings of the 20th International Ornithological Congress, Christ-Church, NZ*, pp. 2149–2158.
- Bairlein, F., Gwinner, E., 1994. Nutritional mechanisms and temporal control of migratory energy accumulation in birds. *Annu. Rev. Nutr.* 14, 187–215.
- Bairlein, F., Simons, D., 1995. Nutritional adaptations in migrating birds. *Isr. J. Zool.* 41, 357–367.
- Berthold, P., 1975. Migration: control and metabolic physiology. In: Farner, D.S., King, J.R. (Eds.), *Avian Biology*. Academic Press, New York, pp. 77–128.
- Berthold, P., 1996. *Control of Bird Migration*. Chapman and Hall, NY.
- Biebach, H., 1996. Energetics of winter and migratory fattening. In: Carey, C. (Ed.), *Avian Energetics and Nutritional Ecology*. Chapman and Hall, NY, pp. 280–323.
- Biebach, H., Friedrich, W., Heine, G., 1986. Interaction of body mass, fat, foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia* 69, 370–379.
- Blem, C.R., 1976. Patterns of lipid storage and utilization in birds. *Am. Zool.* 16, 671–684.
- Blem, C.R., 1980. The energetics of migration. In: Gauthreaux Jr., S.A. (Ed.), *Animal Migration, Orientation, and Navigation*. Academic Press, New York, pp. 175–224.
- Blem, C.R., 1990. Avian energy storage. In: Power, M. (Ed.), *Current Ornithology*. Plenum Press, New York, pp. 59–113.
- Carpenter, F.L., Paton, D.C., Hixon, M.A., 1983. Weight gain and adjustment of feeding territory size in migrant hummingbirds. *Proc. Nat. Acad. Sci.* 80, 7259–7263.
- Castro, G., Stoyan, N., Myers, J.P., 1989. Assimilation efficiency in birds: a function of taxon or food type? *Comp. Biochem. Physiol.* 92A, 271–278.
- Caviedes-Vidal, E., Afik, D., Martinez del Rio, C., Karasov, W.H., 2000. Dietary modulation of intestinal enzymes of the house sparrow (*Passer domesticus*): testing an adaptive hypothesis. *Comp. Biochem. Physiol. A* 125, 11–24.
- Caviedes-Vidal, E., Karasov, W.H., 1996. Glucose and amino acid absorption in house sparrow intestine and its dietary modulation. *Am. J. Physiol.* 40, R561–R568.
- Cherel, Y., Robin, J.P., Maho, Y.L., 1988. Physiology and biochemistry of long-term fasting in birds. *Can. J. Zool.* 66, 159–166.
- Connell, C.E., Odum, E.P., Kale, H., 1960. Fat-free weights of birds. *Auk* 77, 1–9.
- Davis, P., 1962. Robin recaptures on Fair Isle. *Br. Birds* 55, 225–229.
- Dawson, W.R., Marsh, R.L., Yacoe, M.E., 1983. Metabolic adjustments of small passerine birds for migration and cold. *Am. J. Physiol.* 245, R755–R767.
- Diamond, J., 1991. Evolutionary design of intestinal nutrient absorption: enough but not too much. *News Physiol. Sci.* 6, 92–96.
- Drobney, R.D., 1984. Effect of diet on visceral morphology of breeding wood ducks. *Auk* 101, 93–98.

- Dubowy, P.J., 1985. Seasonal organ dynamics in post-breeding male blue-winged teal and northern shovelers. *Comp. Biochem. Physiol.* 82A, 899–906.
- Dykstra, C.R., Karasov, W.H., 1992. Changes in gut structure and function of House Wrens (*Troglodytes aedon*) in response to increased energy demands. *Physiol. Zool.* 65, 422–442.
- El-Wailly, A.J., 1966. Energy requirements of egg-laying and incubation in the zebra finch, *Taeniopygia castanotis*. *Condor* 68, 582–594.
- Evans, P.R., 1966. Migration and orientation of passerine night-migrants in northeast England. *J. Zool. London* 150, 319–369.
- Evans, P.R., 1969. Ecological aspects of migration, and pre-migratory fat deposition in the Lesser Redpoll, *Carduelis flammea cabaret*. *Condor* 71, 316–330.
- Farner, D., Oksche, A., Kamemoto, F., King, J., Cheyney, H., 1961. A comparison of the effect of long daily photoperiods on the pattern of energy storage in migratory and non-migratory finches. *Comp. Biochem. Physiol.* 2, 125–142.
- Feder, M.E., Bennett, A.F., Burggren, W.W., Huey, R.B., 1987. *New Directions in Ecological Physiology*. Cambridge Univ. Press, New York.
- Ferraris, R.P., Diamond, J.M., 1989. Specific regulation of intestinal nutrient transporters by their dietary substrates. *Ann. Rev. Physiol.* 51, 125–141.
- Fry, C.H., Ferguson-Lees, I.J., Dowsett, R.J., 1972. Flight muscle hypertrophy and ecophysiological variation of Yellow Wagtail *Motacilla flava* races at Lake Chad. *J. Zool. Lond.* 167, 293–306.
- Gannes, L.Z., 1999. *Flying, Fasting and Feeding: the Physiology of Bird Migration in Old World Sylvid and Turdid Thrushes*. Princeton University, Princeton, NJ.
- Groscolas, R., 1986. Changes in body mass, body temperature, and plasma fuel levels during the natural breeding fast in male and female emperor penguins, *Aptenodytes forsteri*. *J. Comp. Physiol. B* 156, 521–527.
- Hamilton, K.L., 1985. Food and energy requirements of captive barn owls *Tyto alba*. *Comp. Biochem. Physiol.* 80A, 355–358.
- Hammond, K.A., Diamond, J., 1997. Maximal sustained energy budgets in humans and animals. *Nature* 386, 457–462.
- Hansson, M., Pettersson, J., 1989. Competition and fat deposition in Goldcrests (*Regulus regulus*) at a migration stop-over site. *Vogelwarte* 35, 21–31.
- Herrera, C.M., 1984. Adaptation to frugivory of Mediterranean avian seed dispersers. *Ecology* 65, 609–617.
- Hume, I., Biebach, H., 1996. Digestive tract function in the long-distance migratory garden warbler, *Sylvia borin*. *J. Comp. Physiol. B* 166, 388–395.
- Imondi, A.R., Bird, F.H., 1966. The turnover of intestinal epithelium in the chick. *Poult. Sci.* 45, 142–147.
- Izhaki, I., Safriel, U.N., 1989. Why are there so few exclusively frugivorous birds? Experiments on fruit digestibility. *Oikos* 54, 23–32.
- Jones, P.J., Ward, P., 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch-size in the red-billed Quelea *Quelea quelea*. *Ibis* 118, 547–574.
- Karasov, W.H., 1988. Nutrient transport across vertebrate intestine. In: Gilles, R. (Ed.), *Advances in Environmental and Comparative Physiology*. Springer-Verlag, Berlin, pp. 131–172.
- Karasov, W.H., 1990. Digestion in birds: chemical and physiological determinants and ecological implications. *Stud. Avian Biol.* 13, 391–415.
- Karasov, W.H., 1996. Digestive plasticity in avian energetics and feeding ecology. In: Carey, C. (Ed.), *Avian Energetics and Nutritional Ecology*. Chapman and Hall, New York, pp. 61–84.
- Karasov, W.H., Cork, C.J., 1996. Test of a reactor-based digestion optimization model for nectar-eating Rainbow Lorikeets. *Physiol. Zool.* 69, 117–138.
- Karasov, W.H., Cork, S.J., 1994. Glucose absorption by a nectarivorous bird: the passive pathway is paramount. *Am. J. Physiol.* 267, G18–G26.
- Karasov, W.H., Hume, I.D., 1997. Vertebrate gastrointestinal system. In: Dantzler, W.H. (Ed.), *Handbook of Physiology. Section 13: Comparative Physiology*, 1. Oxford University Press, New York, pp. 409–480.
- Karasov, W.H., Pinshow, B., 1998. Changes in lean mass and in organs of nutrient assimilation in a long-distance migrant at a springtime stopover site. *Physiol. Zool.* 71, 435–448.
- Karasov, W.H., Pinshow, B., 2000. Test for physiological limitation to nutrient assimilation in a long-distance passerine migrant at a springtime stopover site. *Physiol. Biochem. Zool.* 73, 335–343.
- Kehoe, F.P., Ankney, C.D., Alisauskas, R.T., 1988. Effects of dietary fiber and diet diversity on digestive organs of captive mallards (*Anas platyrhynchos*). *Can. J. Zool.* 66, 1597–1602.
- Kendall, M.D., Ward, P., Bacchus, S., 1973. A protein reserve in the pectoralis major flight muscle of *Quelea quelea*. *Ibis* 115, 600–601.
- Kersten, M., Visser, W., 1996. The rate of food processing in the oystercatcher: food intake and energy expenditure constrained by a digestive bottleneck. *Funct. Ecol.* 10, 440–448.
- Ketterson, E.D., King, J.R., 1977. Metabolic and behavioral responses to fasting in the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*). *Physiol. Zool.* 50, 115–129.
- Klaassen, M., 1996. Metabolic constraints on long-distance migration in birds. *J. Exp. Biol.* 199, 57–64.
- Klaassen, M., Biebach, H., 1994. Energetics of fattening and starvation in the long-distance migratory

- garden warbler, *Sylvia borin*, during the migratory phase. *J. Comp. Physiol. B* 164, 362–371.
- Klaassen, M., Kvist, A., Lindstrom, A., 2000. Flight costs and fuel composition of a bird migrating in a wind tunnel. *Condor* 102, 444–451.
- Klaassen, M., Lindstrom, A., 1996. Departure fuel loads in time-minimizing migrating birds can be explained by the energy costs of being heavy. *J. Theor. Biol.* 183, 29–34.
- Klaassen, M., Lindstrom, A., Zijlstra, R., 1997. Composition of fuel stores and digestive limitations to fuel deposition rate in the long-distance migratory Thrush Nightingale, *Luscinia luscinia*. *Physiol. Zool.* 70, 125–133.
- Krapu, G.L., Reinecke, K.J., 1992. Foraging ecology and nutrition. In: Batt, B.D.J., Afton, A.D., Anderson, M.G., Ankney, C.D., Johnson, D.H., Kadlec, J.A., Krapu, G.L. (Eds.), *Ecology and Management of Breeding Waterfowl*. University of Minnesota Press, Minneapolis, pp. 1–29.
- Kuenzi, A.J., Moore, F.R., Simmons, T.R., 1991. Stopover of neotropical landbird migrants on East Ship Island following trans-Gulf migration. *Condor* 93, 869–883.
- Kvist, A., Lindstrom, A., 2000. Maximum daily energy intake: it takes time to lift the metabolic ceiling. *Physiol. Biochem. Zool.* 73, 30–36.
- Langslow, D.R., 1976. Weights of blackcap on migration. *Ring Migration* 1, 78–91.
- LeMaho, Y., Ka, J.V.V., Koubi, H. et al., 1981. Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. *Am. J. Physiol.* 241E, 342–354.
- LeMaho, Y., Robin, J.P., Cherel, Y., Handrich, Y., Groscolas, R., 1991. Proceedings of the 20th International Ornithological Congress. Long-term Fasting in Penguins as a Nutritional Adaptation to Breed or Molt. Christ-Church, NZ, pp. 2177–2185.
- Levey, D.J., Cipollini, M.L., 1996. Is most glucose absorbed passively in northern bobwhite? *Comp. Biochem. Physiol.* 113A, 225–231.
- Levey, D.J., Karasov, W.H., 1989. Digestive responses of temperate birds switched to fruit or insect diets. *Auk* 106, 675–686.
- Levey, D.J., Karasov, W.H., 1994. Gut passage of insects by European Starlings and comparison with other species. *Auk* 111, 478–481.
- Levey, D.J., Martinez del Rio, C., 1999. Test, rejection, and reformulation of a chemical reactor-based model of gut function in a fruit-eating bird. *Physiol. Biochem. Zool.* 72, 369–383.
- Lilja, C., 1987. Mitotic activity of duodenal crypt cells in the young fieldfare (*Turdus pilaris*). *Acta Physiol. Scand.* 131, 163–164.
- Lindgard, K., Stokkan, K.A., Maho, Y.L., Groscolas, R., 1992. Protein utilization during starvation in fat and lean Svalbard ptarmigan (*Lagopus mutus hyperboreus*). *J. Comp. Physiol. B* 162, 607–613.
- Lindstrom, A., Klaassen, M., Kvist, A., 1999. Variation in energy intake and basal metabolic rate of a bird migrating in a wind tunnel. *Funct. Ecol.* 13, 352–359.
- Lindstrom, A., Kvist, A., Piersma, T., Dekinga, A., Dietz, M.W., 2000. Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fueling. *J. Exp. Biol.* 203, 913–919.
- Lindstrom, A., Piersma, T., 1993. Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* 135, 70–78.
- Lopez-Calleja, M.V., Bozinovic, F., Martinez del Rio, C., 1997. Effects of sugar concentration on hummingbird feeding and energy use. *Comp. Biochem. Physiol.* 118A, 1291–1299.
- Marsh, R.L., 1983. Adaptations of the gray catbird *Dumetella carolinensis* to long-distance migration: energy stores and blood substrates. *Auk* 100, 170–179.
- Marsh, R.L., 1984. Adaptations of the gray catbird *Dumetella carolinensis* to long-distance migration: flight muscle hypertrophy associated with elevated body mass. *Physiol. Zool.* 57, 105–117.
- Martinez del Rio, C., 1990. Dietary, phylogenetic, and ecological correlates of intestinal sucrase and maltase activity in birds. *Physiol. Zool.* 63, 987–1011.
- Martinez del Rio, C., Brugger, K., Witmer, M., Rios, J., Vergara, E., 1995. An experimental and comparative study of dietary modulation of intestinal enzymes in European starlings (*Sturnus vulgaris*). *Physiol. Zool.* 68, 490–511.
- Martinez del Rio, C., Cork, S.J., Karasov, W.H., 1994. Modelling gut function: an introduction. In: Chivers, D.J., Langer, P. (Eds.), *The Digestive System in Mammals: Food, Form and Function*. Cambridge University Press, Cambridge, pp. 25–53.
- Martinez del Rio, C., Karasov, W.H., 1990. Digestion strategies in nectar- and fruit-eating birds and the sugar composition of plant rewards. *Am. Nat.* 136, 618–637.
- McLandress, M.R., Raveling, D.G., 1981. Changes in diet and body composition of Canada geese before spring migration. *Auk* 98, 65–79.
- McWilliams, S.R., 1999. Digestive strategies of avian herbivores. In: Adams, N., Slotow, R. (Eds.), *Proceedings of the 22nd International Ornithological Congress*. University of Natal, Durban, South Africa, pp. 2198–2207.
- McWilliams, S.R., Afik, D., Secor, S., 1997. Patterns and processes in the vertebrate digestive system: implications for the study of ecology and evolution. *Trends Ecol. Evol.* 12, 420–422.
- McWilliams, S.R., Caviades-Vidal, E., Karasov, W.H., 1999. Digestive adjustments in cedar waxwings to high feeding rates. *J. Exp. Zool.* 283, 394–407.

- McWilliams, S.R., Karasov, W.H., 1998a. Test of a digestion optimization model: effects of costs of feeding on digestive parameters. *Physiol. Zool.* 71, 168–178.
- McWilliams, S.R., Karasov, W.H., 1998b. Do variable-reward feeding schedules affect digestive performance of migratory birds? *Oecologia* 114, 160–169.
- Miller, M., 1975. Gut morphology of mallards in relation to diet quality. *J. Wildl. Manage.* 39, 168–173.
- Moore, F., Kerlinger, P., 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. *Oecologia* 74, 47–54.
- Moorman, T.E., Baldassarre, G.A., Richard, D.M., 1992. Carcass mass, composition, and gut morphology dynamics of mottled ducks in fall and winter in Louisiana. *Condor* 94, 407–417.
- Moss, R., 1974. Winter diet, gut length, and interspecific competition in Alaskan ptarmigan. *Auk* 91, 737–746.
- Moss, R., 1983. Gut size, body weight, and digestion of winter food by grouse and ptarmigan. *Condor* 85, 185–193.
- Moss, R., Parkinson, J.A., 1972. Digestion of heather (*Calluna vulgaris*) by red grouse (*Lagopus lagopus scoticus*). *Br. J. Nutr.* 27, 285–298.
- Muller, H.C., Berger, D.D., 1966. Analyses of weight and fat variations in transient swainson's thrushes. *Bird-banding* 37, 83–111.
- Murphy, M., 1996. Nutrition and metabolism. In: Carey, C. (Ed.), *Avian Energetics and Nutritional Ecology*. Chapman and Hall, New York, pp. 31–60.
- Nisbet, I.C.T., Drury, W.H., Baird, J., 1963. Weight loss during migration: part 1. Deposition and consumption of fat by the blackpoll warbler. *Bird-banding* 34, 107–138.
- Odum, E.P., Marshall, S.G., Marples, T.G., 1965. The caloric content of migrating birds. *Ecology* 46, 901–904.
- Odum, E.P., Rogers, D.T., Hicks, D.L., 1964. Homeostasis of non-fat components of migrating birds. *Science* 143, 1037–1039.
- Owen Jr., R.B., 1970. The bioenergetics of captive blue-winged teal under controlled and outdoor conditions. *Condor* 72, 153–163.
- Parrish, J.D., 1997. Patterns of frugivory and energetic condition in nearctic landbirds during autumn migration. *Condor* 99, 681–697.
- Pendergast, B.A., Boag, D.A., 1973. Seasonal changes in the internal anatomy of spruce grouse in Alberta. *Auk* 90, 307–317.
- Penry, D.L., Jumars, P.A., 1986. Chemical reactor analysis and optimal digestion. *Bioscience* 36, 310–315.
- Penry, D.L., Jumars, P.A., 1987. Modelling animal guts as chemical reactors. *Am. Nat.* 129, 69–96.
- Piersma, T., 1998. Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight. *J. Avian Biol.* 29, 511–520.
- Piersma, T., Gudmundsson, G.A., Lilliendahl, K., 1999. Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. *Physiol. Biochem. Zool.* 72, 405–415.
- Piersma, T., Klaassen, M., 1999. Methods of studying the functional ecology of protein and organ dynamics in birds. In: Adams, N.J., Slotow, R.H. (Eds.), *Proceedings of the 22nd International Ornithological Congress*, University of Natal, Durban, South Africa, pp. 36–51.
- Piersma, T., Koolhaas, A., Dekinga, A., 1993. Interactions between stomach structure and diet choice in shorebirds. *Auk* 110, 552–564.
- Piersma, T., Lindstrom, A., 1997. Rapid reversible changes in organ size as a component of adaptive behavior. *Trends Ecol. Evol.* 12, 134–138.
- Pigliucci, M., 1996. How organisms respond to environmental changes: from phenotypes to molecules (and vice versa). *Trends Ecol. Evol.* 11, 168–173.
- Ramenofsky, M., 1990. Fat storage and fat metabolism in relation to migration. In: Gwinner, E. (Ed.), *Bird Migration: Physiology and Ecophysiology*. Springer-Verlag, Berlin, pp. 214–231.
- Rappole, J.H., Warner, D.W., 1976. Relationships between behavior, physiology and weather in avian transients at a migration stopover site. *Oecologia* 26, 193–212.
- Ricklefs, R.E., 1996. Avian energetics, ecology, and evolution. In: Carey, C. (Ed.), *Avian Energetics and Nutritional Ecology*. Chapman and Hall, New York, pp. 1–30.
- Sabat, P., Novoa, F., Bozinovic, F., Martinez del Rio, C., 1998. Dietary flexibility and intestinal plasticity in birds: a field and laboratory study. *Physiol. Zool.* 71, 226–236.
- Savory, C.J., 1986. Influence of ambient temperature on feeding activity parameters and digestive function in domestic fowl. *Physiol. Behav.* 38, 353–357.
- Savory, C.J., Gentle, M.J., 1976a. Effects of dietary dilution with fibre on the food intake and gut dimensions of Japanese quail. *Br. J. Poult. Sci.* 17, 561–570.
- Savory, C.J., Gentle, M.J., 1976b. Changes in food intake and gut size in Japanese quail in response to manipulation of dietary fiber content. *Br. J. Poult. Sci.* 17, 571–580.
- Selman, R.G., Houston, D.C., 1996. A technique for measuring lean pectoral muscle mass in live small birds. *Ibis* 138, 348–350.
- Spiller, R.C., Trotman, I.F., Higgins, B.E. et al., 1984.

- The ileal brake inhibition of jejunal motility after ilial fat perfusion in man. *Gut* 25, 365–374.
- Stalmaster, M.V., Gessaman, J.A., 1982. Food consumption and energy requirements of captive bald eagles. *J. Wildl. Manage.* 46, 646–654.
- Starck, J.M., 1996. Phenotypic plasticity, cellular dynamics, and epithelial turnover of the intestine of Japanese quail (*Coturnix coturnix japonica*). *J. Zool. Lond.* 238, 53–79.
- Starck, J.M., 1999. Structural flexibility of the gastro-intestinal tract of vertebrates-implications for evolutionary morphology. *Zoologischer Anzeiger* 238, 87–101.
- Starck, J.M., Kloss, E., 1995. Structural responses of Japanese quail intestine to different diets. *Dtsch. Tierarztl. Wochenschr* 102, 146–150.
- Starck, M., Karasov, W.H., Afik, D., 2000. Intestinal nutrient uptake measurements and tissue damage. Validating the everted sleeve method. *Physiol. Biochem. Zool.* 73, 454–460.
- Stearns, S.C., 1989. The evolutionary significance of phenotypic plasticity. *Bioscience* 39, 436–445.
- Stevens, C.E., Hume, I.D., 1995. *Comparative Physiology of the Vertebrate Digestive System*. Cambridge University Press, Cambridge, UK.
- Swain, S.D., 1992. Flight muscle catabolism during overnight fasting in a passerine bird, *Eremophila alpestris*. *J. Comp. Physiol.* 162B, 383–392.
- Toloza, E.M., Lam, M., Diamond, J., 1991. Nutrient extraction by cold-exposed mice: a test of digestive safety margins. *Am. J. Physiol.* 261, G608–G620.
- Travis, J., 1994. Evaluating the adaptive role of morphological plasticity. In: Wainwright, P.C., Reilly, S.M. (Eds.), *Ecological Morphology: Integrative Organismal Biology*. University of Chicago Press, Chicago, pp. 99–122.
- van der Meer, J., Piersma, T., 1994. Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. *Physiol. Zool.* 67, 305–329.
- Wainwright, P.C., Reilly, S.M., 1994. *Ecological Morphology: Integrative Organismal Biology*. University of Chicago Press, Chicago, IL.
- Walsberg, G.E., Thompson, C.W., 1990. Annual changes in gizzard size and function in a frugivorous bird. *Condor* 92, 794–795.
- West, G.C., 1968. Bioenergetics of captive willow ptarmigan under natural conditions. *Ecology* 49, 1035–1045.