

Chapter 3

Seasonal Metabolic Variation in Birds: Functional and Mechanistic Correlates

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3.1 Introduction

The influence of seasonal changes in temperature and climate on metabolic rates in birds has been a topic of interest to ornithologists and ecophysiologicalists for decades (e.g., Hart 1962; Dawson 1958; Miller 1939). Because metabolic rates increase linearly with temperature in endotherms outside the thermal neutral zone, comparisons of metabolic rates among seasons or species require standardized measurements of metabolic rates. The most common of these standardized metabolic rates used for comparisons of energetics among seasons or species is basal, or resting, metabolic rate. It often serves as a baseline for comparisons of metabolic costs of activities within species, and for comparisons of the “rate of living” among species or species groups (e.g., Wiersma et al. 2007a; White et al. 2007; McKechnie et al. 2006; McKechnie and Wolf 2004; Trevelyan et al. 1990; McNab 1988; Bennett and Harvey 1987; Kersten and Piersma 1987). Theoretically, basal metabolic rate (BMR) is the minimum metabolic rate required for maintenance in endotherms. BMR is measured within the thermal neutral zone under postabsorptive digestive conditions during the resting phase of the daily cycle on resting, nongrowing, nonreproductive animals (McNab 1997). It is doubtful whether truly BMRs can ever be achieved in the laboratory, so the term resting metabolic rate (RMR) is often used to refer to such measurements, even when the standard conditions for BMR have been met. Here, I will revert to the standard terminology and consider BMR as the metabolic rate measured under the standard conditions listed above, recognizing that this may not, in fact, represent truly basal rates (Table 3.1).

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Table 3.1 Definitions of commonly used terms

Term	Definition
Basal metabolic rate (BMR)	Minimum metabolic rate required for maintenance; measured as the metabolic rate at thermoneutrality in resting, postabsorptive, nongrowing birds in the resting phase of the daily cycle
Summit metabolic rate (M_{sum})	Maximum metabolic rate achieved during cold exposure
Maximum metabolic rate (MMR)	Maximum metabolic rate achieved during any form of activity. Maximal metabolic rates during locomotion are generally higher than those during cold exposure in birds
Field metabolic rate (FMR)	Metabolic rate for free-living birds engaged in normal daily activities. When expressed in terms of energy use per day, FMR is the Daily Energy Expenditure (DEE)
Cold tolerance	The time period over which a bird can maintain T_b by thermogenesis (principally shivering) at a given level of cold exposure
Shivering endurance	The time period over which a bird can continue shivering thermogenesis at a given level of cold exposure, essentially equivalent to cold tolerance
Temperature at cold limit (T_{cl})	The temperature producing hypothermia during exposure of an individual bird to a declining series of temperatures
Acclimation	Exposure of birds to controlled climatic conditions <i>in the laboratory</i>
Acclimatization	Exposure of birds to natural climatic conditions <i>in the field</i>

Another standardized measure of metabolic rate is the maximal metabolic rate during activity (MMR). Comparisons of MMR in birds are not currently possible, as MMR during flight has not been convincingly measured for any bird because of technical difficulties associated with verifying that oxygen consumption during sustained flight has actually reached maximum values. However, recent studies employing hovering flight (Chai and Dudley 1995, 1996) or hop-flutter wheels (Wiersma et al. 2007b; Pierce et al. 2005; Chappell et al. 1999) to induce maximum metabolic rates appear potentially promising in this regard, although such measurements are probably not practical for all volant birds. Thus, I will not examine maximal activity-induced metabolic rates in birds in this review. However, a similar standardized metabolic measure that has become more common in recent seasonal comparisons is summit metabolism (M_{sum}) or maximal thermogenic capacity. Here I define M_{sum} as the maximum metabolic rate attained by birds under cold exposure. Historically, summit metabolism measurements were rarely undertaken because of the very cold temperatures required to elicit M_{sum} (but see Saarela et al. 1995; Dawson and Carey 1976; Hart 1962). More recently, helium–oxygen atmospheres (helox) that facilitate heat loss without impairing metabolic function have been used to generate M_{sum} measurements (Rosenmann and Morrison 1974). The utility of M_{sum} measurements emerge not only from the indication that they provide for the maximal capacity for thermogenesis in the cold, but also from the general positive association between M_{sum} and endurance at submaximal levels of cold exposure (Marsh and Dawson 1989). In addition, M_{sum} and MMR are significantly and

positively correlated in some mammals (Hayes and Chappell 1990), so they may both serve as effective general measures of aerobic capacity in endotherms, although M_{sum} and MMR (measured by hop-flutter wheel) were not correlated in tropical birds (Wiersma et al. 2007b).

Most research attention relating to seasonal variation in metabolic rates in birds has been paid to metabolic variation between summer and winter in strongly seasonal climates, as an aspect of seasonal acclimatization to cold and its attendant thermogenic demands. However, the precise nature of the association between variation in metabolic rates and variation in cold tolerance in birds remains uncertain (reviews by Dawson and O'Connor 1996; Dawson and Marsh 1989; Marsh and Dawson 1989). Winter increases in M_{sum} and/or BMR are correlated with improved cold resistance in birds and may be adaptive in this context (O'Connor 1995a; Swanson 1990a). In addition, M_{sum} and cold tolerance are correlated in birds on both intraspecific and interspecific bases (Swanson and Liknes 2006; Swanson 2001).

Surprisingly little effort has been directed toward measurement of metabolic rates of birds in migratory disposition. A substantial amount of effort has been devoted to defining the physiological and biochemical adjustments associated with migration (McWilliams et al. 2004; Gwinner 1990; Dawson et al. 1983a), but this effort has been primarily directed at describing how flight muscles might increase power and endurance during migration and such changes have not been previously tied to changes in organismal metabolism. Recent work, however, has begun to examine potential seasonal variation in basal and summit metabolic rates of migrating birds (Vezina et al. 2007; Battley et al. 2000; Swanson and Dean 1999; Piersma et al. 1995).

Another measure of metabolic rate in free-living birds that has been used for seasonal comparisons is the field metabolic rate (FMR). FMR describes the energetic costs of normal daily activities in birds under natural environmental conditions. FMR is usually measured by two methods, doubly labeled water and time–energy budgets. The theory behind these two methods has been well developed and both methods have been used to measure energy use during various periods of the annual cycle in birds (Speakman 1997; Weathers and Sullivan 1993). The doubly labeled water method measures carbon dioxide production, so it provides a more direct measure of FMR than the time–activity budget method, which sums the metabolic costs of different activities observed in free-living birds. Nevertheless, if metabolic costs of different activities are carefully measured in the lab and microclimates are carefully measured in the field, the time–energy budget and doubly labeled water methods are usually in relatively close agreement (Webster and Weathers 2000; Weathers and Sullivan 1993; Goldstein 1990).

This paper reviews the recent literature on seasonal variation in basal and summit metabolic rates associated with seasonal acclimatization and migratory disposition in birds. In addition, seasonal variation in FMRs will be reviewed in the context of how seasonal changes in energy expenditure, and in the partitioning of energy expenditure, might impact BMR and M_{sum} (or MMR). I will also discuss the potential functional significance of this seasonal variation to meeting the energetic demands of migration and thermogenesis in cold climates. Next, I will discuss the potential

mechanisms underlying seasonal variation in BMR and M_{sum} . I will also try to illuminate some potential topics or avenues for future research. The overall goal is to integrate biochemical and physiological adjustments at the cellular and tissue levels, organismal physiological variation, and ecology.

3.2 The Variable Thermal Environment Encountered by Birds

3.2.1 *Climate and Thermostatic Costs*

Temperature is one of the major modifiers of metabolic level in endothermic animals, so it is necessary to examine the climatic conditions to which birds are exposed throughout their annual cycle. Birds nesting in temperate-zone or arctic latitudes, where climatic conditions deteriorate and productivity is reduced in winter, respond to seasonally changing environments by two major strategies, permanent residency and acclimatization or migration to more favorable climates. Many small mammals exhibit a third strategy, winter dormancy or hibernation, but such a strategy has been claimed for only one bird, the Common Poorwill (*Phalaenoptilus nuttallii*). These birds become inactive and may remain in one location for up to 3 months (Brigham et al. 2006; French 1993; Jaeger 1949). In the torpid condition, skin temperature may drop as low as 2.8°C (Brigham 1992), although body temperature may fluctuate markedly on a daily basis (e.g., up to 11°C per day, French 1993). Despite the energetic savings attributable to such a hibernation strategy, it has not been documented for any other bird species. However, torpor and regulated hypothermia are used by a wide variety of small birds on a daily basis and this can also result in substantial energetic benefit (see McKechnie and Lovegrove 2002, 2006; Reinertsen 1996, for reviews).

Species that are resident in temperate-zone or arctic latitudes, or those that migrate only relatively short distances so that they still winter in cold climates, are faced with marked seasonal changes in cold exposure and thermostatic costs (e.g., Cooper 2000; Wiersma and Piersma 1994). Winter climates in which these birds reside can be severe. Moreover, environmental productivity is reduced in these regions in winter compared to summer and daylength is short, so species employing this strategy are faced with the interacting effects of short days available for foraging, long nights of forced fasting, relatively low food availability, and cold temperatures (Marsh and Dawson 1989). Such factors may combine to make the winter environment thermally stressful for resident birds. If seasonal changes in temperature or climate are a major factor driving seasonal adjustments of physiology, then species wintering in cold climates should demonstrate substantial seasonal physiological adjustment.

Migratory species, particularly those that winter in tropical to subtropical climates, move to more favorable climates in winter and thereby reduce their exposure to the climatic deterioration and declining food base associated with wintering on or near

the breeding grounds. This, in turn, reduces winter thermoregulatory costs relative to those for birds wintering in colder climates (Wiersma and Piersma 1994). As might be expected, based on the severity of winter climate, the percentages of birds migrating varies with latitude such that higher latitudes show an increased proportion of birds moving out of the area in winter. For example, in North America the percentage of birds migrating south in winter varies from 12% in Florida (25°N) to 87% at Ellesmere Island (80°N) (Newton and Dale 1996). Thus, migrating birds escape the potentially stressful environmental conditions present on their breeding grounds during the winter.

During migration, however, birds may encounter adverse weather conditions, although they are still not exposed to the seasonal extremes of temperature that cold climate-wintering species encounter. For birds wintering in tropical or subtropical climates, which migrate later in spring and earlier in fall than shorter-distance migrants (Hagan et al. 1991), average temperatures during spring migration are often lower than those during fall migration (O'Reilly and Wingfield 1995). This seasonal difference is moderated for shorter-distance migrants. For example, mean temperatures surrounding median spring passage dates of the Neotropical migrants Warbling Vireo *Vireo gilvus* and Yellow Warbler *Dendroica petechia* in southeastern South Dakota were 5–6°C colder than temperatures surrounding median fall passage dates (Swanson and Dean 1999). For mild temperate-zone migrants Ruby-crowned Kinglet *Regulus calendula* and Yellow-rumped Warbler *Dendroica coronata*, migrating through the same area, mean temperatures around spring and fall passage dates differed by only 1–2°C.

Because of the differences in seasonal temperature extremes encountered by cold climate residents and migrants, if temperature drives seasonal changes in metabolic rates in birds, then migrants should show less metabolic variation than residents. However, migration is also an energetically expensive endeavor and physiological adjustments promoting endurance muscular activity during migration occur in birds and might influence organismal metabolic rates (Vezina et al. 2007; Dawson et al. 1983a). Knowledge of how such migratory adjustments relate to seasonal variation in organismal metabolic rates is rather rudimentary at present (Vezina et al. 2007; Battley et al. 2000; Swanson and Dean 1999; Piersma et al. 1995).

3.2.2 *Seasonal Variation in Field Metabolic Rates*

For birds wintering in cold climates, higher thermostatic costs in winter might be expected to elevate overall energy demands in winter relative to other seasons. However, it is often assumed that energy expenditure of parent birds should peak during the breeding season, in support of breeding and parental care costs, to maximize the number of offspring produced and thereby maximize fitness. According to this scenario, FMR (or daily energy expenditures, DEE) should be greatest during

the breeding season, or at least during the most expensive stage of the nesting cycle. Two hypotheses have been proposed to describe seasonal patterns of energy expenditure by birds, the increased demand hypothesis and the reallocation hypothesis (Masman et al. 1986). The increased demand hypothesis posits that breeding and parental care activities constitute a higher energetic demand than that at other times of the year, such that FMR during the breeding season, or at least during the most demanding period of the breeding season, is the highest of the annual cycle. The reallocation hypothesis contends that the moderate temperatures and abundant food base during the breeding season reduce thermostatic and foraging costs so that energy used for these purposes can be reallocated to support costs of breeding and parental care. According to this hypothesis, summer and winter FMR should be similar. However, for small birds wintering in cold climates the high costs of thermoregulation over prolonged periods might be expected to elevate FMR in winter relative to other seasons.

Weathers and Sullivan (1993) and Dawson and O'Connor (1996) reviewed seasonal studies of FMR in birds and concluded, for birds studied to that time (eight species total), that FMR during the breeding season was as high or higher than that at other times of the year, thus supporting the increased demand or reallocation hypotheses. Also in support of this conclusion, Anava et al. (2000) documented approximately equal FMR in summer and winter for nonbreeding Arabian Babblers *Turdoides squamiceps* in the northern Arabian Saharan desert in Israel. For breeding Arabian Babblers, FMR was higher in birds during the spring breeding season than nonbreeding birds in summer and winter, and this difference resulted from higher daytime energy expenditure; nocturnal energy expenditure did not vary among breeding, summer, and winter (Anava et al. 2002). Williams (2001) also found stable FMR over the annual cycle in Dune Larks (*Mirafr erythroclamys*) from the Namib desert in southern Africa. However, several recent studies of small birds have documented higher FMR in winter than in summer. Nonbreeding Verdins *Auriparus flaviceps* in southeastern Arizona had 47% higher FMR in winter than in summer, but costs of breeding were not incurred by summer birds in this study (Webster and Weathers 2000). FMR of White-crowned Sparrows *Zonotrichia leucophrys* on the central California coast was 17% higher in winter than during incubation or nestling periods in summer, despite the moderate winter climate at this location (Weathers et al. 1999). In addition, Mountain Chickadees *Poecile gambeli* and Juniper Titmice *Baeolophus griseus* in northern Utah showed 36 and 104% increases in FMR, respectively, in winter relative to summer (Cooper 2000). Carolina Chickadees *Poecile carolinensis* from Ohio also showed elevated FMR in winter relative to summer, with winter values 42% greater than summer values (Doherty et al. 2001). Thus, winter FMR in some birds may be higher than breeding season FMR and these results conflict with those from earlier studies.

Are there any patterns that emerge from these studies on seasonal variation in FMR in birds? Cooper (2000) noted that previous studies of seasonal variation in FMR had largely been conducted on birds wintering in relatively mild winter climates, where winter increases in thermostatic costs would be moderate. In addition, of the

species in the Weathers and Sullivan (1993) and Dawson and O'Connor (1996) reviews, those wintering in relatively cold climates had body masses above 160 g. Because large body size results in low surface area to volume ratios and low thermal conductance, thermostatic costs should vary much less seasonally in these birds than in small birds. Thus, the emerging pattern of seasonal variation in FMR appears to be seasonal stability or higher FMR during the breeding season than during winter for large birds or for birds wintering in mild winter climates, but higher FMR in winter than during the breeding season for small birds wintering in cold climates. This emphasizes the prominent role of thermoregulatory costs in the winter energy budget of small birds in cold climates and underscores the importance of the metabolic adjustments by which small birds meet these demands. These adjustments, in turn, are likely to influence BMR and M_{sum} .

3.3 Patterns and Functional Significance of Seasonal Metabolic Variation

3.3.1 *Thermogenic Mechanisms*

Before discussing patterns of seasonal variation in metabolic rates, a brief review of the mechanisms of heat production in birds is in order because increased thermoregulatory demands have been implicated as a factor driving winter increases in metabolic rates (Dawson and O'Connor 1996). Heat is generated in resting birds primarily, if not exclusively, by shivering (Marsh and Dawson 1989). The flight muscles, pectoralis and supracoracoideus, comprise the largest muscle group in the body of most birds, and range in size from about 15 to 25% of total body mass (Hartman 1961). Flight muscles thus contribute greatly to shivering thermogenesis and, as a consequence, have been the most extensively studied muscle group regarding shivering thermogenesis. However, in some species leg muscles may also contribute importantly to shivering thermogenesis (Marjoniemi and Hohtola 1999; Carey et al. 1989). Birds shiver isometrically so that antagonistic muscle groups work against each other (Hohtola 1982). This has the decided advantage of creating little disruption of the insulative layer at the body surface. Generally, increases in electrical activity in shivering muscles are linearly related to increases in metabolic rate during shivering and EMG activity and oxygen consumption both increase as ambient temperature declines (e.g., Hohtola et al. 1998; Tøien 1992).

Nonshivering thermogenesis (NST) has been claimed for several bird species, based on discrepancies between oxygen consumption and EMG activity (see Reinertsen 1996; Dawson and O'Connor 1996; Duchamp et al. 1993; for reviews). The occurrence of NST in birds, however, is controversial (Hohtola 2002; Marsh 1993) and if it does occur, the site of action is unknown, although skeletal muscle appears to be a likely candidate (Reinertsen 1996). Birds lack brown fat, the principal

site of NST in mammals, and they also lack the uncoupling protein (UCP 1) responsible for dissociation of electron transport from ATP production in the mitochondrion that allows the thermogenic function of brown fat in mammals (Mezentseva et al. 2008; Emre et al. 2007; Brigham and Trayhurn 1994; Saarela et al. 1989a, 1991; Olson et al. 1988). Thus, if NST occurs in birds, its primary site is different from that in mammals. Birds do possess an UCP gene (*avUCP*) that is highly homologous to mammalian *UCP 2* and *UCP 3* and is expressed in skeletal muscle, heart and liver (Mozo et al. 2005; Raimbault et al. 2001; Vianna et al. 2001). Expression of *avUCP* increases in cold-acclimated and glucagon-treated Muscovy ducklings (*Cairina moschata*) (Raimbault et al. 2001). Cold exposure in Swallow-tailed Hummingbirds (*Eupetomena macroura*) elicited torpor and *avUCP* expression increased in torpid birds (Vianna et al. 2001). Moreover, cold exposure in broiler chicks increased plasma triiodothyronine (T_3) levels and *avUCP* expression (Collin et al. 2003a) and treatment of broiler chicks with T_3 increased, whereas treatment with thyroid hormone decreased, *avUCP* expression (Collin et al. 2003b). These data suggest some role for *avUCP* in energy expenditure in birds, mediated by T_3 , but Mozo et al. (2005) suggest that the primary role for *avUCP* may be the control of production of reactive oxygen species by mitochondria, rather than thermogenesis.

Maximum metabolic rates during cold exposure in birds generally range from about 3 to 8-times BMR (Dutenhoffer and Swanson 1996; Saarela et al. 1995; Marsh and Dawson 1989). The largest factorial increment in metabolic rate recorded during cold exposure in birds is from summer acclimatized House Sparrows (*Passer domesticus*) from Wisconsin, USA, where M_{sum} exceeds BMR by ninefold (Arens and Cooper 2005a). Interestingly, winter acclimatized House Sparrows from this same population exhibited a factorial increment of only 6.9. The second largest factorial increment in the cold (8.4) is from a South American hummingbird, the Green-backed Firecrown (*Sephanoides sephanoides*; López-Calleja and Bozinovic 1995). Metabolic expansibility ($M_{\text{sum}}/\text{BMR}$) during cold exposure is usually less than that during locomotion (MMR/BMR), where metabolic expansibilities generally range from about 8 to 14-times BMR for running or flying birds (Brackenbury 1984). Klaassen et al. (2000) suggest that long-term steady-state flights may be somewhat cheaper, as metabolic rates during extended flights in a Thrush Nightingale *Luscinia luscinia* exceeded BMR by only 5.5-times. These values, however, do not represent maximal aerobic metabolic rates during locomotion, which can be much higher. For example, Bundle et al. (1999) recorded a metabolic expansibility for Rheas *Rhea americana* running on an inclined treadmill of 36-times BMR. Flight metabolic expansibility values exceeding 20 have been claimed for some birds, including migrating grebes *Podiceps nigricollis* (based on fat depletion rates; Jehl 1994), pigeons *Columba livia* carrying loads (Gessaman et al. 1991; Gessaman and Nagy 1988), and some small passerines during short flights (Nudds and Bryant 2000; Tatner and Bryant 1986).

The full aerobic capacity of the flight muscles is thus evidently not available for shivering thermogenesis. Marsh and Dawson (1989) suggest three possible reasons

for the difference between M_{sum} and maximum exercise-induced metabolic rate in birds. First, the muscle mass recruited may be less for shivering than for flight if mechanical constraints on force production during shivering exist. Because birds shiver isometrically, force production by the smaller of the antagonistic muscle groups (supracoracoideus in the case of flight muscles) may limit force production by the larger muscle group (pectoralis in the case of flight muscles). The high metabolic expansibility during cold exposure for the only hummingbird for which M_{sum} has been measured, *Sephanoides sephanoides* (López-Calleja and Bozinovic 1995), is noteworthy in this regard because hummingbirds have the largest supracoracoideus mass relative to body mass among birds because of their hovering flight style (Mathieu-Costello et al. 1992). Second, because body temperature of birds is often slightly reduced during shivering at very cold temperatures and slightly elevated during flight, temperature effects on metabolic processes could result in elevated flight metabolic rates relative to shivering metabolic rates. Finally, the nearly constant contraction in shivering muscles may restrict blood flow to the muscle during shivering relative to blood flow to muscles during flight where the muscles intermittently contract and relax. Such a restriction in blood flow could reduce oxygen supply to shivering muscles and thereby limit maximum aerobic metabolic rates during shivering.

Heat produced as a by-product of digestion (heat increment of feeding) or activity may substitute for thermoregulatory heat production in some birds (Dawson and O'Connor 1996). Partial substitution of activity- or digestion-generated heat for thermostatic costs occurs when metabolic rates at temperatures below thermoneutrality are elevated above those for activity or digestion alone, but not to the combined level of activity or digestion costs plus thermostatic costs for resting birds. Complete substitution occurs when metabolic rates for activity or digestion at a given temperature below thermoneutrality are indistinguishable from those for thermoregulation at rest. Partial or complete substitution of activity-induced heat production for thermostatic costs has been documented for White-crowned Sparrows *Zonotrichia leucophrys* (Paladino and King 1984), Verdins *Auriparus flaviceps* (Webster and Weathers 1990), Gambel's Quail *Callipepla gambelii* (Zerba and Walsberg 1992), Red Knots *Calidris canutus* (Bruinzeel and Piersma 1998), Ruby-throated Hummingbirds *Archilochus colubris* (Chai et al. 1998), House Finches *Carpodacus mexicanus* (Zerba et al. 1999), and Black-capped Chickadees *Poecile atricapillus* (Cooper and Sonsthagen 2007). Partial to complete substitution of the heat increment of feeding for thermostatic costs has also been reported for Eurasian Kestrels *Falco tinnunculus* (Masman et al. 1989), House Wren chicks *Troglodytes aedon* (Chappell et al. 1997), Thick-billed Murres *Uria lomvia* (Hawkins et al. 1997), pigeons (Rashotte et al. 1999), and Tawny Owls *Strix aluco* (Bech and Præstang 2004). The net result of this substitution is that overall thermostatic costs are reduced in active or digesting birds. However, Kaseloo and Lovvorn (2003) found that Mallards (*Anas platyrhynchos*) eating grain voluntarily in small meal sizes showed no substitution of the heat increment of feeding for thermoregulation.

3.3.2 *BMR and Seasonal Acclimatization*

The positive relationship between latitude and BMR in terrestrial (Broggi et al. 2007; Weathers 1979) and marine (Ellis 1984) birds suggests that differences in BMR among birds are related to climatic variation. In addition, tropical resident species often have lower BMR than temperate-zone species (Wiersma et al. 2007a; Hails 1983), although some of this variation may be related to habitat, as tropical species from shaded forest areas tend to have average BMR while those from open sunny habitats have reduced BMR (Merola-Zwartjes 1998; Weathers 1997; Vleck and Vleck 1979). In addition, for species that migrate to tropical regions or for those that occupy geographic ranges encompassing both temperate-zone and tropical populations, BMR tends to be lower in the tropics (Kersten et al. 1998; Lindström 1997; Klaassen 1995; Kersten and Piersma 1987).

Laboratory acclimation experiments have shown that temperature can influence BMR, with cold acclimation increasing BMR and warm acclimation decreasing BMR in certain captive species (see McKechnie 2008, for review; also see Gelineo 1964). Although BMR in winter is usually higher than in summer for wild birds in seasonal climates, it may also be lower or seasonally stable (see McKechnie 2008; Dawson and O'Connor 1996, for reviews), so winter increases in BMR are not required for seasonal acclimatization to cold. Weathers and Caccamise (1978) suggested that seasonal variation in BMR is related to body mass, with large birds (>200 g) generally showing winter decreases in BMR, while small birds generally show winter increases in BMR (Fig. 3.1). However, McKechnie (2008) critically reevaluated Weathers and Caccamise's (1978) data and included additional data meeting strict requirements for BMR and found no evidence of a relationship between body mass and the magnitude of seasonal variation in BMR for birds, although he noted that sample sizes for species >30 g were too low at present for definitive conclusions.

How much does BMR vary seasonally or with temperature acclimation in those species showing labile BMR? Gelineo (1964) reported changes in BMR in captive birds ranging from 10 to 85% upon cold acclimation in the laboratory. Similarly, more recent data show cold acclimation-induced increases in BMR ranging from 5 to 42% (McKechnie 2008). Interestingly, BMR of Rufous-collared Sparrows (*Zonotrichia capensis*) showed a greater response to cold acclimation in populations from seasonally variable environments than in those from seasonally stable environments, suggesting that seasonal phenotypic flexibility in BMR is associated with climatic variability (Cavieres and Sabat 2008). The maximum degree of seasonal variation in BMR for wild birds to date was documented for House Sparrows, where BMR was 64% higher in winter than in summer (Arens and Cooper 2005a). According to the allometric equation of Weathers and Caccamise (1978), winter BMR/summer BMR ratios of 1.24, 1.16, and 1.05 would be expected for birds of 10, 25, and 100 g body mass, respectively.

Because winter elevations of BMR in small birds are often correlated with improvements in cold tolerance (e.g., Liknes et al. 2002; Liknes and Swanson 1996;

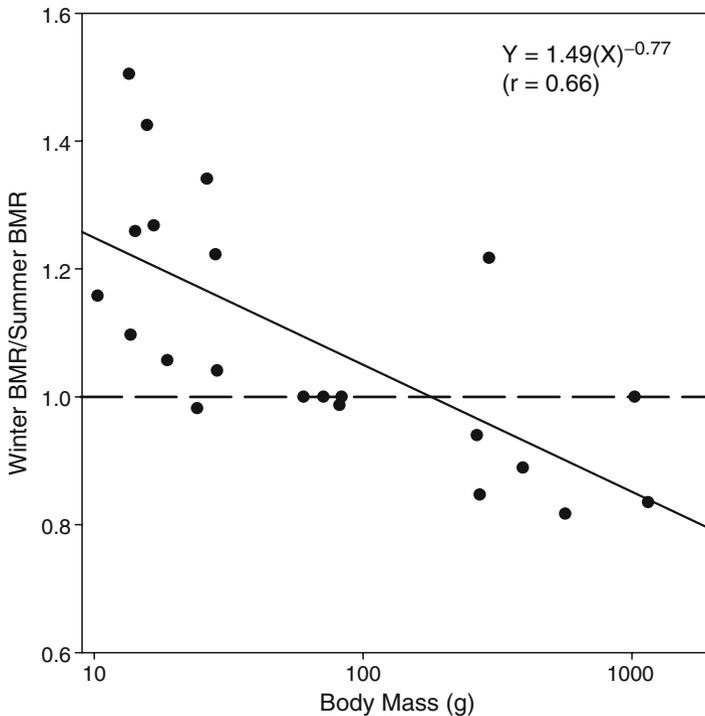


Fig. 3.1 Relationship between body mass and winter/summer BMR ratio in birds. The *dashed line* represents equality between summer and winter BMR. Birds less than about 200 g tend to show elevated BMR in winter relative to summer, while the opposite is generally true for larger birds. Redrawn from Weathers and Caccamise (1978), with permission

Cooper and Swanson 1994; Swanson 1991a; Weathers and Caccamise 1978), this suggests that changes in BMR are functionally correlated with changes in cold tolerance. Dawson and O'Connor (1996) suggested that an elevation of BMR in winter appears unnecessary and energetically expensive for cold defense given the substantial capacity of birds for regulatory thermogenesis. They mentioned two possibilities by which winter increases in BMR could benefit cold tolerance in birds directly. First, winter increases in BMR could serve as an emergency response for protection of peripheral tissues from cold injury. Second, an elevation of BMR could lower the threshold temperature for initiation of shivering, thus decreasing energetic costs of thermoregulation. Neither of these possibilities seem particularly likely, as shivering thermogenesis should provide sufficient protection of peripheral tissues from cold injury and an elevated BMR entails an energetic cost that offsets the benefit from a decreased threshold for shivering thermogenesis. Regarding the relationship of increases in BMR with increases in cold tolerance, Dawson and O'Connor (1996) suggest that it is currently impossible to distinguish whether increases in BMR in winter contribute to increases in cold tolerance, are a by-product

of them, or are a separate response. The by-product possibility seems most likely, as the increased metabolic machinery required for enhanced thermogenesis in winter probably entails higher maintenance costs (Swanson 1991a). Such a relationship should be manifested by a positive correlation between BMR and M_{sum} in birds. Some studies have found that BMR and M_{sum} are significantly correlated in birds on an interspecific basis (Rezende et al. 2002; Dutenhoffer and Swanson 1996), but Wiersma et al. (2007b) found no significant interspecific correlation between M_{sum} and BMR for tropical birds. To my knowledge, the relationship between BMR and M_{sum} on an intraspecific basis is unstudied in birds. Potentially pertinent to this question, however, Chappell et al. (1999) found that BMR and maximal exercise-induced metabolic rates were significantly and positively correlated in juvenile House Sparrows, but not in adults.

Most treatments of seasonal variation in BMR in birds have focused on its association with winter acclimatization, but variation in BMR related to the energetics of reproduction might also be expected. In this regard, decrements of BMR in the nonmigratory season or with summer acclimatization are common in birds (Dawson and O'Connor 1996). Such decreases in BMR during periods of the year where energy demands for migration or thermoregulation are reduced may be directly adaptive, functioning to decrease maintenance costs of metabolically active tissues during these periods. Ambrose and Bradshaw (1988) found that White-browed Scrubwrens (*Sericornis frontalis*) from arid environments exhibited a BMR that was 19% lower in summer than in winter, while scrubwrens from more mesic environments did not undergo seasonal variation in BMR. In addition, birds from the arid environments had lower BMR than birds from the more mesic environments in summer, but not in winter. These data suggest that the decrease in summer BMR for scrubwrens from arid environments could be directly adaptive, allowing reductions in energy expenditure, heat production, and respiratory evaporative water loss in hot, dry environments (Ambrose and Bradshaw 1988).

Another physiological adjustment during the breeding season that could contribute to decreases in BMR is mass loss during reproduction. This is a common occurrence among birds, although such mass losses are often restricted to females that are largely responsible for chick brooding and provisioning (Moreno 1989). Two alternative hypotheses have been proposed to explain reproductive mass losses in birds, the cost of reproduction hypothesis and the adaptive mass loss (or programmed anorexia) hypothesis (e.g., Golet and Irons 1999). The cost of reproduction hypothesis contends that the heavy workload associated with reproduction, incubation, brooding, and chick provisioning results in nutritional stress and decreases energetic condition, particularly in female birds. Thus, the decline in body condition and fat stores is viewed as a cost to reproduction. According to this hypothesis, mass loss should be greatest during the period of heaviest workload (i.e., feeding nestlings). Patterns of mass loss consistent with this hypothesis have been documented for a number of bird species (e.g., Nagy et al. 2007; Williams et al. 2007; Moe et al. 2002; Holt et al. 2002; Chastel and Kersten 2002; Murphy et al. 2000; Golet and Irons 1999; Bryant 1988; Nur 1984). Alternatively, mass loss during breeding could be adaptive if it reduces energetic costs (BMR and flight

costs) of adults involved in chick rearing. According to this hypothesis, mass loss should not be coincident with the period of highest workload, but should occur prior to or at the initiation of chick provisioning so that flight costs (and BMR) are lower during this period. A number of studies have documented this pattern of mass loss in breeding birds (e.g., Blem and Blem 2006; Kullberg et al. 2002; Cichon 2001; Phillips and Furness 1997; Sanz and Moreno 1995; Croll et al. 1991; Ricklefs and Hussell 1984; Freed 1981; Norberg 1981).

Variation of BMR in birds has been correlated with variation in lean mass or with variations in organ masses in several studies (e.g., Liu and Li 2006; Vezina and Williams 2003, 2005; Bech and Ostnes 1999; Chappell et al. 1999; Piersma et al. 1996a; Scott et al. 1996; Daan et al. 1990). Furthermore, a number of studies have estimated the reductions in BMR and flight costs potentially attributable to reproductive mass losses. These reductions range from about 5 to 25% for BMR and from about 4 to 10% for flight costs (Phillips and Furness 1997; Jones 1994; Croll et al. 1991). However, these estimates were generated from allometric equations predicting metabolic rates as a function of body mass and changes in body composition associated with reproductive mass losses were not quantified. Thus, these indirect estimates are of little value for describing the energetic consequences of breeding season mass losses. If mass losses were primarily from metabolically inactive tissues (e.g., fat), the reductions in BMR may be overestimated. However, loss of muscle protein during the egg-laying period has been documented for a number of birds, although its occurrence is not universal (Cottam et al. 2002; Houston et al. 1995; Jones 1991), and muscle protein levels depleted during the laying period may remain low during incubation (Mawhinney et al. 1999). Regardless of how breeding season mass losses are accomplished, significant energetic savings could accrue from decreases in flight costs and BMR during the reproductive season (Norberg 1981).

Few studies have directly measured variation in RMR over the breeding season in birds to evaluate how such changes might associate with variation in body mass. Nilsson and Råberg (2001) found that RMR in Great Tits (*Parus major*) increased, relative to winter levels, by 12% during nest building, 27% during egg production, and 20% during chick provisioning stages of the nesting cycle. RMR also varied among nonbreeding, egg-laying, and chick provisioning periods in European Starlings (*Sturnus vulgaris*), but relative RMR among the stages differed among years, with each stage being highest during one of 3 years of measurement (Vezina and Williams 2002). Black-legged Kittiwakes (*Rissa tridactyla*) exhibited a 26% reduction in RMR during the chick provisioning stage compared to pre-breeding and incubation stages of the nesting cycle, and this was associated with a concomitant increase in FMR and decrease in body mass (Fyhn et al. 2001). The body mass decrease between incubation and chick provisioning in kittiwakes is accompanied by reductions in plasma triiodothyronine levels and kidney metabolic intensity (Rønning et al. 2008), suggesting that a downregulation of metabolic intensity, in addition to decreased body mass, may contribute to the reduced BMR during chick rearing. However, Vezina and Williams (2005) found that mass-specific metabolic intensity (measured by citrate synthase activity) did not vary consistently with mass

changes in several organs across the breeding season in starlings, so mass and metabolic intensity of organs do not necessarily vary in tandem. This result is also supported by the finding that Red Knots (*Calidris canutus*) show a reduced BMR, despite increases in body mass, lean mass and gizzard mass when switched to a lower quality diet (Piersma et al. 2004).

3.3.3 BMR and Migratory Disposition

Migration involves sustained bouts of an energetically expensive behavior (flight) that are not immediately balanced by feeding and resting. Thus, migration results in physiological changes promoting endurance flight in birds (McWilliams et al. 2004; Gwinner 1990; Dawson et al. 1983a). Organismal metabolic rates might be expected to increase with migratory disposition because of the physiological adjustments promoting endurance flight. Several studies have examined seasonal variation in BMR (on a whole-organism basis) associated with migration (Table 3.2). Piersma et al. (1995) found that arctic-breeding Red Knots *Calidris canutus* held as outdoor-captives on the western European wintering grounds, demonstrated seasonal variation in BMR (up to 2.1-fold), with values in late spring and early summer (spring migration and initiation of breeding) higher than the annual minimum value during winter (Fig. 3.2). Similarly, Weber and Piersma (1996) showed that BMR in outdoor captive knots decreased markedly, along with mass, over a 31-day period following the attainment of peak mass associated with the spring migration period. Lindström (1997) found that BMR was higher in populations of autumn migrants than in populations on the African wintering grounds for three species of shorebirds, although the Sanderling (*Calidris alpina*) showed no seasonal

Table 3.2 Variation in BMR associated with migratory disposition in birds

Species	Mass (g)			BMR (mL O ₂ ·min ⁻¹)			H/L	References
	Annual			Annual				
	Spring	Low	Fall	Spring	Low	Fall		
Shorebirds								
<i>Calidris canutus</i>	165	115 ^a	115	3.97	2.06 ^a	2.24	2.1	Piersma et al. 1995
<i>C. alpina</i>	–	35	44	–	1.04	1.58	1.51	Lindström 1997
<i>C. ferruginea</i>	–	52	51	–	1.64	1.85	1.27	Lindström 1997
<i>C. alba</i>	–	47	47	–	1.58	1.58	1.0	Lindström 1997
<i>Arenaria interpres</i>	–	100	87	–	1.67	2.75	1.64	Lindström 1997
Passerines								
<i>Dendroica coronata</i>	13	–	11	0.84	–	0.64	1.31	Swanson and Dean 1999

The Annual Low column refers to the time period providing the lowest BMR over the annual cycle. For the shorebirds above, which are arctic-breeders and tropical-winterers, this period is in winter

^aValues estimated as averages for three individuals from Fig. 3 in Piersma et al. 1995

H/L: the annual high BMR divided by the annual low BMR

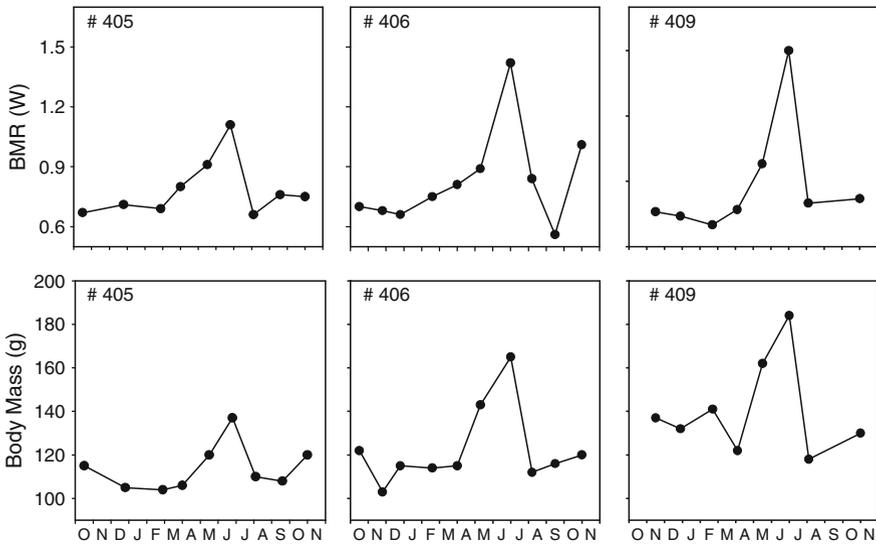


Fig. 3.2 Annual variation in body mass and BMR (in Watts) for three individual captive Red Knots, *Calidris canutus*. Both mass and BMR increased during the spring migration period and peaked during late June/early July, which coincides with the early breeding season on their arctic breeding grounds. Redrawn from Piersma et al. (1995), with permission

variation in BMR. Redshanks *Tringa totanus* also demonstrated elevated BMR in association with migratory fattening (Scott et al. 1996). Recently, Vezina et al. (2007) demonstrated that BMR in Red Knots varied over the cycle of fattening and mass loss surrounding the spring migration period and that changes in BMR were positively associated with changes in body mass and pectoral muscle mass. In addition to the shorebird data, BMR in Yellow-rumped Warblers increased by 31% in spring relative to fall migration (Swanson and Dean 1999).

The general pattern emerging from these studies is that whole-organism BMR does increase with migratory disposition in birds, at least during spring migration, and that elevated BMR accompanies the increment in body mass during migration (Fig. 3.2). Because only a few species have been studied, these conclusions regarding seasonal variation in BMR with migratory disposition must remain tentative at present. Further research, including BMR measurements from a wider variety of taxa, is needed to determine if these general patterns are robust. Additional specific research questions in need of study include: (1) Is the migratory elevation of BMR detected in shorebirds common to other taxa as well? (2) How does BMR compare between spring and fall migration? (3) Does variation of BMR with migration differ between short-distance and long-distance migrants, perhaps as a result of differential storage and use of protein and fat prior to and during migratory flights (Piersma and Jukema 2002; Klaassen et al. 1997; Klaassen 1996; Klaassen and Biebach 1994)?

The elevated BMR associated with migratory disposition in many birds suggests that a general elevation of metabolism supports an increased capacity for endurance flight. Most likely, BMR tracks changes in the total aerobic capacity of migrants, which presumably increases in association with the high and sustained energy demands of migration (Vezina et al. 2007; Weber and Piersma 1996). In this respect, increases in BMR with migratory disposition do not directly promote enhanced endurance flight, but instead are indicative of adaptation of total aerobic capacity (Piersma 2002; Piersma et al. 1995, 1996a). That is, migration-induced increases in BMR result from increased maintenance costs of tissues involved in support (e.g., heart, gut, kidney) of the high energetic demands of peripheral effector organs (i.e., skeletal muscles) during migration (Piersma et al. 1996a, 1999). Moreover, as mass declines (along with flight and maintenance costs) during long-distance migratory flights, BMR may concurrently decline (Battley et al. 2000; Klaassen and Biebach 1994).

3.3.4 M_{sum} and Seasonal Acclimatization

A general pattern emerging from seasonal studies of both M_{sum} and cold tolerance in birds is that those species showing marked winter enhancement of cold tolerance also show significant increases in M_{sum} (Arens and Cooper 2005a; Liknes et al. 2002; Cooper 2002; Liknes and Swanson 1996; O'Connor 1995a; Cooper and Swanson 1994; Swanson 1990a; Marsh and Dawson 1989; Dawson and Smith 1986). Cold acclimation also increased M_{sum} and cold tolerance in Red Knots (Vezina et al. 2006). This suggests that M_{sum} and cold tolerance in birds are positively associated. Consistent with such a relationship, birds exhibiting only minor seasonal adjustment of cold tolerance also demonstrate little or no seasonal variation in M_{sum} (Swanson and Weinacht 1997; Dawson et al. 1983b). However, geographic variation in cold tolerance in small birds is not necessarily congruent with geographic variation in M_{sum} , suggesting that M_{sum} is a rather imprecise indicator of cold tolerance (Swanson 1993; Dawson et al. 1983b). Moreover, significant improvement of cold tolerance in winter in small birds can occur without or with only minor winter elevation of M_{sum} (Saarela et al. 1989b, 1995; Dawson and Smith 1986; Dawson et al. 1983b).

Marsh and Dawson (1989) and Dawson and Marsh (1989) reviewed the literature to that date on seasonal variation in M_{sum} and cold tolerance in small birds. They concluded that the major physiological adjustment associated with winter acclimatization in small birds was a seasonal increase in shivering endurance, rather than changes in thermogenic capacity. However, changes in endurance are associated with changes in aerobic capacity in vertebrates generally (Bennett 1991), so the relatively minor seasonal changes in M_{sum} accompanying seasonal changes in cold tolerance (i.e., shivering endurance under cold exposure) in birds seem somewhat unusual in this regard. Marsh and Dawson (1989) and Dawson and Marsh (1989) also noted that seasonal variation in M_{sum} in most birds amounted to

less than about 15% and that such seasonal changes were lower in birds than in mammals, which sometimes exceeded 50%.

Much of the data used to formulate the conclusion of relatively minor seasonal adjustments in M_{sum} in small birds came from studies of cardueline finches, including the well-studied American Goldfinch *Carduelis tristis* (Dawson and Smith 1986; Dawson and Carey 1976) and the House Finch *Carpodacus mexicanus* (Dawson et al. 1983b). Dawson and Carey (1976) found no significant seasonal difference in mass-specific peak metabolic rates in goldfinches exposed to less than -60°C in air, despite winter birds tolerating these temperatures for up to 8 h while summer birds became hypothermic in less than 1 h. However, whole-organism peak metabolic rates in winter in these goldfinches were 32% higher than in summer. Dawson and Smith (1986) argued persuasively that whole-organism metabolic rates are actually the more pertinent measure for seasonal comparisons, largely because of seasonal differences in fattening. These authors detected a 16% elevation of M_{sum} in goldfinches in winter relative to spring, but M_{sum} in spring birds was measured in April, which has colder temperatures than summer months, so 16% might underestimate the full degree of seasonal variation in M_{sum} in these birds. Indeed, in American Goldfinches from South Dakota, whole-organism M_{sum} in winter exceeds that in summer by 31% (Liknes et al. 2002), a value similar to the whole-organism seasonal difference in peak metabolic rate documented by Dawson and Carey (1976). Thus, American Goldfinches appear to exhibit a greater degree of seasonal variation in M_{sum} than previously credited them. Dawson et al. (1983b) found no seasonal differences in M_{sum} from House Finches in California or Colorado, but O'Connor (1995a) found a 30% elevation of whole-organism M_{sum} in winter relative to summer in House Finches from Michigan. In addition, recent studies on a wider diversity of avian taxa have revealed that relatively large seasonal changes in M_{sum} are common among small birds, with winter increments of M_{sum} relative to summer commonly exceeding 25%, and exceeding 50% in some species (Liknes and Swanson 1996; Table 3.3). Thus, winter elevations of M_{sum} in birds and mammals appear less disparate than previously recognized. Finally, M_{sum} may also vary among winters or even within a winter in small birds and such variation is inversely correlated with temperature (Swanson and Olmstead 1999). This suggests that temperature exerts a proximate influence on M_{sum} in these birds.

The general positive relationship between M_{sum} and cold tolerance in birds suggests that the physiological changes underlying increases in M_{sum} may be important to winter acclimatization. M_{sum} cannot be sustained indefinitely, as birds become hypothermic after some time at a cold exposure eliciting peak thermogenesis (e.g., O'Connor 1995a). However, some fraction of M_{sum} can be maintained indefinitely, allowing survival of prolonged cold periods where energy demands for thermogenesis are high (Marsh and Dawson 1989). The fraction of M_{sum} that can be sustained for prolonged periods may be related to the relative provision of ATP to shivering muscles from fats or carbohydrates or from aerobic or anaerobic metabolism. In mammals, carbohydrates play an increasingly important role in ATP provision as exercise intensity increases, and lactate accumulates at high

Table 3.3 Variation in M_{sum} associated with seasonal acclimatization in birds

Species	Mass (g)		M_{sum} (mL O ₂ ·min ⁻¹)		W/S	References
	Summer	Winter	Summer	Winter		
American Goldfinch (Michigan)	12.8	14.4	4.20	4.83	1.15	Dawson and Smith 1986
(S. Dakota)	12.4	13.8	4.27	5.61	1.31	Liknes et al. 2002
House Finch (California)	21.0	21.6	5.34	5.83	1.09 ^a	Dawson et al. 1983b
(Colorado)	21.8	21.7	6.54	6.73	1.03 ^a	–
(Michigan) ^b	21.1	21.6	5.46	7.12	1.30	O'Connor 1995a
(S. Dakota)	21.3	21.0	6.03	6.54	1.08 ^a	Swanson and Liknes 2006
Eurasian Siskin	12.8	13.2	4.18	4.53	1.08	Saarela et al. 1995
Eurasian Greenfinch	27.1	26.6	6.19	5.19	0.84 ^a	–
Evening Grosbeak	58.0	62.1	12.33	14.50	1.18	Hart 1962
European Starling	79.6	89.8	17.33	18.83	1.09	–
House Sparrow (Ontario)	27.1	29.4	7.0	10.0	1.43	–
(Wisconsin)	26.4	27.6	8.4	10.9	1.29	Arens and Cooper 2005b
(S. Dakota)	26.8	27.1	8.4	9.3	1.11	Swanson et al. 2009
Black-capped Chickadee	12.4	13.4	4.78	6.49	1.36	Cooper and Swanson 1994
Black-capped Chickadee	13.2	13.0	4.39	6.00	1.37	Swanson and Liknes 2006
Dark-eyed Junco	16.9	18.2	5.78	7.39	1.28	Swanson 1990a
White-breasted Nuthatch ^d	19.8	21.3	5.18	8.04	1.55	Liknes and Swanson 1996
White-breasted Nuthatch	19.6	21.8	4.87	6.21	1.28	Swanson and Liknes 2006
Downy Woodpecker	25.0	26.6	6.62	10.04	1.52	Liknes and Swanson 1996
Downy Woodpecker	25.8	26.0	7.73	7.19	0.93 ^a	Swanson and Liknes 2006
Northern Bobwhite	220	230	20.19	22.02	1.09 ^a	Swanson and Weinacht 1997
Mountain Chickadee	11.4	11.3	4.26	5.37	1.26	Cooper 2002
Juniper Titmouse	16.3	17.1	5.23	5.73	1.10	–
Northern Cardinal	41.4	48.3	8.10	10.91	1.35	Swanson and Liknes 2006

The W/S column is the ratio of M_{sum} in winter divided by M_{sum} in summer

^aSeasonal values did not differ significantly

^bMichigan House Finches were tested at -10°C in helox, so values may not represent actual summit metabolism. However, all birds became hypothermic at the end of these tests suggesting that metabolic rates closely approached summit metabolism

^cValues from Hart (1962) are reported as presented in Marsh and Dawson (1989)

^dSummer values for nuthatches are mid-summer values, which were significantly lower than early/late summer values (20.5 g, 6.20 mL O₂·min⁻¹) in this study

exercise intensities (e.g., 85% of maximum aerobic capacity), indicating an anaerobic contribution to ATP provision at these levels of exercise (Roberts et al. 1996), but this does not appear to be the case for birds, where fat serves as the major fuel for both shivering and locomotion at all levels of intensity (Vaillancourt et al. 2005; McWilliams et al. 2004).

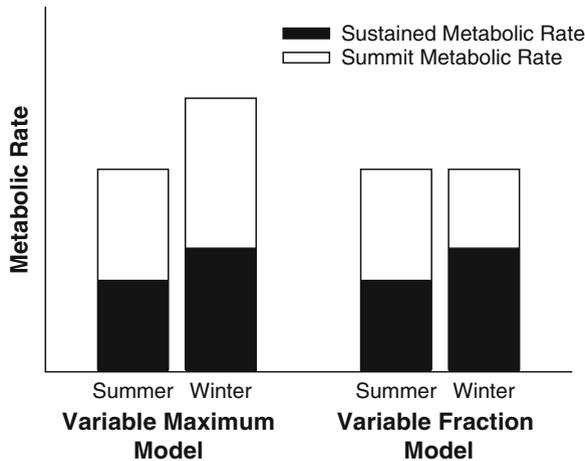


Fig. 3.3 Variable fraction and variable maximum models for how shivering endurance and M_{sum} are related on a seasonal basis. The entire extent of the bars represents M_{sum} , while the filled portions of the bars indicate the metabolic rates that can be sustained indefinitely (some percentage of M_{sum}). The variable fraction model suggests that winter birds can sustain a higher fraction of M_{sum} than summer birds, thereby increasing shivering endurance at cold temperatures and improving cold tolerance. The variable maximum model suggests that M_{sum} varies seasonally and that sustaining a seasonally constant fraction of M_{sum} elevates sustainable levels of thermogenesis and thereby improves cold tolerance. The two models are not mutually exclusive. From Liknes et al. (2002)

Birds could presumably increase cold tolerance (i.e., shivering endurance) in winter by increasing the fraction of M_{sum} that could be sustained relative to that in summer (variable fraction model, Fig. 3.3). Alternatively, birds could sustain a seasonally constant fraction of M_{sum} but increase M_{sum} in winter (variable maximum model, Fig. 3.3). These two models explaining seasonal differences in shivering endurance are not mutually exclusive and the end result of both models is an increase in sustained heat production in winter relative to summer (Liknes et al. 2002). For mammals, interspecific differences in endurance are mediated by differences in aerobic capacity, rather than by differences in the fraction of maximum aerobic metabolic rate that can be sustained (Roberts et al. 1996). Marsh and Dawson (1989) suggested that because seasonal changes in M_{sum} in birds tested to that date were relatively minor (mostly <15%), winter increments of cold tolerance and shivering endurance were mediated through the ability of winter birds to sustain higher fractions of M_{sum} than summer birds, consistent with the variable fraction model. Recent data indicating larger seasonal variations in M_{sum} , however, are more consistent with the variable maximum model (e.g., Liknes et al. 2002). According to this model, species sustaining a seasonally constant fraction of M_{sum} would increase heat production in winter relative to summer for any given fraction of M_{sum} sustained. If we assume that shivering endurance is seasonally stable for any given fraction of M_{sum} sustained, a winter increase in M_{sum} would affect an

increase in cold tolerance because sustainable levels of heat production would be higher in winter than in summer. Such an increase in sustained heat production would seem to be the functionally significant feature of winter increments of M_{sum} to cold tolerance and acclimatization (Liknes et al. 2002; Liknes and Swanson 1996; O'Connor 1995a). Furthermore, if a higher fraction of M_{sum} could be maintained in winter than in summer, as Marsh and Dawson (1989) suggest, then this could further improve cold tolerance in winter birds.

Because large winter increases in cold tolerance in birds may occur with only relatively minor winter increases in M_{sum} (Dawson and Smith 1986; Dawson and Carey 1976; Hart 1962) and intraspecific geographic variation in M_{sum} does not necessarily parallel geographic variation in cold tolerance, the precise nature of the relationship between cold tolerance (i.e., increased shivering endurance) and M_{sum} in birds is uncertain. Swanson (2001) demonstrated that mass-independent M_{sum} and shivering endurance (measured as time to hypothermia under a standardized cold stress in helox) were positively correlated for Dark-eyed Juncos (*Junco hyemalis*), American Tree Sparrows (*Spizella arborea*), and Black-capped Chickadees (*Poecile atricapillus*) overwintering in South Dakota, although the variation in M_{sum} explains only a portion of the variance in endurance ($R^2=0.11-0.54$). Moreover, mass-adjusted M_{sum} was positively associated with cold tolerance on an interspecific basis for 25 bird species (Swanson and Liknes 2006). Thus, the general positive correlation between M_{sum} and cold tolerance (i.e., shivering endurance) in birds is consistent with the general rule among vertebrates of a positive association between expanded aerobic capacities and enhanced endurance at submaximal levels of activity (Bennett 1991; Marsh and Dawson 1989).

3.3.5 M_{sum} and Migratory Disposition

Because physiological adjustments for migration and winter acclimatization both promote endurance muscular activities (long-distance flight and prolonged shivering, respectively) and organismal M_{sum} generally increases in winter, it might be expected that migratory disposition could influence M_{sum} . Seasonal variation in M_{sum} associated with migration has been documented in four passerine migrants (Table 3.4, Swanson and Dean 1999; Swanson 1995). For Warbling Vireos *Vireo gilvus* and Yellow Warblers *Dendroica petechia*, per-bird M_{sum} was elevated (18 and 23%, respectively) during spring migration relative to summer and fall migration periods, which do not differ significantly. M_{sum} in Ruby-crowned Kinglets *Regulus calendula* and Yellow-rumped Warblers *Dendroica coronata* was measured only during spring and fall migration periods and was significantly greater in spring than in fall for warblers (20%) and for male kinglets (11%), but not for female kinglets. The general pattern emerging from these studies is that M_{sum} is elevated during spring migration, relative to other seasons, at least in the territory-establishing sex. Interestingly, the degree of seasonal variation in M_{sum} associated with migration shows broad overlap with the percent increases in M_{sum} associated with winter

Table 3.4 Variation in M_{sum} associated with migratory disposition in passerine birds

Species	Mass (g)			M_{sum} (mL O ₂ ·min ⁻¹)			S/F ^a	References
	Spring	Sum	Fall	Spring	Sum	Fall		
Warbling Vireo	14.4	13.6	14.1	5.00	4.19	4.26	1.18	Swanson 1995
Ruby-crowned Kinglet (male)	6.3	–	6.0	2.63	–	2.37	1.11	Swanson and Dean 1999
Ruby-crowned Kinglet (female)	5.6	–	5.7	2.17	–	2.14	1.01	–
Yellow Warbler	10.0	9.1	9.5	3.46	2.89	2.73	1.23	–
Yellow-rumped Warbler	12.7	–	11.8	4.49	–	3.75	1.20	–

^aRatio calculated as spring M_{sum} divided by fall M_{sum} or pooled fall and summer M_{sum}

acclimatization (0–55%, but most values <35%, Table 3.3). In addition to these studies on passerines, Vezina et al. (2007) found that M_{sum} and cold tolerance in captive Red Knots changed in tandem with body mass and pectoralis muscle size changes over the period encompassing spring migration, and that this relationship was independent of thermal acclimation. More studies measuring seasonal trends in M_{sum} associated with migratory disposition on a wider variety of taxa are needed. Specific research questions in need of testing include: (1) Is the general pattern so far documented for passerines and Red Knot robust? (2) Do fall migratory adjustments in M_{sum} generally differ from those during spring or does variation in M_{sum} relate to differing migration strategies? (3) Are the percent changes in M_{sum} associated with migration and winter acclimatization similar? (4) Does M_{sum} change with the duration of migration (i.e., approaching the migratory destination), as rates of migration sometimes do (Ellegren 1993)?

The potential significance for the general pattern of a spring increment in M_{sum} in migratory birds is less obvious than the increase in M_{sum} associated with winter acclimatization because most migrants are not exposed to the seasonal extremes of temperature encountered by residents of cold climates. Swanson (1995) and Swanson and Dean (1999) presented two hypotheses, the cold acclimatization hypothesis and the flight adaptation hypothesis, to explain the pattern of seasonal variation in M_{sum} associated with migration documented for passerine migrants. The cold acclimatization hypothesis posits that selection for improved cold hardiness during spring migration relative to other seasons is responsible for the spring increment of M_{sum} . Many migrants are subject to colder temperatures during spring migration and upon arrival on breeding grounds than during the remainder of the breeding season or during fall migration (Swanson and Dean 1999; O'Reilly and Wingfield 1995; Wiersma and Piersma 1994). Thus, provided that increases in M_{sum} are related to increases in cold hardiness (see above), elevated M_{sum} and cold resistance during spring could be beneficial from a thermoregulatory standpoint.

Alternatively, the flight adaptation hypothesis suggests that the spring increment of M_{sum} is a by-product of selection for improved endurance flight during the spring rush to the breeding grounds. Faster flight velocities, longer flight durations,

or shorter stopover periods between successive flights could all produce a faster pace of migration in spring than in fall. The intensity, duration, and frequency of exercise training appear to be important in eliciting metabolic adjustments associated with improved muscular endurance in mammals and/or birds (Butler and Turner 1988; Harms and Hickson 1983; Hickson 1981). Thus, behaviors resulting in a faster pace of migration might be expected to produce improved flight endurance in migrating birds.

For the flight adaptation hypothesis to be a valid explanation for the patterns of seasonal variation in M_{sum} associated with migration documented for passerines by Swanson (1995) and Swanson and Dean (1999), spring rates of migration must exceed rates of migration in fall. This appears to be the case for several Old World passerine migrants and spring migration rates can exceed fall migration rates by two- to threefold in these species (Fransson 1995; Pearson and Lack 1992). Data are not available to test whether seasonal differences in migration rates exist for New World migrants, but some indirect evidence suggesting a faster pace of migration in spring than in fall has been reported (Swanson and Dean 1999; Morris et al. 1994; Winker et al. 1992).

One method of testing whether M_{sum} variation associated with migration conforms better to cold acclimatization or flight adaptation hypotheses is to examine seasonal variation in M_{sum} in migrants with differing migration strategies. Swanson and Dean (1999) used this method to compare seasonal variation M_{sum} in the mild temperate-zone migrants, Ruby-crowned Kinglet and Yellow-rumped Warbler, with that in the Neotropical migrants, Warbling Vireo, and Yellow Warbler. Mild temperate-zone migrants migrate earlier in the spring and later in the fall than Neotropical migrants (Hagan et al. 1991), so they are exposed to lower average and extreme temperatures, increased probabilities of encountering cold or adverse weather, and are subject to reduced variation between spring and fall migration periods than are Neotropical migrants. Swanson and Dean (1999) found that mild temperate and Neotropical migrants demonstrated similar mass-independent M_{sum} and similar levels of seasonal variation in M_{sum} , despite the differences in thermal environments encountered. These data are not consistent with the cold acclimatization hypothesis and suggest that factors other than temperature acclimatization, perhaps adaptation for endurance flight, are responsible for the migration-induced changes in M_{sum} . The data of Vezina et al. (2007) for captive Red Knots provide a more direct test of the flight adaptation hypothesis and the increases in M_{sum} and cold tolerance during the period of spring migratory fattening and pectoralis muscle hypertrophy, irrespective of thermal acclimation, also support the idea that elevated thermogenic capacity is a by-product of migratory disposition. Even if cold acclimatization is not the selective factor responsible for the spring increment of M_{sum} in migratory birds, elevated M_{sum} and accompanying increases in cold tolerance could still presumably benefit thermoregulation in these birds if they encounter cold temperatures or adverse climatic conditions during migration or upon arrival on breeding grounds. However, the spring increment of M_{sum} in the passerine migrants studied by Swanson (1995) and Swanson and Dean (1999) was not uniformly associated with improved cold resistance.

3.4 Mechanistic Correlates of Seasonal Variation in Metabolic Rates

Adjustments contributing to seasonal changes in whole-organism basal, summit, or MMRs could occur at several levels within the bird (Fig. 3.4). BMR is largely a function of central organs (e.g., brain, heart, gut, and kidney), while maximal and summit metabolic rates are largely functions of skeletal muscle activity (Hoppeler and Weibel 1998; Bennett 1991; Taigen 1983). Consequently, adjustments promoting changes in MMR or M_{sum} might not promote similar changes in BMR. Thus, M_{sum} and BMR may not show corresponding seasonal or migration-induced variation in birds. Such a discrepancy between seasonal variation in BMR and M_{sum} has been demonstrated in some birds (O'Connor 1995a; Dawson and Smith 1986; Hart 1962). On the other hand, BMR and M_{sum} are phenotypically correlated in birds independent of mass and phylogeny (Rezende et al. 2002; Dutenhoffer and Swanson 1996; but see Wiersma et al. 2007b), so physiological and biochemical adjustments influencing M_{sum} in birds may generally influence BMR or vice versa.

Because seasonal or migration-induced changes in BMR in birds apparently reflect increased maintenance costs for support of elevated metabolic capacities (M_{sum} and MMR) (Piersma et al. 1995, 1996a; Swanson 1991a), a review of potential limits to aerobic metabolism is needed before examination of mechanistic responses underlying changes in BMR and metabolic capacities can proceed. Organismal metabolic capacities are potentially limited at several steps along the

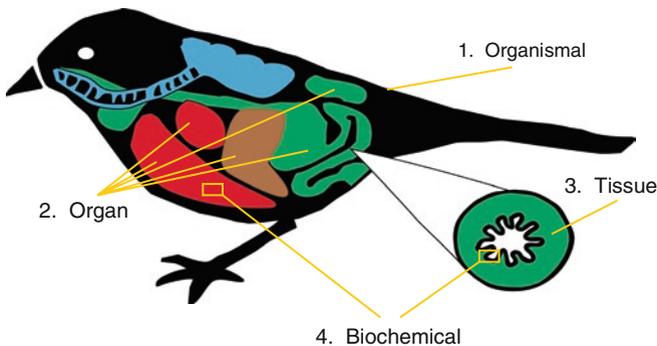


Fig. 3.4 Adjustments potentially mediating seasonal variation in basal, summit, or MMRs can occur from the whole-organism to the biochemical levels within the bird. At the whole-organism level, changes in fattening or thermal conductance, along with changes in organismal metabolic rates, could markedly influence flight or shivering endurance. Such organism-level adjustments in basal or MMRs could themselves be mediated by changes in masses of metabolically active nutritional or exercise organs. Variation at the cell or tissue level, such as cellular hypertrophy or changes in capillary density in the muscle or luminal surface area of the intestine, could complement organ-level adjustments to enhance metabolic or nutritional support capacities. Finally, contributions from biochemical changes, such as increased catabolic enzyme activities, increased capacities of metabolic substrate transport, or increased intestinal transporter uptake rates, could influence mass-specific metabolic intensities of organs and thereby impact organismal metabolic rates

pathways for provision and use of oxygen and metabolic substrates (Hoppeler and Weibel 1998; Suarez 1998). Limits might be imposed by oxygen diffusing capacity in the lung, substrate mobilization from storage depots, transport capacity of oxygen and substrates to tissues, capillarity of muscles, transport of oxygen and substrates into muscle cells, intracellular transport to mitochondria, availability of intracellular

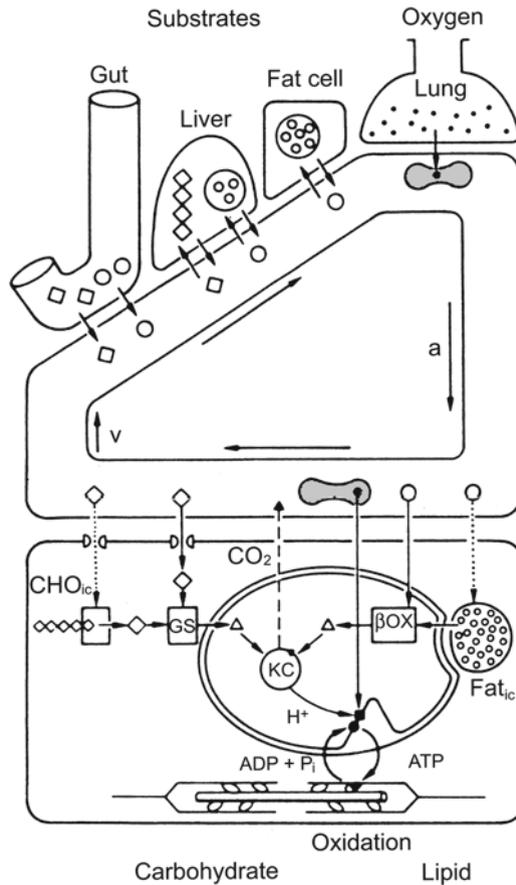


Fig. 3.5 Diagram illustrating the interacting structures and pathways involved in the processing, transport, and use of oxygen and substrates during oxidative metabolism. Substrates enter the bloodstream from the gut or from storage depots, while oxygen enters at the lung. Both oxygen and substrates are delivered to the muscle cell and are transported into the mitochondria for oxidative metabolism. Limitations to aerobic capacity might be imposed by oxygen diffusing capacity in the lung, substrate mobilization from storage depots, transport capacities of oxygen or substrates to muscle cells, capillarity of muscles and transport of oxygen and substrates into muscle cells, intracellular transport to mitochondria, availability of intracellular substrate stores to supplement extracellular supply, or cellular oxidative capacity. *CHO* carbohydrates; *GS* glycolysis; *KC* Krebs cycle; *β OX* β -oxidation; *Fat_{ic}*, intracellular lipid deposits; *a* arterial; and *v* venous. *Open circles* indicate lipids, *open squares* indicate carbohydrates, and *closed dots* indicate oxygen. Reprinted from Hoppeler and Weibel (1998), with permission

substrate stores to supplement extracellular supply, or cellular energy use (Fig. 3.5). Interspecific studies of mammals suggest that the following factors are important to MMRs: lung volume, stroke volume of the heart and blood oxygen carrying capacity, capillarity of muscles, transport of oxygen into muscle cells, intracellular substrate supplies in the muscle, and muscle mitochondrial volume (Hoppeler and Weibel 1998). Thus, limitations to aerobic capacity appear at a number of levels and limits may vary under differing conditions for activity. This suggests that the capacities for any one level of the integrated system do not greatly exceed capacities at other levels, a concept known as symmorphosis (Taylor and Weibel 1981). Symmorphosis, or at least correlated changes in some steps of pathways affecting organismal performance, appears to be generally applicable to limits on aerobic performance in vertebrates, including birds (Seymour et al. 2008; Suarez 1998; Bennett 1991). Thus, elevated organismal aerobic capacity is often accompanied by changes in several components of energy processing, transport, and use.

Nevertheless, metabolism of the skeletal muscle cells determines the aerobic energy demand during maximal metabolism (Hoppeler and Weibel 1998; Bennett 1991). With regard to energy demand, seasonal or migration-induced variation in summit metabolic rates could conceivably result from either (or both) changes in metabolic intensity (i.e., mass-specific alteration of metabolism) or masses of muscles active in shivering. Factors involved in regulating muscle metabolic intensity include mitochondrial volume, mitochondrial cristae surface area, and concentrations of catabolic enzymes (Suarez 1998). The flight muscles (pectoralis and supracoracoideus) are probably primary determinants of MMRs during both migratory flights and prolonged shivering, but the leg muscles may also be important for shivering in some species (Vittoria and Marsh 1996; Duchamp and Barre 1993; Marsh and Dawson 1989; Carey et al. 1989; Aulie and Tøien 1988). Thus, if variation in metabolic intensity is associated with changes in aerobic capacity, it should occur at these sites. Such variation would alter the metabolic capacity of skeletal muscles without corresponding changes in muscle mass. Regulatory enzymes especially important to control aerobic capacity include citrate synthase (CS), a regulatory enzyme of the Krebs cycle, and cytochrome c oxidase (CCO), which is the terminal step in the electron transport chain. Activities of both of these enzymes have been used as indices of mass-specific aerobic capacity of tissues (e.g., Vezina and Williams 2005; Liknes 2005; Weber and Piersma 1996; O'Connor 1995b; Marsh and Dawson 1982). Enzyme activities typically used as indicators of carbohydrate and lipid provision capacities to the Krebs cycle in birds are phosphofructokinase-1 (PFK-1), a regulatory step for glycolysis, and β -hydroxyacyl-CoA dehydrogenase (HOAD), a regulatory step in the β -oxidation pathway for catabolism of free fatty acids (FFA) (e.g., Liknes 2005; Guglielmo et al. 2002; O'Connor 1995b; Marsh and Dawson 1982; Marsh 1981).

Whole-organism variation in aerobic metabolic capacity could also occur without changes in metabolic intensity by variation in the masses of skeletal muscles (Daan et al. 1990). During migratory periods or season-long cold exposure, increases in energy demand resulting from increased mass and activity of skeletal muscles

would also entail increased processing and provision of energy to support elevated metabolic rates. The heart, gut, digestive organs, and kidney might undergo seasonal or migration-induced adjustment to meet these heightened energy demands and such changes in these central organs would presumably influence BMR.

3.4.1 Seasonal or Migration-Induced Changes in Transport Capacities for Oxygen

The principle of symmorphosis dictates that elevated energy demand by the skeletal muscles during migration or winter should be accompanied by increases in other systems involved in energy provisioning. Critical steps in the provision of energy to active muscles involve the transport and delivery of oxygen and substrates to muscles. Seasonal or migration-induced variation in metabolic rates would therefore be expected to be associated with alterations in oxygen and substrate transport mechanisms. Oxygen carrying capacity of the blood is determined by the hemoglobin concentration, which in turn is related to the hematocrit, or packed cell volume, of the blood. Hematocrit was elevated by 11% and oxygen carrying capacity by 9% in Dark-eyed Juncos in winter relative to summer (Swanson 1990b). In White-crowned Sparrows, hematocrit was elevated in winter and during spring migration relative to other periods of the year (deGraw et al. 1979). Moreover, migratory Bartailed Godwits (*Limosa lapponica*) had higher hematocrit and hemoglobin content than allometrically predicted, and both increased in birds that improved their energetic condition during stopover, suggesting that high levels are associated with readiness for departure on migratory flights (Landys-Ciannelli et al. 2002; Piersma et al. 1996b). Hematocrit was also positively correlated with MMR during treadmill running in female, but not male, Red Junglefowl *Gallus gallus* (Hammond et al. 2000). In contrast, Breuer et al. (1995) found that four species of Australian passerines all showed seasonally constant hematocrit, but winter increases in erythrocyte number, suggesting smaller erythrocytes with greater surface area in winter relative to summer. These authors speculated that the smaller erythrocytes in winter could increase efficiency of gas exchange and oxygen transport in support of winter thermogenic demands. Hematocrit also showed little seasonal variation in captive Ruff *Philomachus pugnax* and Red Knot during the annual cycle, despite maintenance of typical annual cycles of body mass and molt in these birds (Piersma et al. 2000). In a recent review of hematocrit variation in birds, Fair et al. (2007) concluded that hematocrit generally, but not universally, increased in winter relative to summer for birds in temperate climates.

Transport of oxygen from blood to working muscles is also important to aerobic muscle function and depends, among other factors, on the vascularization of the muscle (high vascularity decreases diffusion distance) and the gradient for diffusion. In addition, oxygen transfer from blood to muscle can be facilitated by muscle myoglobin because its affinity for oxygen is higher than that of hemoglobin. In an interspecific study of pectoralis muscle capillary density in 15 species of European

passerines, Lundgren and Kiessling (1988) found that capillary density was higher in long-distance migrants when compared with short-distance migrants or residents, suggesting that increased capillary density is important to endurance flight. Swim training increased both the maximum oxygen consumption during swimming (27%) and the capillary to muscle fiber ratio (20%) in leg muscles of Tufted Ducks *Aythya fuligula* (Butler and Turner 1988). Cold acclimation in the pigeon increased capillary density in pectoralis muscle, but no such change occurred between flying and sedentary birds (Mathieu-Costello et al. 1994, 1998). Treadmill training in Bar-headed Geese *Anser indicus* increased leg muscle myoglobin content by 20–31% in different thigh muscles (Saunders and Fedde 1991). Captive Tufted Ducks in an outdoor aviary that underwent a natural training regimen that included diving and flying had higher myoglobin content in pectoralis and leg muscles (38–55%) than untrained indoor captives (Butler and Turner 1988). In addition, European Starlings had higher myoglobin content in both heart and pectoralis muscle shortly after arrival from migration when compared to wintering birds in Spain (Palacios et al. 1984). In general, both the capacity of the blood to transport oxygen and the ability to unload oxygen to the tissues seem to increase with activity training, migration, or cold exposure in birds. In contrast to these results, however, American Goldfinches showed no difference in capillary to muscle fiber ratios in the pectoralis between winter and late spring (Carey et al. 1978).

Oxygen extraction efficiency (EO_2) may vary under cold exposure in birds and seasonal changes in EO_2 could contribute to variation in oxygen delivery to working muscles among seasons (Arens and Cooper 2005a; 2005b). Only two species have been studied to date with regard to seasonal changes in EO_2 . Seasonally stable EO_2 under severe (helox) and moderate cold exposure was documented for House Sparrows during the active phase of the daily cycle, but moderate cold exposure resulted in higher EO_2 in winter than in summer during the rest phase, when thermogenic demands are typically greatest (Arens and Cooper 2005a, b). Black-capped Chickadees showed winter increases in EO_2 relative to summer under severe cold stress (Cooper and Same 2000).

3.4.2 Seasonal or Migration-Induced Changes in Transport Capacities for Substrates

Prolonged shivering and endurance flights are both fueled largely by lipid (Dawson et al. 1983a) and birds rely on circulatory lipids to fuel sustained exercise to a greater degree than mammals (McWilliams et al. 2004; Weber et al. 1996), so transport capacities for lipids might be expected to increase with winter acclimatization or migratory disposition. Because lipids are relatively insoluble in plasma, they are generally carried in the blood bound to carrier proteins. FFA are generally bound to plasma albumin and triglycerides (TG) are bound to apoproteins, mainly as very low-density lipoproteins (VLDL) for transport to muscle (Fig. 3.6; McWilliams et al. 2004; Stevens 1996; Ramenofsky 1990). Plasma FFA levels are generally

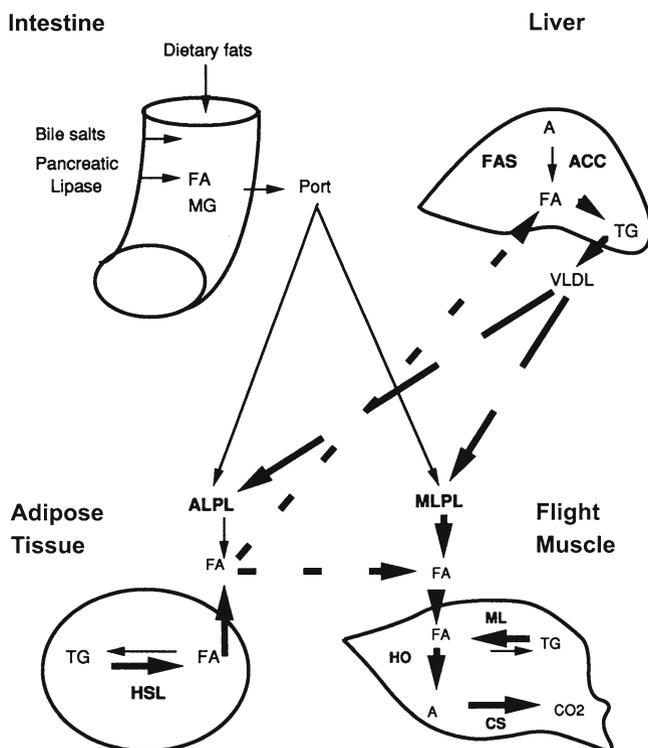


Fig. 3.6 Pathways for lipid mobilization and use as a metabolic substrate for migration. The *heavy lines* indicate major metabolic pathways operating during migration. Lipids are mobilized from stored fat and transported to liver and flight muscle as free fatty acids (FA) bound to plasma albumin. Triglycerides (TG) from the liver may also be released into the blood and bound to apo-proteins to form very low-density lipoproteins (VLDL). VLDLs can be hydrolyzed by muscle lipoprotein lipase (MLPL) for transfer into the muscle cell as FA. Enzymes are shown in *bold*. MG monoacylglycerol; Port portomicrons; HSL hormone-sensitive lipase; ALPL adipose lipoprotein lipase; FAS fatty acid synthetase; ACC acetyl-CoA carboxylase; ML muscle lipase; HO β -hydroxyacyl-CoA dehydrogenase; and CS citrate synthase. Reprinted from Ramenofsky (1990), with permission

elevated during cold exposure (Liknes 2005; O'Connor 1995b; Swanson 1991b; Marsh et al. 1984; Marsh and Dawson 1982) and sustained flights or hop-flutter wheel exercise (Pierce et al. 2005; Landys et al. 2005; Jenni-Eiermann et al. 2002; Gannes et al. 2001; Jenni-Eiermann and Jenni 1992, 2001) in birds, although plasma levels under such conditions often do not vary seasonally. Moreover, plasma levels of albumin did not change between winter and late spring in House Finches, despite improved cold tolerance and elevated M_{sum} in winter birds (O'Connor 1995b). Plasma TG and VLDL were elevated during active migratory flights when compared to resting or foraging birds in European Robins *Erithacus rubecula*, Pied Flycatchers *Ficedula hypoleuca*, and Garden Warblers *Sylvia borin* (Jenni-Eiermann and Jenni 1992). Moreover, Bar-tailed Godwits captured immediately

following migratory flights had elevated TG levels compared to inactive fasting birds, also suggesting that elevated TG levels may support the high metabolic demands of flight (Landys et al. 2005). This raises the possibility that the transport of TG via VLDL might be a general mechanism for seasonal variation in lipid transport associated with migration or winter acclimatization in birds. However, TG levels did not show similar elevation with flight for pigeons (Schwilch et al. 1996; Bordel and Haase 1993) or Red Knots (Jenni-Eiermann et al. 2002). Neither did TG levels increase with hop-flutter wheel exercise in Red-eyed Vireos *Vireo olivaceus* (Pierce et al. 2005) or with severe cold exposure (in either summer or winter) in Black-capped Chickadees, House Sparrows, and White-breasted Nuthatches *Sitta carolinensis* (Liknes 2005). Thus, seasonal modulation of lipid supply to working muscles via TG and VLDL does not appear to be a common mechanism supporting high levels of muscular activity among birds.

Muscle lipoprotein lipase (MLPL), present in the capillary endothelial wall, catalyzes the hydrolysis of plasma TG to FFA and glycerol, which can then be taken up by the muscle cells (Ramenofsky 1990). Peak MLPL activity in captive Dark-eyed Juncos during the spring migratory period occurred when birds were exhibiting migratory restlessness, suggesting an increased supply of lipid to muscles during periods of migratory flight (Ramenofsky 1990). Seasonal changes in MLPL activity might allow modulation of uptake of lipids by muscles. Pectoralis lipoprotein lipase activity, however, did not vary between premigratory and wintering Rosy Pastors (*Sturnus roseus*) from India (George and Vallyathan 1964). Savard et al. (1991) also failed to document any difference in peak MLPL activity between migratory and nonmigratory juncos. Furthermore, mean MLPL activity was higher in outdoor captive Dark-eyed Juncos during early molt than during migration (Ramenofsky et al. 1999). On the other hand, diel rhythms of MLPL activity in juncos were apparent during migration, but not during winter or molt, with nocturnal values associated with migratory restlessness greater than diurnal values (Ramenofsky et al. 1999). MLPL activity declined overnight in juncos exhibiting nocturnal migratory restlessness, concomitant with an increase in adipose tissue lipolysis, suggesting a relatively steady supply of FFA to muscles during nocturnal activity (Savard et al. 1991). Thus, although lipids are the primary fuel source for prolonged shivering and migratory flights, conclusive demonstration of enhanced capacities of circulatory lipid transport to working muscles during migration or winter in birds is lacking.

Another potential regulatory point for lipid metabolism is the delivery of fatty acids from the plasma across the sarcolemma into the muscle cell. Fatty acid transporters account for much of this delivery (McWilliams et al. 2004), so could function as sites of migration-induced or seasonal variation. Sarcolemmal fatty acid transporters in birds and mammals include plasma membrane-bound fatty acid binding protein (FABP_{pm}) and fatty acyl translocase (FAT/CD36) (Sweazea and Braun 2006; Bonen et al. 2004; Abumrad et al. 1999; Luiken et al. 1999). McFarlan (2007) recently studied migratory variation in sarcolemmal fatty acid transporters in White-throated Sparrows (*Zonotrichia albicollis*) and found that gene expression in the pectoralis muscle for both FABP_{pm} and FAT/CD36 increased in migratory

birds from Ontario relative to wintering birds from southern Mississippi, with fall migrants showing higher expression than spring migrants. Pectoralis FABP_{pm} protein levels also increased in migratory sparrows relative to winter, but spring and fall protein levels did not differ. These data suggest that sarcolemmal fatty acid transporters may be an important regulatory site for phenotypic flexibility in overall fatty acid flux rates during prolonged muscular exercise in birds.

A limited amount of information is available regarding migration-induced variation in intracellular transport of lipids to the mitochondrial matrix, where β -oxidation of fatty acids occurs. In exercising mammals, maximum delivery of extracellular carbohydrate and lipid to the muscle cells occurs at moderate workloads, about 40–50% of MMR. Higher work rates require reliance on intracellular substrate stores, which are higher in athletic species than in sedentary species of mammals (Hoppeler and Weibel 1998). Heart-type fatty acid binding protein (H-FABP) facilitates the intracellular transport of fatty acids within the skeletal muscle cell (Pelsers et al. 1999). H-FABP is a prominent cytosolic protein in pectoralis muscle and heart of migrating Western Sandpipers *Calidris mauri* where it is found at levels several-fold higher than in nonvolant mammals (Guglielmo et al. 1998). Guglielmo et al. (1998) further suggest that modulation of muscle H-FABP expression could serve as an important mechanism for enhancing extracellular lipid use during migratory flights. In Barnacle Geese *Branta leucopsis* pectoralis H-FABP increases throughout development and is further increased, in wild birds but not in captives, just prior to migration suggesting a relationship between H-FABP and aerobic capacity (Pelsers et al. 1999). In addition, increases in pectoralis H-FABP and/or H-FABP expression have been documented during migration for Western Sandpipers (Guglielmo et al. 2002) and White-throated Sparrows (McFarlan 2007) and during winter for Black-capped Chickadees and White-breasted Nuthatches, although H-FABP remained seasonally stable in House Sparrows (Liknes 2005). H-FABP was also seasonally stable in the supracoracoideus muscle for Black-capped Chickadees, White-breasted Nuthatches and House Sparrows (Liknes 2005). These data suggest that intracellular lipid transport via H-FABP in the pectoralis is generally elevated by the increased metabolic demands of winter and, particularly, migration, so intracellular fatty acid transport may be another key regulatory site for phenotypic flexibility of metabolism in birds.

Few data are available to assess whether intracellular lipid stores in avian muscle are as important as they are in mammals for support of high aerobic workloads. The volume density of intracellular lipid droplets in pigeon pectoralis muscle approximately doubled after cold exposure compared to controls, but flight activity did not promote a similar change relative to sedentary controls (Mathieu-Costello et al. 1994, 1998). Intracellular lipid in the pectoralis muscle of Eared Grebes *Podiceps nigricollis* approximately doubled during hypertrophy following the flightless molt period and just prior to fall migration (Gaunt et al. 1990). Piersma et al. (1999) detected little change in the fat content of flight muscles during staging in red knots, despite marked changes in the size of the muscles, suggesting little change in intracellular fat content. Intramuscular lipid in pectoralis muscles of Black-capped Chickadees, White-breasted Nuthatches and House Sparrows from the cold winter

climate of South Dakota was seasonally stable (Liknes 2005). Thus, available data are equivocal with regard to whether intracellular lipid in avian muscle increases with increasing energy demands. The absence of consistent increases in intracellular lipid with increasing energy demand is, perhaps, not surprising given the primary reliance of birds on exogenous fat stores to fuel sustained exercise (McWilliams et al. 2004).

The final step in lipid delivery to the mitochondria is transport of FFA across the mitochondrial membrane into the matrix where β -oxidation enzymes are housed. Transport of FFA into the mitochondrial matrix is catalyzed carnitine acyl CoA transferase (CAT), but may also involve FAT/CD36, which occurs on the mitochondrial membrane in mammals, may be physically associated with CAT, and functions in transport of long-chain fatty acids into the mitochondria in exercising muscle (Holloway et al. 2006; Campbell et al. 2004). In Semipalmated Sandpipers *Calidris pusilla* that were ready to depart on migration following a stopover period, carnitine oleoyl CoA transferase activity was significantly elevated relative to birds that were not in migratory disposition (Driedzic et al. 1993). Similarly, carnitine palmitoyl transferase increased in migratory relative to nonmigratory Western Sandpipers (Guglielmo et al. 2002). These data suggest that the capacity for FFA transport into the mitochondrion is enhanced with migratory disposition, but whether this result applies to other migrants or to birds wintering in cold climates is unknown. Based on the limited information available, it appears that intracellular transport of FFA to the mitochondrial matrix may vary with energy demand in birds, so this would seem to be a profitable avenue for further research relating to seasonal or migration-induced adjustments in metabolic rate.

3.4.3 Seasonal or Migration-Induced Changes in Mass-Specific Metabolic Intensity

Mass-specific adjustment of metabolic intensity could result from elevated mitochondrial density in tissues or from enhanced mass-specific activities of catabolic enzymes. Mitochondrial density in muscle as a function of cold acclimation, migration, or flight activity has only been investigated for a few species and these data suggest that mitochondrial density does increase positively with energy demand. Pectoralis muscle mitochondrial density increased concomitantly with muscular hypertrophy during the premigratory phase in three species of *Calidris* sandpipers (Evans et al. 1992). Mitochondrial density in pectoralis muscle also increased with hypertrophy in Eared Grebes during the period following molt and immediately prior to fall migration (Gaunt et al. 1990). Flight activity and cold acclimation both increased mitochondrial volume density in pigeon pectoralis muscle (Mathieu-Costello et al. 1994, 1998).

If mass-specific aerobic capacity of muscles increases during migration or winter acclimatization, such changes would need to be supported by an increased flux of substrates, principally lipid and carbohydrates, into the Krebs cycle. Thus,

increased activities of enzymes in β -oxidation and glycolysis pathways might be expected with development of migratory disposition or with winter acclimatization. Winter acclimatized American Goldfinches showed elevated mass-specific activities of PFK-1 and HOAD in pectoralis muscle relative to their summer counterparts, but hexokinase (HK) activity (an indicator of catabolism of glucose from plasma) was seasonally stable (Yacoe and Dawson 1983; Marsh and Dawson 1982). In House Finches, mass-specific activities of pectoralis muscle HK, PFK-1, and HOAD were all seasonally stable, while leg muscle showed seasonally stable HK and PFK-1, but winter increases in HOAD (O'Connor 1995b; Carey et al. 1989). Black-capped Chickadees exhibited elevated mass-specific and total HOAD activities in winter compared to summer for pectoralis and leg muscles, but not for supracoracoideus, and HOAD activity was seasonally stable in all these muscles for White-breasted Nuthatches and House Sparrows (Liknes 2005). For the same three species, activity of PFK-1 was seasonally stable in pectoralis, supracoracoideus and leg muscles (Liknes 2005).

Guglielmo et al. (2002) documented a 12% increase in pectoralis HOAD activity during migration in Western Sandpipers. Elevation of mass-specific activities of pectoralis HOAD in migratory compared with nonmigratory individuals is commonly reported for passerine migrants (Lundgren 1988; Lundgren and Kiessling 1985, 1986; Marsh 1981), but such elevation does not occur universally. Migratory Sedge Warblers *Acrocephalus schoenobaenus*, Reed Buntings *Emberiza schoeniclus*, and Yellowhammers *Emberiza citrinella* showed seasonally constant activities of pectoralis HOAD (Lundgren 1988; Lundgren and Kiessling 1985). Glycolytic enzyme activities (PFK-1 or pyruvate kinase) in pectoralis are unchanged or decrease with migratory disposition in most species (Lundgren 1988; Lundgren and Kiessling 1985; Marsh 1981), but increases have been reported in migratory Semipalmated Sandpipers *Calidris pusilla* (Driedzic et al. 1993) and juvenile Reed Warblers *Acrocephalus scirpaceus* (Lundgren and Kiessling 1986). Generalizing from these data, an increased capacity for lipid oxidation in pectoralis muscle is common, but not universal, to both winter acclimatization and migration in birds, but alteration of carbohydrate oxidation capacity is less regularly associated with these conditions.

For alterations in substrate catabolism to be important to changes in mass-specific aerobic capacity, enzyme activities in Krebs cycle and oxidative phosphorylation pathways would also need to be adjusted to permit changes in flux through these pathways. Current data are equivocal with reference to whether seasonal or migration-induced variation in mass-specific activities of oxidative enzymes underlie changes in aerobic capacity, as some species show changes while others do not. Muscovy ducklings, *Anas barbariae*, exhibited increased activities of CS and CCO in pectoralis and hindlimb muscles after cold acclimation (Vittoria and Marsh 1996; Barré et al. 1987). Black-capped Chickadees and House Sparrows showed elevated CS activity in pectoralis and/or supracoracoideus muscles (but not in leg muscles) in winter relative to summer (Liknes 2005). Likewise, European Tree Sparrows *Passer montanus* showed elevated pectoralis CCO activity in winter compared to summer (Zheng et al. 2008). European

Starlings had higher mass-specific and total pectoralis CS activity at the end of winter than during the egg-laying period, and total activity was also higher at the end of winter than during the chick-rearing period (Vezina and Williams 2005). Treadmill training elevated CS activity in leg muscles of the Tufted Duck relative to untrained individuals (Butler and Turner 1988). Combined pectoralis and leg muscle CS activity was positively correlated with MMR during treadmill running in male, but not female, Red Junglefowl (Hammond et al. 2000). Reed Warbler, European Robin *Erithacus rubecula*, Eurasian Blackbird *Turdus merula*, and Reed Bunting all showed elevated pectoralis muscle activities of CS and CCO in migratory relative to nonmigratory individuals (Lundgren and Kiessling 1985, 1986). Activities of CS and CCO in the pectoralis were also increased during migration in Goldcrests *Regulus regulus*, Great Tits *Parus major*, and Yellowhammers (Lundgren 1988) and pectoralis CS activity also increased during migration in Western Sandpipers (Guglielmo et al. 2002). These results suggest that alterations of mass-specific oxidative enzyme activities might function to elevate aerobic capacity in migrants or cold acclimatized birds.

In contrast to these data, however, are a number of studies documenting no mass-specific variation of oxidative enzyme activities with migration or cold acclimatization. Neither House Finches nor American Goldfinches exhibited differences in mass-specific CS activity of the pectoralis muscle associated with seasonal acclimatization, although leg muscle in House Finches did show a winter increment of CS activity (O'Connor 1995b; Carey et al. 1989; Yacoe and Dawson 1983; Marsh and Dawson 1982). CS activities in pectoralis, supracoracoideus, and leg muscles of White-breasted Nuthatches were also seasonally stable (Liknes 2005). Furthermore, American Goldfinches show no seasonal variation in the activity of succinate dehydrogenase, another Krebs cycle enzyme (Carey et al. 1978), and pectoralis muscle homogenates and isolated mitochondria show no seasonal variation in their capacity to oxidize fats or carbohydrates (Yacoe and Dawson 1983). Mass-specific succinate dehydrogenase activity in the pectoralis also did not vary between migratory and nonmigratory Rosy Pastors (George and Vallyathan 1964). Gray Catbirds *Dumetella carolinensis* demonstrated no variation in mass-specific CS or CCO activities in flight muscles between migratory and nonmigratory individuals (Marsh 1981). No differences in mass-specific pectoralis CS activity were evident between migratory and nonmigratory Sedge Warblers (Lundgren and Kiessling 1985). In addition, Semipalmated Sandpipers and Red Knots showed no migration-induced variation in mass-specific CS or CCO activities, respectively, in flight muscles (Weber and Piersma 1996; Driedzic et al. 1993). Thus, while cold, activity, or migration-induced increments of mitochondrial density or mass-specific oxidative enzyme activities do occur in some species, their occurrence is far from universal, and such changes do not appear to be required for migration or cold acclimatization.

It might also be expected that nutritional organs would show increases in metabolic intensity associated with migratory disposition or cold acclimatization to assist in support of the elevated energy demands of migration and thermoregulation in the cold. There are few data to address this possibility, but some studies have

examined catabolic enzyme activities in the heart associated with migration and digestive enzyme activity and nutrient uptake capacities in the gut associated with cold acclimation. Stable or decreasing mass-specific aerobic capacity of the heart, as indicated by CS or CCO activities, with migratory disposition occurs in Semipalmated Sandpipers and Red Knots (Weber and Piersma 1996; Driedzic et al. 1993). Heart CS activity was also seasonally stable in European Starlings (Vezina and Williams 2005). Cold acclimation in Cedar Waxwings *Bombycilla cedrorum* produced no changes in digestive enzyme activities or nutrient uptake rates per unit intestine (McWilliams et al. 1999). Intestinal carrier-mediated glucose uptake was higher in cold-acclimated, exercised House Wrens than in warm-acclimated sedentary controls, but carrier-mediated glucose transport was an order of magnitude lower than passive glucose transport and proline-uptake rates in the gut did not vary between groups (Dykstra and Karasov 1992). Thus, the few available data suggest that mass-specific metabolic intensity of central organs does not vary substantially with migration or cold acclimatization. In contrast, Zheng et al. (2008) documented higher CCO activity in winter than in summer in liver of Eurasian Tree Sparrows.

3.4.4 Seasonal or Migration-Induced Changes in Organ Masses and Their Influence on Organismal Metabolic Rates

Because mass-specific increases in metabolic intensity do not seem to vary consistently with metabolic demands of migration or winter thermogenesis in birds, an alternative or additional strategy for elevating metabolic rates to meet these demands is to increase the masses of the tissues involved in provision and use of energy. A number of recent studies have examined the relationship between variation in masses of organs and variation in BMR in birds. The interspecific study of Daan et al. (1990) revealed that BMR in birds was correlated with lean dry masses of heart and kidney, but not with masses of other organs. BMR was also correlated with daily energy expenditure in this study, prompting the authors to conclude that organ mass is adjusted to meet daily energetic demands and that BMR varies accordingly with the adjusted organ masses. BMR varied positively with lean mass in Red Knots, but this relationship was mostly associated with variation in masses of stomach and intestine (Piersma et al. 1996a). In Tree Swallows *Tachycineta bicolor*, BMR was positively associated with kidney mass, but was negatively associated with pectoralis and intestine masses and showed no relationship with heart mass (Burness et al. 1998). Intestine length and liver mass were positively correlated with BMR in nestling European Shags *Phalacrocorax aristotelis*, but BMR showed no relationship with heart or kidney masses (Bech and Ostnes 1999). BMR was positively associated with gut, liver, kidney, and pectoralis masses in House Sparrows (Chappell et al. 1999). BMR was positively associated with intestine and lung masses in male Red Junglefowl and with spleen mass in females (Hammond et al. 2000). Cold-acclimated Hoopoe Larks *Alaemon alaudipes* showed elevated BMR relative to warm-acclimated birds and BMR was positively associated with

masses of liver, kidney, intestine and stomach (Williams and Tieleman 2000). Vezina and Williams (2003) studied variation in BMR and organ masses during the breeding season in female European Starlings and found that BMR was positively associated with oviduct mass during the laying period, with liver and gizzard masses during the chick-rearing period, and with pectoral muscle mass during the nonbreeding (end of winter) season. In contrast, BMR decreased while gizzard mass increased in Red Knots shifted from soft to hard-shelled food (Piersma et al. 2004). These studies indicate that changes in organ masses can influence BMR in birds and although individual organs are not positively associated with BMR in every case, important contributors to BMR variation appear to include kidney, liver, heart, and gut masses.

Given that variation in masses of central organs can influence BMR in birds, it is instructive to examine how central organ masses vary with migratory disposition or with winter acclimatization. Increment of heart mass is a regular component of development of migratory disposition in birds (Piersma 1998). Similarly, gut mass increases are commonly associated with elevated energy expenditures and resultant increases in daily food intake in birds (McWilliams and Karasov 2001; Karasov 1996). For long-distance migratory shorebirds, and presumably for other long-distance migrant species as well, immediately prior to departure on migratory flights “exercise organs” (i.e., pectoralis muscle and heart) increase in mass, while “nutritional organs” (i.e., stomach, intestine, and liver) decrease in mass (Landys-Ciannelli et al. 2003; Battley et al. 2001; Piersma 1998). Instructive in this regard is a study of body composition variation during a 24-day migratory stopover in Red Knots on the southern coast of Iceland (Piersma et al. 1999). During the first 7-days of the stopover period, knots showed little change in overall body mass, although heart, stomach, and liver masses increased. Over the next 10-days, body mass increased rapidly as the birds accumulated fat stores and masses of kidneys, liver, and intestine increased, along with a decrease in stomach mass. During the final 7-days before departure, body mass increased slowly and pectoral muscle and heart masses also increased, while stomach, intestine, liver, and leg muscle masses decreased (Fig. 3.7). Similar patterns of organ mass variation have been documented for Great Knot *Calidris tenuirostris* (Battley et al. 2001) and Bar-tailed Godwit (Landys-Ciannelli et al. 2003).

Also interesting are examinations of the body composition of birds immediately before and/or after long-distance migratory flights. Biebach (1998) and Bauchinger et al. (2005) studied migratory Garden Warblers before and after crossing the Sahara desert (a 2–3-day flight period) and found that this crossing resulted in decreases in most organ masses, with breast and leg muscle masses decreasing from 14 to 25% and digestive organ masses decreasing from 34 to 57%. Lean dry masses of most organs (excepting brain and lung) decreased following a 5,400-km migratory flight from Australia to China in Great Knots (Battley et al. 2000). Similarly, individual Red Knots showed decreases in pectoral muscle size and body mass following extended flights in a laboratory wind tunnel (Lindström et al. 2000) and a Thrush Nightingale showed decreases of about 20% in both BMR and body mass following 12-h wind tunnel flights (Lindström et al. 1999).

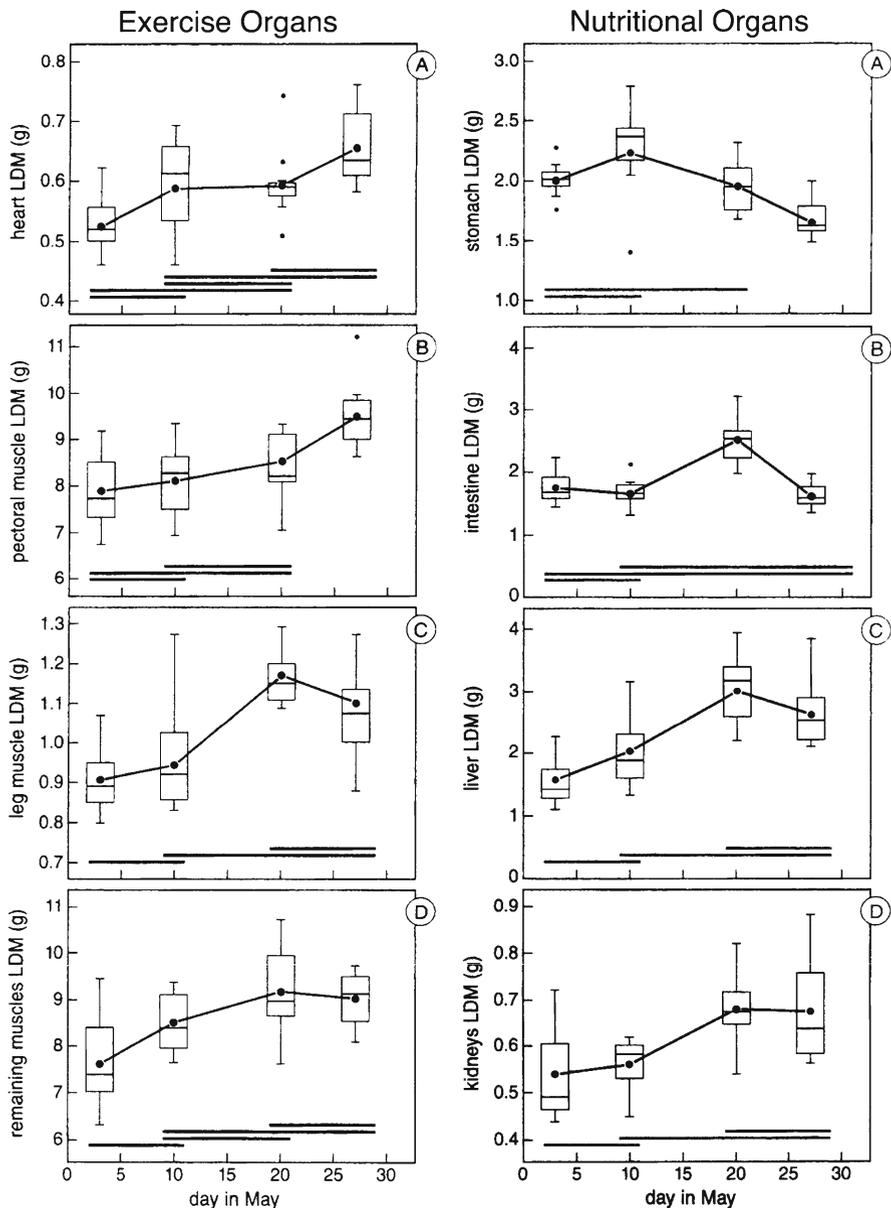


Fig. 3.7 Variation in lean dry mass of exercise (*left*) and nutritional (*right*) organs over a 24-day stopover during spring migration (May) in Red Knots, *Calidris canutus*. The *large dots* represent mean values, while the *horizontal lines* within the boxes represent median values. Boxes provide 25% quartiles around the median, while *error bars* indicate the range of values. Where *small dots* are present, they represent outlier values. *Heavy horizontal lines* indicate values not significantly different from each other. Reprinted from Piersma et al. (1999), with permission

Bar-tailed Godwits just prior to takeoff on long-distance migratory flights had small gizzard, gut, liver, and kidney masses relative to nonmigrating individuals (Piersma and Gill 1998). Migration in Western Sandpipers, a short-hop migrant, resulted in increases in masses of pectoralis muscle, heart, gizzard, pancreas, liver, and ceca, with relatively greater increases in digestive than in exercise organs (Guglielmo and Williams 2002).

Seasonal changes in gut mass, with higher values in winter, are common among birds, but these changes are usually associated with diet switches to less digestible food and gut mass increases on diets of low digestibility (Karasov 1990). However, there is evidence that cold, and its attendant thermoregulatory demands, can result in increments of gut mass in birds. Cold acclimation resulted in a 30% increase in intestinal length in Japanese Quail *Coturnix coturnix* (Fenna and Boag 1974). Dykstra and Karasov (1992) showed that cold acclimation in House Wrens produced a 21% increase in small intestine length. Moreover, cold-acclimated Cedar Waxwings increased masses of digestive organs by 22–53% over warm-acclimated controls (McWilliams et al. 1999). Winter acclimatized Rufous-collared Sparrows *Zonotrichia capensis* exhibited dry mass increases of 27 and 45% for crop and intestine, respectively, and this occurred despite the larger fraction of insects relative to seeds in the diets of winter birds relative to their summer counterparts (Novoa et al. 1996). Liknes (2005) documented winter increases, relative to summer, in intestine mass for Black-capped Chickadees, in liver and gizzard masses for House Sparrows, and in gizzard mass for White-breasted Nuthatches. Eurasian Tree Sparrows showed elevated BMR in winter along with increases in masses of liver, gizzard, and intestine (Zheng et al. 2008; Liu and Li 2006). Finally, Swanson (1991b) showed that liver wet mass in winter acclimatized Dark-eyed Juncos increased by 39% relative to summer acclimatized birds. Even though it is difficult to tease apart the factors driving the increase in gut and digestive organ masses during winter (i.e., diet or energetic demands of thermoregulation), elevated masses of the gut and digestive organs in winter may entail an energetic cost for maintenance, thereby driving up BMR in winter.

In summary, changes in central organ masses, and sometimes flight muscle masses, can influence BMR in birds and such changes are associated with migration and seasonal acclimatization. Thus, seasonal and migration-induced changes in body composition appear to be a mechanism by which similar variation in BMR can be modulated (e.g., Piersma 1998, 2002).

Can similar seasonal or migration-induced variation in organ masses help account for the seasonal patterns of variation in aerobic capacity or M_{sum} documented for birds? Changes in M_{sum} could presumably result from alterations in masses of skeletal muscles, especially those prominently involved in shivering (i.e., flight muscles). Few studies have directly examined correlations between aerobic capacity or M_{sum} and organ masses in birds. However, Chappell et al. (1999) investigated correlations between organ masses and maximum oxygen consumption during hop-flutter exercise in House Sparrows. In this study, breast muscle and heart masses were significantly and positively correlated with aerobic capacity,

although they explained only 17% of the variation in aerobic capacity. Hammond et al. (2000) demonstrated that maximum oxygen consumption during treadmill running in Red Junglefowl was positively correlated with intestine mass in females and with heart and pectoralis mass in males. In addition, M_{sum} was positively correlated with breast muscle size in both cold-acclimated and migratory Red Knots (Vezina et al. 2006, 2007). These data suggest that masses of flight muscles and heart, among other factors, can have an important influence on aerobic capacity or M_{sum} in birds.

If we accept that variation in masses of skeletal muscle and heart can influence aerobic capacity and M_{sum} in birds, to determine if such changes can assist in explaining seasonal patterns of variation in M_{sum} we need to examine how muscle and heart masses change with migration and winter acclimatization. Flight muscle and heart hypertrophy are common in migratory birds during premigratory and migratory periods (Landys-Ciannelli et al. 2003; Piersma 1998; Dawson et al. 1983a). This hypertrophy may occur rapidly, over a period as short as a few days (Lindström et al. 2000; Piersma et al. 1999; Jehl 1997; Fry et al. 1972). Increases in pectoralis muscle mass associated with the development of migratory disposition can be as high as 35% (Piersma et al. 1999; Jehl 1997; Evans et al. 1992; Marsh 1984; Baggott 1975). The degree of pectoralis muscle hypertrophy can even exceed these levels in species rebuilding muscle following a flightless molt period prior to migration (Gaunt et al. 1990). Increments of heart mass are also commonly associated with preparedness for departure on migratory flights in birds (Landys-Ciannelli et al. 2003; Piersma 1998) and interspecific modeling studies have revealed that heart mass and associated stroke volume changes are important to adaptive specializations of aerobic capacity (Bishop and Butler 1995).

Pectoralis muscle hypertrophy is also a common aspect of winter acclimatization, at least in small birds with marked winter increases in M_{sum} (Liknes 2005; Cooper 2002; O'Connor 1995b; Swanson 1991b). These studies indicate that percent changes in pectoralis muscle mass often rather closely parallel percent changes in M_{sum} (Fig. 3.8). In contrast to these data, however, House Finches from Colorado showed no seasonal variation in pectoralis muscle mass, but this population also exhibited no seasonal difference in M_{sum} and only modest winter improvement of cold tolerance (Carey et al. 1989; Dawson et al. 1983b). Seasonal variability in heart mass associated with winter acclimatization in birds has received little study, but heart mass did increase in winter relative to summer for three species of small passerines (Black-capped Chickadees, White-breasted Nuthatches, and House Sparrows) from South Dakota (Liknes 2005).

In summary, available data indicate that flight muscle and/or heart do increase in mass with migratory disposition and winter acclimatization in birds. These adjustments likely impact aerobic capacity and M_{sum} during these periods of the annual cycle, as suggested by the data for winter acclimatized birds. In addition, because flight muscles comprise such a large fraction of total body mass in volant birds, hypertrophy of these muscles might also elevate BMR and such a correlation has been demonstrated in some birds (Vezina and Williams 2003; Chappell et al. 1999).

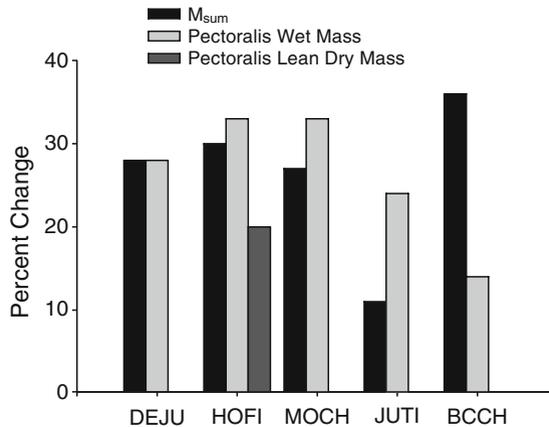


Fig. 3.8 Percent increases in pectoralis muscle mass and M_{sum} in winter relative to summer in passerine birds for which both values have been measured. Data are from the following studies: Dark-eyed Junco (DEJU, Swanson 1990a; 1991b), House Finch (HOFI, O'Connor 1995a, b), Mountain Chickadee and Juniper Titmouse (MOCH and JUTI, Cooper 2002), and Black-capped Chickadee (BCCH, Cooper and Swanson 1994, E.T. Liknes and Swanson, unpublished data). Pectoralis muscle mass values are mostly for wet mass because this is the most common measure reported in the literature, although lean dry mass is probably the better metric. O'Connor (1995b) provided seasonal measurements of pectoralis lean dry mass for House Finches, so I also included this value in the figure

3.5 Suggestions for Future Research

Seasonal patterns of variation in BMR and M_{sum} associated with winter acclimatization in birds have been well described. However, more research is needed to better describe patterns of variation in BMR and M_{sum} during the different stages of reproduction (e.g., Vezina and Williams 2005). Moreover, the functional significance of metabolic variation during reproduction and how such variation might be related to variation in FMR is in need of further study (e.g., Vezina and Williams 2003). BMR variation associated with migration has been well documented in shorebirds, but migration-associated variation in BMR is practically unstudied in other migratory birds. Further study is also required to document if emerging patterns of migration-induced M_{sum} variation are broadly applicable. Measurement of MMR variation associated with migration would also be fruitful, although current techniques measuring MMR during hovering flight or in hop-flutter wheels (Chappell et al. 1999; Chai and Dudley 1995, 1996) might not accurately represent MMR during horizontal flight typical of migration.

Several topics related to the relationship between organ masses, tissue metabolic intensity, and organismal metabolic rates in birds deserve further research attention. First, additional detailed experiments examining potential variation in both metabolic intensity (e.g., CS, CCO, HOAD activities, and/or mitochondrial density) and organ masses of nutritional and exercise organs, along with measurement of BMR

and M_{sum} , or at least in species for which BMR and M_{sum} are known to vary with migration or season, are needed. To date, the only birds for which most of these parameters have been measured are Red Knots during migration (Piersma et al. 1995, 1996a, 1999; Weber and Piersma 1996) and American Goldfinches and House Finches during winter acclimatization (O'Connor 1995a, b; Carey et al. 1989; Dawson et al. 1983b; Yacoe and Dawson 1983; Marsh and Dawson 1982; Dawson and Carey 1976). Recent studies examining organ mass changes and metabolic intensity of European Starlings during the breeding season (Vezina and Williams 2005) and several species of small passerines during seasonal acclimatization (Zheng et al. 2008; Liknes 2005) are steps in the right direction.

Second, virtually all studies of variation in organ masses have so far been carried out on samples from populations during different seasons or different stages of migration, rather than the ideal method of tracking organ masses in individual birds over time. Following temporal variation in organ masses in individual birds has not been possible because, as Lindström and Piersma (1993, p. 70) point out, "one cannot kill a bird twice" for examination of body composition on individual birds during periods of changing energy demands. However, Dietz et al. (1999a) used ultrasonography to demonstrate that organ masses in individual captive Red Knots did change over time in association with the development of migratory disposition. Lindström et al. (2000) also used ultrasonography to document changes in pectoral muscle size associated with flight, fasting, and fueling in individual knots. To date, ultrasonography has been validated for measurement of breast muscle size in birds as small as medium-sized shorebirds, but it is likely applicable to smaller species as well. Thus, recent technological developments, including ultrasonography (Lindström et al. 2000; Dietz et al. 1999a, 1999b) and high field MRI (Anderson et al. 2000), may allow successful noninvasive tracking of organ size changes in individual birds over time. Studies using such techniques during the development of migratory disposition or during exposure to cold temperatures would nicely complement current data and coupling organ size data with metabolic measurements would allow assessment of how tightly changes in organ masses and metabolism are linked in individual birds. Indeed, Vezina et al. (2006, 2007) tracked changes in breast muscle size during cold acclimation and development of migratory disposition using ultrasonography and correlated these changes with BMR and M_{sum} . In addition, such studies could show how rapidly mass and metabolism could be adjusted to meet changing energetic demands.

A third area where additional research is needed is to determine if body composition or metabolic intensity alterations confer differences in endurance flight or cold hardiness. Current data suggesting such changes are largely correlative. Experiments monitoring cold or exercise training effects on flight or shivering endurance, BMR, M_{sum} , and MMR in association with measurements of organ mass and metabolic intensity variation would be useful in this regard. Additionally, the question of whether exercise training influences thermogenic capacity or endurance, or whether cold acclimation increases maximum exercise-induced metabolism or exercise endurance has not been addressed in birds. Potentially relevant in this regard is the finding that M_{sum} and MMR during activity were significantly and

positively associated in deer mice *Peromyscus maniculatus* (Hayes and Chappell 1990). Cold acclimation increases peak metabolism during exercise in some mammals (Turner et al. 1995; Hayes and Chappell 1986) and exercise training elevates M_{sum} or cold tolerance in others (McDonald et al. 1988; Harri et al. 1984; Strømme and Hammel 1967). However, in some mammals exercise training does not influence M_{sum} (Conley et al. 1985). Moreover, extrapolation of mammalian results to birds is complicated by the prominent role of brown fat and NST in mammalian thermoregulation in the cold. The only relevant study for birds of which I am aware is Vezina et al. (2007), which documented that increases in body mass and flight muscle size associated with migratory disposition in Red Knots were positively correlated with M_{sum} .

Because fat is the principal fuel for both long-distance migratory flights and prolonged shivering, additional studies of what factors might limit fat catabolism, and thereby influence organismal metabolic rates, during migratory flights and shivering are needed. Recent studies suggest that intracellular transport or transport across sarcolemmal and mitochondrial membranes may be critical steps in regulating lipid catabolism (McWilliams et al. 2004). Research addressing variation in these steps with migration is in its infancy (McFarlan 2007; Guglielmo et al. 2002; Pelters et al. 1999) and even less is known about variation in these steps with seasonal acclimatization (Liknes 2005). Another factor relating to fat catabolism and organismal metabolic rates that warrants further study is the impact of fatty acid composition of depot fat on aerobic performance in birds. Pierce et al. (2005) studied Red-eyed Vireos and showed that diets lower in unsaturated fatty acids (but higher in 18:2n6 content) produced fat stores with similar fatty acid composition, and that birds with lower unsaturated fatty acid content (but higher 18:2n6 content) had elevated MMR during hop-flutter wheel exercise. How such differences in fatty acid composition are regulated naturally in birds and how such differences might impact migratory performance or M_{sum} would be a fruitful area for additional research.

The cellular and molecular mechanisms regulating muscle and organ mass changes with migration and seasonal acclimatization have received very little study to date. A potential candidate for regulation of muscle mass changes is myostatin, a member of the TGF- β superfamily of growth factors, which is a potent autocrine/paracrine inhibitor of muscle growth in mammals (Lee 2004) and birds (Kim et al. 2006, 2007). Myostatin is synthesized in skeletal muscle in an inactive form that requires proteolytic removal of the N-terminal signal sequence and the propeptide to produce the active C-terminal fragment (Lee and McPherron 2001; McPherron and Lee 1997). Cleavage of the latent complexes to the mature form that binds to myostatin receptors is required for myostatin activity. Metalloproteinases, including BMP-1/tolloid family members TLL-1 and TLL-2, can activate myostatin (Wolfman et al. 2003; Huet et al. 2001). Swanson et al. (2009) documented winter decreases in myostatin and TLL-1 gene expression in pectoralis muscle of House Sparrows, a species showing winter increases in pectoralis muscle mass. These results are consistent with a role for myostatin in promoting pectoralis muscle hypertrophy in winter and additional research examining how expression and

protein levels of myostatin and its metalloproteinase activators vary with migration and seasonal acclimatization would likely be productive.

Finally, one proposal for what limits maximal thermogenic capacity in birds is the amount of muscle recruited (Marsh and Dawson 1989). Because birds shiver isometrically (Hohtola 1982), force production by the smaller of the antagonistic muscle pair (supracoracoideus in the case of flight muscles) may limit force production by the larger muscle. Thus, for winter acclimatized birds, measurement of relative seasonal changes in mass and metabolic intensity of pectoralis and supracoracoideus muscles could illuminate mechanisms for enhancing thermogenic capacity and cold hardiness. Relatively larger seasonal changes in the supracoracoideus muscle might be expected if the smaller of the muscle pair is actually a limiting factor to thermogenic capacity. Such a scenario would not be expected in migrating birds because pectoralis and supracoracoideus muscles contract sequentially rather than isometrically during flight. Indeed, in Gray Catbirds, mass-specific cytochrome c concentrations and CS activities in the pectoralis were approximately double values for the supracoracoideus, although supracoracoideus CS activity was weakly, but positively, correlated with premigratory fattening (Marsh 1981). However, the relative masses of pectoralis and supracoracoideus muscles vary during the annual cycle in Red Knots, although such variation is not necessarily associated with migration (Piersma and Dietz 2007). Measurements of relative masses and metabolic intensities of pectoralis and supracoracoideus muscles during winter acclimatization and migration are needed.

3.6 Summary and Conclusions

In this paper, I have reviewed the evidence for seasonal and migration-induced variation in metabolic rates in birds. I have also tried to draw some generalizations about the importance of variation in BMR and M_{sum} to the ecology of wintering and migrating birds and attempted to link seasonal or migration-induced variation in organismal metabolic rates with physiological and biochemical variation at the cellular and tissue levels. Several conclusions that I believe are noteworthy have emerged from this body of work.

First, increments of M_{sum} in winter acclimatized small birds relative to their summer counterparts appear to be greater than previously recognized, and such increments are a common component of winter acclimatization in these birds. Thus, it seems probable that the mechanistic adjustments underlying winter increases in shivering endurance (i.e., cold tolerance) also promote increases in M_{sum} . Elevated M_{sum} in winter should increase heat production for any given fraction of M_{sum} that is sustained during shivering, and this would appear to be the functionally significant aspect of winter increases in M_{sum} to improved cold hardiness. However, variation in BMR does not necessarily track changes in cold tolerance and M_{sum} in birds, so its precise relation to winter improvements in cold resistance is uncertain and may vary among species.

Second, BMR and M_{sum} (and presumably maximal exercise-induced metabolic rates) also vary with migratory disposition in birds, although spring and fall migratory

periods do not necessarily induce identical changes in organismal metabolism. From the limited available data, migration-induced changes in M_{sum} appear better explained as a by-product of adjustments for endurance flight, rather than for adjustment to cold temperatures. Nevertheless, higher M_{sum} in spring migrants may benefit birds if they encounter cold or adverse weather during migration or during arrival on the breeding grounds. Migration-induced changes in BMR appear, in general, to track changes in energy demand during the migratory period.

Third, mechanistic changes underlying variation in metabolic rates in birds could occur at several levels of the interacting system for energy processing, transport, and use. Some levels of this interacting system have received far more study than others, but some preliminary conclusions have emerged from this body of work. The ability to transport oxygen in the blood and to deliver it to working muscles seems to parallel energy demands from the tissues in species studied to date. Lipid transport and delivery to muscle cells does not appear to vary consistently with season or migratory disposition. Intracellular transport of lipid to the mitochondria, as well as intracellular stores of lipid, do seem positively related to energy demands, but this topic has been very little studied. Mass-specific aerobic capacity of muscles does not vary consistently with migration or winter acclimatization, nor does the metabolic intensity of central organs. Organ mass changes, however, do occur regularly with migration and winter acclimatization and this variation appears to occur in an adaptive manner, with larger central organ and muscle masses as needs for energy processing and/or use increase. Such changes in organ masses appear to serve as a vehicle by which whole-organism changes in aerobic capacity and metabolic rates are affected.

In summary, some aspects relating to variation in metabolic rates in birds and their underlying mechanisms have been well studied, but other aspects have received little attention. Thus, some of the preceding generalizations must be regarded as preliminary. More research needs to be conducted to thoroughly evaluate these generalizations and I have tried to outline some potentially valuable research approaches toward this end throughout the review. Data from such studies should help solidify our understanding of how seasonal metabolic variation in birds is mediated and whether or not such variation occurs in an adaptive manner.

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