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Sources and significance of variation in basal, summit and maximal metabolic rates in birds

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Abstract The rates at which birds use energy may have profound effects on fitness, thereby influencing physiology, behavior, ecology and evolution. Comparisons of standardized metabolic rates (e.g., lower and upper limits of metabolic power output) present a method for elucidating the effects of ecological and evolutionary factors on the interface between physiology and life history in birds. In this paper we review variation in avian metabolic rates [basal metabolic rate (BMR; minimum normothermic metabolic rate), summit metabolic rate (M_{sum}; maximal thermoregulatory metabolic rate), and maximal metabolic rate (MMR; maximal exercise metabolic rate)], the factors associated with this variation, the evidence for functional links between these metabolic traits, and the ecological and evolutionary significance of avian metabolic diversity. Both lower and upper limits to metabolic power production are phenotypically flexible traits, and vary in association with numerous ecological and evolutionary factors. For both inter- and intraspecific comparisons, lower and upper limits to metabolic power production are generally upregulated in response to energetically demanding conditions and downregulated when energetic demands are relaxed, or under conditions of energetic scarcity. Positive correlations have been documented between BMR, M_{sum} and MMR in some, but not all studies on birds, providing partial support for the idea of a functional link between lower and upper limits to metabolic power production, but more intraspecific studies are needed to determine the robustness of this conclusion. Correlations between BMR and field metabolic rate (or daily energy expenditure), in birds are variable, suggesting that the linkage between these traits is subject to behavioral adjustment, and studies of the relationship between field and maximal metabolic rates are lacking. Our understanding of avian metabolic diversity would benefit from future studies of: (1) the functional and mechanistic links between lower and upper limits of metabolic power output; (2) the environmental and ecological cues driving phenotypically flexible metabolic responses, and how responses to such cues might impact population responses to climate change; (3) the shapes of metabolic reaction norms and their association with environmental variability; and (4) the relationship of metabolic variation to fitness, including studies of repeatability and heritability of minimum and maximum metabolic power output[*Current Zoology* 56 ( ): – , 2010].

Received Jan. 20 , 2010; accepted Apr. 20, 2010

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1 Introduction

The rates at which birds use energy have far-reaching implications for understanding their physiology, behaviour, ecology and evolution. Because of the host of biotic and abiotic factors that influence the total energy used by birds per unit time, ecological and evolutionary physiologists often focus on standardized metabolic rates for elucidating the patterns and processes that contribute to avian metabolic diversity. Standardized metabolic parameters that have been widely used are the lower and upper limits of metabolic output in resting birds (basal metabolic rate, BMR, and summit metabolism, M_{sum}, respectively) and the maximum metabolic rate achieved during intense exercise (maximal metabolic rate) (e.g., Lasiewski and Dawson, 1967; McNab, 1988; 2009; Swanson, 1995; Chappell et al., 1996; Rezende et al., 2002; Tieleman et al., 2003a; McKechnie and Wolf, 2004; White et al., 2007a; Wiersma et al., 2007a; Swanson and Garland, 2009). Standardized metabolic rates (particularly BMR) are often interpreted as reflecting the overall pace of life of a species or population (Wikelski et al., 2003; Wiersma et al., 2007b). There is also increasing interest in the links between standardized metabolic rates and behavioral traits; for instance, a recent analysis identified a positive correlation between BMR and flight initiation distance, a key measure of risk-taking behavior (Møller, 2009).

The metabolic rates of an individual bird are determined by several interacting sources of phenotypic variation, namely a) allometric scaling with body mass, b) phylogenetic inertia reflecting patterns of evolutionary descent, c) adaptation through natural and/or sexual selection, and d) phenotypic plasticity. The goal of this paper is provide an overview of the variation that exists in the lower and upper limits of avian metabolic power output, as well as the various sources of phenotypic variation that contribute to metabolic diversity. We review inter- and intraspecific variation in basal, summit, and maximal metabolic rates, the ecological correlates of each trait, and the available information on scaling, phylogenetic inertia, metabolic adaptation and phenotypic plasticity. We then discuss the functional links between these parameters, and highlight emerging questions regarding the physiological, ecological and evolutionary significance of avian metabolic diversity.

2 Basal Metabolic Rate

Basal metabolic rate (BMR) is the minimum resting metabolic rate of a postabsorptive, non-reproductive normothermic endotherm during the rest-phase of its circadian cycle, i.e., measured under conditions that do not elicit increases in metabolic rate associated with thermoregulation, digestion, activity, circadian rhythms, reproduction, or other energy-demanding activities such as moult or growth (McNab, 1997; Speakman et al., 2004). BMR represents the sum of maintenance energy requirements of organs and tissues, with the majority of BMR (e.g, ~ 70% in mammals smaller than 100 g) accounted for by organs such as the liver, brain, kidneys and heart (Daan et al., 1990; Wang et al., 2001; Suarez and Darveau, 2005). Because BMR represents the lower limit of metabolic power output in a normothermic individual, it has been widely used as a parameter for comparing metabolic power output both within and among bird species (e.g., Tieleman et al., 2003a, b; Wikelski et al., 2003; White et al., 2007). In terms of practical considerations, BMR is easier to measure than other standardized metabolic rates suitable for comparative analysis (e.g, summit metabolic rates – see below), and can readily be measured at remote field sites with a minimum of equipment (e.g., McNab, 2005; Smit and McKechnie, 2010).

Brody and Proctor (1932) provided the earliest comparative analysis of variation in avian BMR, and since then data have been obtained for ~ 530 bird species in 26 orders and 97 families (McNab, 2009). Reported BMR values vary approximately 790-fold from 0.08 W in the 6.8-g glossy swiftlet (*Collocalia esculenta*, McNab and Bonaccorso, 1995) to 63.05 W in the 92.4-kg common ostrich (*Struthio camelus*, Withers, 1983). There is also considerable variation that is independent of body mass (Fig. 1); for example, the BMR reported for the 74-g green woodhoopoe *Phoeniculus purpureus* is 0.174 W (Boix-Hinzen and Lovegrove, 1998, but see also Williams et al., 1991), whereas the corresponding value for the similarly-sized 72.5-g Bohemian waxwing *Bombycilla garrulous* is 0.954 W (Kendeigh et al., 1977), a 5.5-fold difference.

2.1 Scaling

The single largest source of phenotypic variation in avian BMR is body mass. The allometric scaling of BMR is described by an exponential equation of the form $BMR = aM_b^b$, where M_b is body mass and a and b are the y-intercept and scaling exponent, respectively. Reported values for b vary, but are typically in the range of 0.65–0.75. The earliest interspecific analysis of the relationship between BMR and body mass yielded a b-value of 0.64 (Brody and Proctor 1932), but King and Farner (1961) subsequently obtained a value of 0.74, much closer to the exponents obtained in early analyses of mammalian BMR. Lasiewski and Dawson (1967) showed that passerines generally have higher BMR than non-passerines of the same size, and that after controlling for these differences, $b \approx 0.72$, with similar values subsequently obtained by Aschoff and Pohl (1970). More recently, McNab (2009) analysed the largest data set to date (533 species) and after including a passerine/non-passerine categorical variable, obtained $b = 0.721$. Bennett and Harvey (1987) fitted a regression model to BMR values for families, rather than species, and obtained a b-value of 0.67. Recent analyses using phylogenetically independent regression models have obtained overall b-values of 0.635 (Reynolds and Lee, 1996), 0.677 (Tieleman and Williams, 2000), 0.677 (McKechnie and Wolf, 2004) and 0.707 (McKechnie et al., 2006). The latter authors also found variation in avian BMR scaling exponents correlated with the origin of the birds used for metabolic measurements, such that captive-raised populations exhibited a significantly shallower exponent (0.670) compared to wild-caught populations (0.744). Other analyses, however, have reported exponents close to 0.670 for wild-caught birds (e.g., White et al., 2007a).

Intraspecific scaling exponents for avian BMR tend to be larger than interspecific exponents. For instance, among waders migrating between the Eurasian Arctic and Africa, interspecific exponents in reduced major axis (RMA) regressions ranged from 0.62–0.74, whereas intraspecific exponents ranged from 0.93–4.21 (Kvist and Lindström, 2001). Other studies have reported similar results (Daan et al., 1990; Battley et al., 2001). Since most of these studies involved migrating birds, the high intraspecific BMR exponents are thought to reflect body mass increases involving predominantly metabolically active tissues during stopovers (Kvist and Lindström, 2001). The BMR of red knots *Calidris canutus* varied in parallel with changes in the thickness of pectoral muscle during a migratory cycle of mass gain and loss (Vézina et al., 2007), although similar correlations were not evident in knots acclimated to various air temperatures (Vézina et al., 2006).

The processes underlying metabolic scaling patterns among all organisms remain the topic of heated debate, with an exponent of 0.67 predicted from surface area–volume ratios (Rubner, 1883; Dodds et al., 2001), an exponent of 0.75 predicted from the fractal geometry of nutrient and oxygen supply networks (West et al., 1999; 2002), and a range of *b*-values predicted by allometric cascade models involving multi-level regulation of energy supply and demand (Darveau et al., 2002; Suarez and Darveau, 2005). The observations that a) avian scaling exponents vary with the origin of populations used for metabolic measurements (McKechnie et al., 2006), b) there is no universal allometric exponent in birds and other organisms (White et al., 2007b), and c) intraspecific scaling exponents are often much higher than interspecific exponents, collectively suggest that patterns of avian BMR scaling are best explained by allometric cascade models (Darveau et al., 2002; Suarez and Darveau, 2005). Future work on avian metabolic scaling should focus on sampling a wider range of taxa (at present, BMR measurements are available for only ~ 5 % of extant species), comparing exponents for minimum (BMR) and maximum (M_{sum} and MMR) metabolic rates, and examining more closely the influence of phenotypic flexibility on scaling exponents.

2.2 Phylogeny

Among the earliest evidence for broad-scale BMR variation among higher avian taxa was the finding that the BMR of passerines (order Passeriformes) is ~ 65% higher than that of other avian orders (i.e., non-passerines) (Lasiewski and Dawson, 1967; Zar, 1968; but see also Prinzinger and Hänssler, 1980). Zar (1968) demonstrated further significant inter-order variation, with Apodiformes and Anseriformes, for instance, exhibiting higher BMR than Galliformes and Strigiformes. Similar conclusions were drawn by Aschoff and Pohl (1970), and more recently, McNab (2009). These findings reiterate the need to account for phylogenetic relationships when identifying metabolic adaptation. Bennett and Harvey (1987) partitioned variation in avian BMR among taxonomic levels, with most variation (67 %) existing among families within orders.

The differences in BMR between passerines and non-passerines have been repeatedly scrutinized in phylogenetically independent (PI) analyses that account for the non-independence of biological data on account of hierarchical patterns of evolutionary descent from common ancestors (Felsenstein, 1985).

Reynolds and Lee (1996) reanalyzed avian metabolic rates using several PI approaches, namely independent contrasts (Felsenstein, 1985) and PI analysis of co-variance (Garland et al., 1993). Their analyses showed that the BMR of passerines is not significantly different than that of non-passerines once phylogeny is controlled for. Garland and Ives (2000) verified Reynolds and Lee's (1996) findings, but also showed that rates of evolution for body mass and BMR differ significantly between passerines and non-passerines. The conclusions of both the aforementioned studies held in a later analysis that used much more rigorous data inclusion criteria (McKechnie and Wolf, 2004). It should be noted, however, that all the above analyses assumed relationships among higher avian taxa as proposed in the DNA-DNA hybridization phylogeny of Sibley and Ahlquist (1990). Their findings still need to be verified using the new Hackett et al. (2008) phylogeny and new phylogenetically informed multiple regression models (Lavin et al., 2008).

2.3 Adaptation

Whereas early analyses did not reveal any clear link between BMR and climate (Scholander et al., 1950), positive correlations between avian metabolic rates and latitude were subsequently documented in landbirds (Weathers, 1979) and seabirds (Ellis, 1984). The notion that tropical birds generally have lower BMR than their temperate-zone counterparts has received strong support in a recent study that found that BMR in 69 tropical species is significantly lower than that of 59 species from temperate latitudes, and that in 13 phylogenetically matched temperate/tropical species pairs, BMR was consistently lower in the tropical representatives (Wiersma et al., 2007b). Correlations with specific microclimates and plumage thermal properties have also been documented, including ~25 % lower BMR in species that typically forage in the sun compared to species that forage in the shade (Hails, 1983; Weathers, 1979), and a correlation with plumage coloration (lower BMR in species with dark plumage) among herons (Ellis, 1980). Broad-scale negative correlations between avian BMR and temperature have recently been reported in analyses of large global data sets (~ 130 spp.) (White et al., 2007a; Jetz et al., 2008), with a 20 °C difference in mean annual temperature associated with a 48 % difference in predicted BMR (Jetz et al., 2008).

A number of studies have identified correlations between BMR and broad habitat categories, ecological traits (e.g., mode of prey capture, flightlessness), and/or diet type (Bennett and Harvey, 1987; McNab, 1988, 1994,2000, 2003, 2009). Diet-correlated BMR variation was reported by McNab (1988, 2005, 2009), with relatively low BMR in frugivores, folivores and aerial insectivores and relatively high BMR in granivores, nectarivores and species feeding on terrestrial invertebrates. However, Bennett and Harvey (1987) found no significant association with diet among nonpasserine families, and a review of intra-specific studies of the influence of secondary compounds, digestibility, and energy content on BMR found mixed support for the idea of consistent diet-related variation in BMR (Cruz-Neto and Bozinovic, 2004). One taxon in which there is strong evidence for a link between BMR and ecological characteristics is the caprimulgids; a PI analysis revealed that the BMR of seven species of nightjars and allies is significantly lower than that of other birds (Lane et al.,2004). One ecological factor thought to select for low normothermic energy requirements in this group of birds is the large fluctuations in aerial insect prey that are associated with variation in temperature and/or rainfall (Jetz et al., 2003; Ashdown and McKechnie, 2008).

In contrast to early work primarily involving species from North American deserts (Bartholomew and Cade, 1963; Dawson and Bartholomew, 1968), recent analyses that included data from Old World deserts have revealed significantly lower BMR in desert species (Tieleman and Williams, 2000; Tieleman et al. 2002), a finding thought to reflect the greater age of many Old World deserts, and consequently the time available for physiological traits to evolve (Tieleman and Williams, 2005). For instance, whereas the Namib Desert of southwestern Africa is thought to be ~ 80 million years old (Ward et al., 1983), the Sonoran Desert is only ~ 8 million years old, and the latter's expansion into Arizona and California thought to have occurred only 9,000 years ago (Van Devender, 2000). BMR was also negatively related to increasing habitat aridity among 12 species of Old World larks (Alaudidae) (Tieleman et al., 2003a). Although scarce and unpredictable rainfall and resultant spatially and temporally unpredictable food supplies have often been invoked as a major factor driving the evolution of reduced metabolic rates in desert organisms (Louw and Seely, 1982; Lovegrove, 2000, 2003; Williams and Tieleman, 2005), two recent analyses suggest that temperature, rather than primary productivity, is the strongest correlate of avian BMR (White et al., 2007a; Jetz et al., 2008).

A fundamental limitation of the correlational studies discussed above is that observed BMR variation may reflect phenotypic plasticity as well as adaptation. Evidence for genotypic divergence in BMR is relatively rare, not least because of the logistics involved in conducting the common garden experiments necessary to demonstrate adaptation (i.e., experiments involving species and/or populations raised under identical conditions, in order to eliminate phenotypic plasticity as a source of phenotypic variation). Stonechats *Saxicola torquata* raised in common garden conditions exhibited significant geographical variation in BMR, with mass-specific BMR lowest in a non-migrating population from equatorial Africa, intermediate in European birds (Ireland and Austria, short-distance and partial migrants, respectively) and highest in a migratory population from Kazakhstan (Wikelski et al., 2003). However, the validity of these results has been questioned by Tieleman (2007), who showed that the air temperature at which the former authors measured metabolic rate was in fact below the stonechats' thermoneutral zones (TNZ), and that true BMR measured within the TNZ did not differ among populations once variation in body mass was taken into account. There is also evidence from common garden experiments for adaptation in BMR in great tits *Parus major*: a southerly population exhibited significantly higher BMR than northern birds (Broggi et al., 2005). However, wild-caught great tits exhibited BMR variation in the opposite direction, with higher BMR in individuals from a more northerly site (Broggi et al., 2004).

Arguments for adaptation in avian BMR assume (usually implicitly) that this trait is subject to selection, yet little is known about its repeatability within individuals and populations and heritability across generations. Selection could potentially act on BMR directly, since the latter represents maintenance energy demands and thus a significant component of overall energy requirements, and/or indirectly via the sizes and/or metabolic intensities of specific organs. Significant BMR repeatabilities of 0.22 - 0.87 have been found in a number of species (Versteegh et al., 2008), with significant long-term (across years) repeatabilities reported for great tits (Broggi et al., 2009) and zebra finches *Taeniopygia guttata* (Rønning et al., 2005). The heritability of avian BMR has received much less attention. A captive population of zebra finches exhibited a whole-animal BMR heritability of 0.25, although the conditional heritability of BMR (i.e., heritability independent of additive genetic variance in body mass) was only 0.04 (Rønning et al., 2007). Contrasting results were recently obtained in a wild population of blue tits *Cyanistes caeruleus*, which exhibited non-significant additive variance in body mass, but a high heritability (0.59) of whole-animal resting metabolic rate (Nilsson et al. 2009). A study of the quantitative genetics of BMR in stonechats also found significant heritabilities, as well as indications that whole-animal BMR, mass-specific BMR and body mass can evolve independently of each other (Tieleman et al., 2009a).

2.4 Phenotypic flexibility

Basal metabolic rate is not fixed within individuals, but exhibits a high degree of phenotypic plasticity (reviewed by McKechnie, 2008; Swanson in press), although the properties of avian BMR reaction norms (a reaction norm is the range of phenotypic trait values that can be produced by a single genotype; Schlichting and Pigliucci, 1998) remain far from clear. Numerous studies have demonstrated short-term, reversible BMR variation (i.e., phenotypic flexibility, Piersma and Drent 2003) in the contexts of migration, seasonal acclimatization or thermal acclimation under laboratory conditions. We follow Piersma and Drent (2003) and numerous other authors in defining acclimatization as the adjustment of traits in response to natural environments, and acclimation as the adjustment of traits in response to artificial environments. In contrast, almost nothing is known about the influence of non-reversible developmental plasticity (Piersma and Drent, 2003) on avian BMR, although it is tempting to speculate that the differences in BMR scaling between wild-caught and captive-raised birds arise in part from developmental factors (McKechnie et al., 2006). Because we have recently reviewed patterns of phenotypic flexibility in avian BMR (McKechnie, 2008; Swanson in press), here we provide only summaries of recent developments.

Birds exhibit considerable phenotypic flexibility in BMR associated with seasonal acclimatization, with north-temperate species exhibiting winter increases of up to 64% in whole-animal BMR (Arens and Cooper, 2005) and 40 % in mass-specific BMR (Liknes and Swanson, 1996). In contrast, species from sub-tropical latitudes tend to exhibit lower BMR in winter. Five species in southern Africa’s Kalahari Desert, for instance, exhibited BMR values 17 – 35 % lower during winter compared to summer (Smit and

McKechnie, 2010). The magnitude and direction of seasonal adjustments correlate strongly with air temperature during winter; a multiple regression model that included the mean air temperature during the coldest month of the year as a predictor variable explained more variation in winter BMR / summer BMR than did a model that included latitude (Smit and McKechnie, 2010). Similarly, BMR in amethyst sunbirds *Chalcomitra amethystina* from eastern South Africa was lower in winter than summer (Lindsay et al., 2009a; 2009b), but mass-specific BMR in outdoor-captive red-winged starlings *Onychognathus morio* in South Africa was 22% higher in winter than in summer (Chamane and Downs, 2009). Smit and McKechnie (2010) hypothesized that winter increases in BMR in species in cold environments reflect winter enhancements in thermogenic capacity, whereas the decreases in BMR in species from lower latitudes reflect metabolic down-regulation in response to decreased food availability during winter.

Numerous studies have documented BMR changes in the context of short-term (days to weeks) thermal acclimation under laboratory conditions, with cold temperatures generally resulting in higher BMR, and *vice versa* (e.g., Williams and Tieleman, 2000; Tieleman et al., 2003b; Klaassen et al., 2004; McKechnie et al., 2007). However, the links between metabolic responses to thermal acclimation and those seen during seasonal acclimatization remain unclear. For instance, BMR in rufous-collared sparrows *Zonotrichia capensis* was 19 % higher in 15 °C- *versus* 30 °C-acclimated birds, but winter- and summer-acclimatized birds did not show any significant difference (Maldonado et al., 2009). The divergent BMR patterns between acclimated and acclimatized birds in the latter study support the argument that temperature is not the primary factor driving seasonal metabolic adjustments in species from lower latitudes (Smit and McKechnie, 2010). One potentially important environmental cue of seasonal metabolic adjustments, but which has received relatively little attention, is photoperiod. There is limited evidence that BMR is influenced by photoperiod, with pigeons acclimated to short photoperiod (20 D 4 L) exhibiting significantly higher BMR than birds acclimated to 12 L 12 D (Haim et al., 1979). However, BMR did not change with photoperiod manipulation in Japanese quail (Saarela and Heldmaier, 1987).

The question of whether the avian capacity for phenotypic metabolic adjustments is correlated with environmental conditions and subject to selection was raised by Tieleman et al. (2003b), who hypothesized that larks inhabiting unpredictable desert environments exhibit greater phenotypic flexibility in BMR than species inhabiting more predictable mesic habitats. In the aforementioned study, desert species did not show greater BMR flexibility in response to acclimation to two air temperatures than mesic species, but Tieleman et al.'s data do not rule out several other potential interspecific differences in the properties of BMR reaction norms (McKechnie, 2008). More recently, significant intraspecific variation in acclimation responses correlated with habitat characteristics was documented in rufous–collared sparrows (Cavieres and Sabat, 2008). Whereas populations from sites at 33 °S and 40 °S increased BMR in response to acclimation to low air temperatures, a population from an arid site at 27 °S with relatively little seasonal variation in air temperature did not (Cavieres and Sabat, 2008). Such intraspecific differences in BMR reaction norms reiterate the need for further studies examining variation in phenotypic flexibility within and among species.

An important consideration in future studies of avian BMR reaction norms should be the number of different sets of experimental conditions to which birds are acclimated. In most studies, birds are acclimated to one of two air temperatures (e.g., Williams and Tieleman, 2000; Tieleman et al., 2003b; Klaassen et al., 2004; Maldonado et al., 2009). Whereas some potential differences in phenotypic flexibility among populations and/or species can be assessed using these data, several properties of BMR reaction norms (including their approximate shape) require data for three or more experimental treatments (McKechnie et al., 2007; McKechnie, 2008). Studies involving acclimation to just one set of conditions (e.g., Lindsay et al., 2009a; 2009b) should be avoided, since their results are very difficult to interpret in the framework of reaction norms describing the relationship between BMR and environmental determinants of acclimation. In summary, although numerous studies have documented considerable phenotypic flexibility in avian BMR, the shapes of relationships between BMR and determinants of acclimation/acclimatization (e.g., air temperature) remain largely unknown, as does the rapidity with which BMR is adjusted. A better understanding of the properties of BMR reaction norms is a prerequisite for elucidating the contribution of phenotypic flexibility to avian metabolic diversity.

3 Cold- and Exercise-induced Maximal Metabolic Rates

Summit metabolic rate (M_{sum}), referred to by some authors as peak cold-induced metabolic rate (PMR_c), is defined as the maximum aerobic resting metabolic rate elicited by cold exposure in endotherms, and is therefore equivalent to maximal thermogenic capacity. Heat production in birds is primarily accomplished via shivering (Hohtola and Stevens, 1986; Marsh and Dawson, 1989; Hohtola et al., 1998; Marjoniemi and Hohtola, 1999), although recent studies suggest that non-shivering thermogenesis, likely originating in muscle, may also contribute to thermogenic capacity, especially in young birds (Duchamp and Barre, 1993; Duchamp et al., 1993; Bicudo et al., 2002; Toyomizo et al., 2002; but see Hohtola, 2002). Thus, M_{sum} is primarily a function of muscular activity during shivering. Summit metabolic rates are usually measured in an atmosphere consisting of 21% oxygen/79% helium (helox), with the high thermal conductivity of helium facilitating heat loss without impairing gas exchange (Rosenmann and Morrison, 1974; Holloway and Geiser, 2001). Helox produces temperatures eliciting maximal heat production at relatively modest air temperatures, which helps protect against freezing damage to tissues in experimental animals. The end-point of these cold-exposure experiments is hypothermia, which strongly suggests that birds have indeed reached maximal levels of heat production (Swanson et al., 1996). Typically, M_{sum} exceeds BMR by 4 to 8-fold in birds (Swanson in press).

Maximal metabolic rate (MMR) is defined as the maximum aerobic metabolic rate elicited by exercise, which in birds can be studied by measuring metabolic rates during flight (for volant species, Hails, 1979; Norberg, 1996), running (for terrestrial species, Fedak et al., 1974; Taylor et al.,1982; Bundle et al., 1999;

Seymour et al., 2008), or in hop-flutter chambers (Chappell et al., 1996; 1999; Hammond et al., 2000) (Fig. 1). Flight metabolic rates for birds in wind tunnels are typically measured either with a respiratory mask, with doubly labeled water, or by estimation from mass loss for flying birds (see Norberg 1996 for review). In all these conditions, it is difficult to determine if flight metabolic rates represent maximal metabolic rates because it is not known if birds are actually performing maximally. Maximum flight metabolic rates generally exceed BMR by 8 to 14-fold for flying birds (Brackenbury, 1984; Marsh and Dawson, 1989). For birds running on treadmills, treadmill speed can be increased until birds show signs of exhaustion, which is a better indication that maximal running metabolic rates have been attained. MMRs while running range from 2 to 17 times BMR for a variety of terrestrial birds, but may reach 36 times BMR in rheas (*Rhea americana*, Bundle et al., 1999). MMRs measured in wind tunnels and on treadmills both require training of captive birds before metabolic data can be obtained, so these methods are not appropriate for measuring exercise-induced maximal metabolic rates on wild birds. Hop-flutter chambers get around the training problem and also produce exhaustion as an end-point, so maximal metabolic rates can be verified. MMR in hop-flutter wheels typically exceeds BMR by only about 10-fold (Chappell et al., 1999; Hammond et al., 2000; Pierce et al., 2005; Price and Guglielmo, 2009; Wiersma et al., 2007a), so this activity, like cold-exposure, probably doesn't use the full aerobic potential of the flight muscles, but because birds are exhausted at the completion of the tests, this method does maximize aerobic potential of muscle fibers supporting the hop-flutter exercise, and should provide good measures of general aerobic capacity.

The capacity for sustained activity (i.e., endurance) is directly and positively associated with maximal metabolic capacity in animals generally (Bennett, 1991) and selection on maximal metabolic rates is likely focused on increased endurance (i.e., increased shivering endurance promotes increased cold tolerance, Marsh and Dawson, 1989; Swanson, 2001). In addition, physiological adjustments promoting enhanced maximal exercise performance also promote elevated levels of sustained exercise performance, such as migratory flights (McWilliams et al., 2004; Price and Guglielmo, 2009). Thus, it might be expected that peak metabolic rates, whether induced by cold or exercise, would be more tightly correlated with environmental variability and/or energy demands than BMR. Consistent with this idea, neither BMR nor M_{sum} for house finches *Carpodacus mexicanus* from the mild Mediterranean climate of southern California, USA, varied with season (Dawson et al., 1983), but for house finches from the colder continental climate of Michigan, USA, BMR was seasonally stable, but M_{sum} was elevated in winter birds (O'Connor, 1995). However, in most small birds from markedly seasonal climates both BMR and M_{sum} increase in winter (McKechnie, 2008; Swanson in press).

4 Factors Affecting M_{sum}

4.1 Scaling

A major contributor to variability in M_{sum}, like BMR, is body mass (e.g., Schmidt-Nielsen, 1984; Fig. 1). A number of studies have examined interspecific scaling of M_{sum} in birds, some including a wide diversity of avian taxa and some including fewer taxa. Exponents for the interspecific relationship between body mass and M_{sum} in birds range from 0.503 to 0.832 (Table 1), and these exponents are generally similar to those scaling relationships for BMR (see above).

4.2 Phylogeny

Phylogenetic position may also influence M_{sum} in birds. Similar to recent comparative studies of BMR (Reynolds and Lee, 1996; Garland and Ives, 2000; Rezende et al., 2002), M_{sum} in passerines and non-passerines does not differ significantly, either for conventional or phylogenetically informed analyses (Rezende et al., 2002). However, significant phylogenetic signal (i.e., more similar trait values among closely related species than among distantly related species, signifying an influence of phylogenetic affinity on trait values) was present for mass-adjusted M_{sum} data in summer-acclimatized birds (Swanson and Garland, 2009; Swanson and Bozinovic unpubl. data), but not for analyses including both summer and winter birds (Rezende et al., 2002; Blomberg et al., 2003). The ability to detect phylogenetic signal in studies including both summer and winter birds is likely compromised by seasonal phenotypic flexibility in M_{sum}, so the conflicting results regarding phylogenetic signal for M_{sum} in these studies is, perhaps, not surprising. Phylogeny is also a significant effector of M_{sum} in birds in multiple regressions with body mass, winter temperature, migratory strategy and clade (i.e., phylogeny) as independent variables (Swanson and Garland 2009; Swanson and Bozinovic unpubl. data). In addition, M_{sum} differs between the two major suborders of passerine birds, with oscine passerines having higher M_{sum} than suboscine passerines for both conventional and phylogenetically informed statistical approaches (Swanson and Bozinovic unpubl. data).

4.3 Adaptation

4.3.1 Temperature and Climate Temperature and climate (i.e., long-term temperature patterns) are significant effectors of M_{sum} in interspecific comparative studies (Wiersma et al., 2007b; Swanson and Garland, 2009). These interspecific comparisons require that M_{sum} be standardized to reduce impacts of seasonal metabolic flexibility, so comparative studies of M_{sum} have focused on summer acclimatized birds because summer represents the period where M_{sum} is at an annual minimum in temperate-zone species. Wiersma et al. (2007b) compared M_{sum} between tropical and temperate-zone birds from a wide taxonomic representation using both conventional and phylogenetically informed comparative analyses. These authors found that tropical birds had an average M_{sum} that was 34% lower than temperate-zone birds after accounting for mass and phylogeny. BMR was also lower in tropical birds, so metabolic capacity appears to be reduced in tropical birds relative to their temperate counterparts, which is consistent with their slower pace of life (i.e., reduced clutch sizes, delayed maturity, slow growth rates, etc). Swanson and Garland (2009) examined the impact of several variables, including winter temperature, across a wide taxonomic sampling and found that winter temperature was significantly negatively related to M_{sum}, such that birds wintering in cold climates had higher M_{sum} than those wintering in warm climates. A similar result was found by Swanson and Bozinovic (unpubl. data) when comparing M_{sum} among 60 species of passerine birds. Thus, temperature has a pervasive and consistent effect on M_{sum} in birds, with birds inhabiting cold climates for at least part of the year having higher M_{sum} than birds restricted to warm climates.

Several studies have also examined intraspecific geographic variation in M_{sum} in broadly distributed bird species. House finches *Carpodacus mexicanus* from California and Colorado, USA, exhibit seasonally stable M_{sum} (Dawson et al., 1983), but those from Michigan, USA, show elevated M_{sum} in winter relative to summer (O'Connor, 1996). However, winter M_{sum} for finches from the cold winter climates of Colorado and Michigan are higher than those from California, and the absence of a seasonal difference in Colorado finches is due to higher M_{sum} during summer than the other populations (O'Connor, 1996). Swanson (1993) compared M_{sum} in winter-acclimatized dark-eyed juncos *Junco hyemalis* from the cold winter climate of South Dakota, USA, and the milder winter climate of western Oregon, USA, and found that South Dakota juncos tolerated colder temperatures during helox cold exposure than Oregon juncos, but M_{sum} did not vary between the two populations. Olson et al. (2010) examined winter M_{sum} and distribution patterns in black-capped *Poecile atricapillus* and Carolina *Poecile carolinensis* chickadees and found that whole-organism M_{sum}, but not mass-adjusted M_{sum}, was higher in black-capped than in Carolina chickadees, consistent with the more northerly distribution of the former species. Among black-capped chickadees, M_{sum} and body mass were higher in birds from South Dakota, USA, than from Wisconsin or Ohio, USA, despite similar winter climates among these locations. Olson et al. (2010) argue that the limited woodland cover and windy conditions in South Dakota, relative to Wisconsin and Ohio, might result in elevated convective heat losses in South Dakota chickadees, which might favor higher thermogenic capacities and body mass. Thus, data from some of these intraspecific geographic studies support the general inverse association between cold temperatures and M_{sum} documented for interspecific comparative studies and intraspecific acclimation and acclimatization studies, but M_{sum} and winter climates are not uniformly inversely correlated in all geographic comparisons.

4.3.2 Migration A migratory life history does not appear to influence M_{sum} during the non-migratory season, as Swanson and Garland (2009) found that migratory strategy (migrant vs. non-migrant) was not a significant effector of M_{sum} in summer-acclimatized birds. This is similar to the result for BMR noted previously (Jetz et al., 2008), where migratory strategy was associated with elevated BMR, but when temperatures on the breeding grounds were included in statistical models, BMR differences between migrant and non-migrant birds disappeared. This result suggests that differences in BMR between migrants and non-migrants were primarily explained by colder summer climates for migratory species.

4.4 Phenotypic flexibility

4.4.1 Temperature Perhaps the most prominent factor affecting M_{sum} variability in birds, outside of body mass, is temperature. Most species of small birds inhabiting markedly seasonal climates show winter increases in M_{sum} on the order of 25%–50% that are correlated with improved winter cold tolerance (reviewed by Swanson in press). As noted previously, recent studies indicate that BMR is seasonally stable or increases in summer relative to winter in many species inhabiting tropical and subtropical climates

(Maldonado et al., 2009; Smit and McKechnie, 2010), but seasonal phenotypic flexibility of M_{sum} for birds in tropical and subtropical climates has not been investigated.

4.4.2 Migration Migration also influences phenotypic flexibility in M_{sum}, with generally higher M_{sum} during spring migratory periods than during summer or winter (in mild climates) non-migratory periods (Swanson, 1995; Swanson and Dean, 1999; Vézina et al., 2007). The selective factor driving the increase in M_{sum} during migration appears to be selection for flight endurance and capacity, with thermogenic capacity increasing as a by-product (Swanson and Dean, 1999; Vézina et al., 2007). Nevertheless, the elevated thermogenic capacity may provide thermoregulatory benefits (i.e., improved cold tolerance) should migrating birds encounter cold temperatures en route to breeding grounds. An interesting related question is whether differences in flight capacity among bird groups result in differences in M_{sum}. For example, do aerial insectivores, which spend much of their active time during the year on the wing, even during non-migratory periods, generally have higher M_{sum} than species that don't spend as much time flying? This hypothesis has not been tested for birds and such tests would provide a fruitful avenue for future research.

4.4.3 Captivity Long-term captivity affects BMR in birds (McKechnie et al., 2006), but such an influence has not been studied for M_{sum}, primarily because most measures of M_{sum} for birds have been derived from wild populations. To avoid possible captivity effects on M_{sum} most measurements of M_{sum} in birds have been generated on the day of capture or on birds held overnight. If birds are held captive for periods longer than 1–2 days before measurement, it is important to verify the absence of a short-term captivity impact on M_{sum} to use these data for comparative purposes. Few studies have addressed this relationship in birds. Hill et al. (1993) examined M_{sum} variation in winter-acclimatized black-capped chickadees *Poecile atricapillus* from Michigan, USA, and found no significant differences in M_{sum} for up to 18 d after capture, suggesting little impact of short-term captivity on M_{sum}. Swanson (unpubl. data) measured M_{sum} on summer-acclimatized (mid August- mid September) American goldfinches, *Carduelis tristis*, from South Dakota, USA, held as indoor captives for periods of up to four weeks after initial capture. M_{sum} in these birds was elevated after 12-21 d and remained elevated when birds were measured again a week later. These data, contrary to those of Hill et al. (1993), suggest that short-term captivity may influence M_{sum} in birds. Thus, how short-term captivity might influence M_{sum} in birds remains an open question, and which environmental conditions might affect the short-term response of M_{sum} to captivity would be an interesting topic for additional research.

One of the principal findings stemming from these data is that M_{sum} is a flexible physiological trait. Factors consistently influencing M_{sum} variation in birds include body mass and temperature or climate. M_{sum} in birds is positively correlated with body mass (with similar scaling relationships to BMR) and negatively related to temperature, over both short and long durations. Several other factors may affect M_{sum} in birds, but are not consistent effectors. These include phylogeny, geography, and captivity. Phylogeny may influence M_{sum} differences among certain taxa, but other taxa do not show consistent differences in M_{sum}, and determining what functional, ecological, and evolutionary factors may underlie such phylogenetic differences will necessitate additional study. Similarly, M_{sum} does not consistently vary with short-term captivity, and defining the influence of captive housing conditions on M_{sum} variation will require further research. Moreover, the impact of captive origin on M_{sum} in birds has not been investigated, so whether M_{sum} in captive-raised birds differs from their wild counterparts, as does BMR (McKechnie et al., 2006), is unknown. Intraspecific variation in M_{sum} in birds may vary geographically, with colder regions producing higher M_{sum}, but such a relationship does not occur universally, suggesting that physical or behavioral responses may also impact biogeographical patterns in birds. Finally, whether birds engage in migration or not does not appear related to interspecific M_{sum} variation in birds, despite intraspecific increases in M_{sum} during migration, the latter likely a result of physiological adjustments promoting higher flight capacity in migrants.

5 Factors Affecting MMR

Exercise-induced MMR is generally higher than M_{sum} in birds and is also allometrically related to body size, with scaling exponents for MMR generated by flying, running, or in hop-flutter wheels ranging from 0.649 to 0.813 (Table 1). These scaling relationships are broadly similar to those for M_{sum} and BMR in birds (Fig. 1), suggesting similar overall scaling of both resting and maximal metabolic rates, despite the variable contributions of different physiological systems to basal and maximal metabolic rates (Darveau et al., 2002; Suarez and Darveau, 2005). Other ecological factors affecting MMR in birds are rarely studied, at least partially due to the difficulty in verifying that maximum exercise-induced metabolic rates have been attained. However, climate (or life history differences associated with climate) does appear to influence MMR generated in hop-flutter wheels. Wiersma et al. (2007a) found that tropical birds (mostly passerines) had, on average, a 39% lower MMR than temperate birds, with greater differences for smaller birds. This suggests that climate can influence not only thermogenic capacity, but also metabolic capacity in general.

6 Linking Variation in BMR, M_{sum} and MMR

A positive phenotypic correlation between BMR and MMR (i.e., aerobic capacity) is a central tenet of the aerobic capacity model for the evolution of endothermy (Bennett and Ruben, 1979). A few studies have examined interspecific phenotypic correlations between BMR and M_{sum} for birds. However, metabolic rates during maximal shivering intensity in birds range from about 4–8 times BMR, whereas maximal metabolic rates recorded during flight or other exercise generally exceed BMR by 10-fold or more (Marsh and Dawson, 1989; Swanson in press). Thus, examination of the relationship between BMR and M_{sum} may not be the most appropriate test for addressing the assumption of the aerobic capacity model of a link between resting and maximal metabolic rates. Very few studies have investigated the relationship between BMR and exercise MMR in birds (Chappell et al., 1999; Hammond et al., 2000; Wiersma et al., 2007a).

6.1 Phenotypic correlations of BMR and M_{sum}

Significant positive correlations between residuals of BMR and M_{sum} were documented in interspecific comparative studies of passerine birds (Dutenhoffer and Swanson, 1996) and of a variety of avian orders (Rezende et al., 2002). Thus, those species with high BMR also showed high M_{sum} in these studies. In contrast, Wiersma et al. (2007a) found no significant correlation between BMR and M_{sum} for tropical birds (mostly passerines). Thus, interspecific studies to date provide mixed support for a phenotypic link between BMR and M_{sum} in birds. In comparing the results of these studies, it is noteworthy that positive phenotypic correlations were found in studies where data were obtained largely from temperate-zone birds, whereas no relationship was found for tropical species, which likely face little selective pressure for high levels of regulatory thermogenesis (Wiersma et al., 2007a; b; Swanson and Garland, 2009). Determining whether climate provides a consistent and widespread influence on the correlation between BMR and M_{sum} will require further study.

Most small bird species from markedly seasonal climates show winter increases in both BMR and M_{sum} (McKechnie, 2008, Swanson in press), suggesting that these traits are phenotypically correlated on an intraspecific basis. Moreover, Swanson and Olmstead (1999) showed parallel changes in BMR and M_{sum} among winters that were associated with severity of the winter. However, no studies have directly examined the intraspecific relationship between BMR and M_{sum} in birds (Wiersma et al., 2007a). Future studies investigating potential intraspecific phenotypic associations between BMR and M_{sum} (and MMR) in birds are needed.

6.2 Phenotypic correlations of BMR and M_{sum} with MMR

The only study examining the interspecific relationship between BMR and MMR in birds is that of Wiersma et al. (2007a) who measured BMR and exercise-induced (hop-flutter wheel) MMR in a variety of tropical birds (mostly passerines). In this study, mass-independent residuals of MMR were significantly positively correlated with those for BMR, but MMR residuals were not correlated with M_{sum} residuals for species for which both MMR and M_{sum} were measured. Chappell et al. (1999) and Hammond et al. (2000) examined intraspecific correlations between BMR and MMR (hop-flutter wheel exercise) for house sparrows and red junglefowl *Gallus gallus*, respectively. BMR and MMR were significantly and positively correlated in juvenile sparrows, but not for adult sparrows or for junglefowl. These studies thus provide only partial support for the assumptions of the aerobic capacity model for the evolution of endothermy. These studies also suggest that exercise-induced and cold-induced metabolic rates may not correlate similarly with BMR. MMR is generally higher than M_{sum} in birds (Marsh and Dawson, 1989). For example, MMR for tropical birds in Wiersma et al. (2007a) exceeded M_{sum} by 47% on average, although both MMR and M_{sum} were lower in tropical than in temperate species. It seems likely that different muscle groups are used to generate maximum metabolic rates during shivering and hop-flutter wheel exercise or that blood flow patterns to muscles might differ between the two activities, and what impact this might have on correlations between BMR, M_{sum} and MMR is a topic worthy of additional study.

7 The ecological Relevance of BMR, M_{sum} and MMR

The metabolic rates of free-ranging birds in natural habitats are between BMR and MMR during activity and between BMR and M_{sum} when resting (except during periods of facultative hypothermia, when metabolic rate may be far below BMR). The ecological significance of M_{sum} is intuitively obvious, since it is a direct measure of maximum thermoregulatory heat production. Likewise, MMR is a key determinant of maximum exercise intensity during, for example, predator avoidance or long-distance migration. The ecological relevance of BMR, on the other hand, is less obvious. This has led to suggestions that a) we should focus on field metabolic rate [FMR, usually measured using the doubly-labeled water method (Nagy, 1980; Speakman, 1997)] rather than BMR if we want to understand how evolution shapes avian energy demands (C. Martinez del Rio, *pers. comm.*), and b) that comparative BMR analyses are largely phenomenological (Ricklefs et al., 1996). The ecological relevance of BMR is particularly pertinent in light of the current interest in the role of metabolic machinery in mediating life-history trade-offs (Ricklefs and Wikelski, 2002; Wikelski et al., 2003; Tieleman et al., 2006).

Some studies have found significant correlations between avian BMR and FMR residuals (Daan et al., 1990; Daan et al., 1991; Koteja, 1991), but Ricklefs et al. (1996) found a significant correlation for mammals but not for birds in a PI analysis. The lack of a direct quantitative relationship between BMR and FMR is also illustrated by Tieleman and Williams' (2000) observation that FMR is reduced by ~ 50 % in desert birds compared to non-desert species, whereas BMR is only ~ 17 % lower, emphasizing the importance of behaviour in determining FMR. Similarly, the relationship between FMR and latitude remains unclear. Although tropical wrens exhibit lower FMR than their temperate-zone counterparts (Tieleman et al., 2006), a recent analysis of the relationship between avian FMR and latitude revealed that some tropical species exhibit FMR values that are relatively high, and comparable to those of species at higher latitudes (see Fig. 1 in Anderson and Jetz, 2005). Collectively, these studies suggest that BMR cannot be viewed as a direct index of overall energy requirements. Careau et al. (2008) recently argued that one reason for this weak relationship is that behavioural traits related to animal personality exert a much stronger influence on daily energy expenditure than on standardized resting metabolic rates such as BMR. According to this argument, the energetic consequences of inter-individual variation in traits such as activity, exploration, boldness and aggressiveness are more likely to be manifested in overall energy demands (i.e., FMR), than in resting metabolic rates measured under conditions that attempt to exclude these traits' influences (i.e., BMR) (Careau et al., 2008).

Studies linking BMR variation to body composition and/or acclimation to specific conditions collectively suggest that the usefulness of BMR lies primarily in the fact that it provides an easily measureable indicator of the overall state of a bird's physiological machinery. Changes in BMR within individual birds, for instance, reflect changes in the masses and/or metabolic intensities of various organs, and are often correlated with environmental variation in energy supply and/or energy demand. Although the functional links between BMR, M_{sum} and MMR remain unclear and require further studies, the existence of clear zoographical patterns in the direction and magnitude of seasonal changes in BMR (Smit and McKechnie, 2010) reinforces the idea that BMR is a convenient indicator of overall metabolic adjustments, even if BMR variation is merely a by-product of changes in overall metabolic capacity. It may be that BMR has greater ecological significance for species inhabiting relatively warm climates. The lower limit of metabolic heat production probably has little direct ecological relevance for a small, temperate-zone bird wintering at high latitudes, but many tropical species regularly experience environmental temperatures that fall within their TNZs, conditions under which BMR becomes the major determinant of heat loads and rates of respiratory water loss.

In summary, BMR represents a significant, albeit variable, fraction of total energy demands, and the clear correlations between BMR and climatic and organismal traits strongly suggest that, even if for many species BMR is not a physiological trait with direct ecological relevance, it nevertheless provides a good indicator of how selection has operated on metabolic machinery. Similar correlations of climatic and organismal traits with M_{sum} and MMR, which are likely targets for more direct selection, at least under conditions of high energetic demands, reiterate that these standardized metabolic rates are worthwhile subjects for study when attempting to understand the links between physiology and life history in birds.

8 Future Research Directions

Several avenues of future research are necessary to further our understanding of avian metabolic diversity and its ecological and evolutionary implications. First and foremost, BMR has been measured in vastly more species than has M_{sum} or MMR, and we are much more constrained by limited data sets when seeking environmental and phylogenetic correlates of the latter two variables compared to the former.

A critical gap in current knowledge concerns the functional linkages between BMR, M_{sum} and MMR. Only one study has examined linkages among all three of these variables (Wiersma et al., 2007a), and studies examining the interspecific correlations between BMR and M_{sum} in birds have produced conflicting results with positive correlations for temperate species (Dutenhoffer et al., 1996; Rezende et al., 2002), but no correlation for tropical species (Wiersma et al., 2007a). These results also raise the interesting possibility that climate could influence the correlation between BMR and M_{sum}, but verifying this possibility will require additional research. Few studies have directly examined the linkages between BMR and maximum metabolic power output within species (Chappell et al., 1996; 1999; Hammond et al., 2000) and BMR and MMR are correlated in some cases but not in others. Thus, additional studies measuring all three standard metabolic measures, using hop-flutter wheels or flight tunnels to measure MMR, are needed, particularly at the intraspecific level. Results from such studies will help to either validate or invalidate the critical assumption of the aerobic capacity model for the evolution of endothermy (Bennett and Ruben, 1979) that lower and upper limits of metabolic power output are phenotypically linked. Moreover, such studies will shed light on the question of whether cross-training effects occur in birds (i.e., does flight training influence shivering capacity and vice versa?) and if such effects have ecological relevance. If correlations among lower and upper limits of metabolism are documented in birds, as some evidence suggests, another productive area of research would be to examine the functional bases for such correlations using molecular (e.g., candidate genes), genomic (e.g., microarrays) and mechanistic approaches to document changes in gene and protein expression and their effects in response to factors inducing metabolic variation in birds.

Recent studies suggest that seasonal patterns of phenotypic flexibility in BMR differ between birds inhabiting temperate-zone and tropical or subtropical climates (Smit and McKechnie, 2010). No studies have yet examined whether M_{sum} or MMR show similar differential seasonal trends with climate, and such studies are needed to more completely document the effects of climatic variability on phenotypic flexibility in metabolism. Few studies have examined this relationship in birds and those that have documented either no correlation (Tieleman et al., 2003b) or positive correlations (Cavieres and Sabat, 2008) between physiological flexibility (e.g., BMR and total evaporative water loss) and environmental variability (aridity, temperature, and/or seasonality). Studies addressing similar questions for M_{sum} or MMR in response to these and other climatic factors, especially those using common garden approaches (e.g., Wikelski et al., 2003; Tieleman et al., 2003; Broggi et al., 2005; Cavieres and Sabat, 2008), would be beneficial in understanding the relationship between climatic variability and phenotypic flexibility in birds. In addition, more information on the environmental cues driving metabolic variation is needed (Carey and Dawson, 1999). Studies addressing the relative importance of ultimate (e.g., photoperiod) and proximate (e.g., temperature) cues to metabolic variation in birds would be useful in this regard. A related issue concerns differences between metabolic responses to acclimation and acclimatization. Whereas the vast majority of species investigated to date increase BMR when acclimated to cold air temperatures under artificial conditions, winter acclimatization in sub-tropical species appears to involve the opposite response (Smit and McKechnie, 2010). Winter usually involves a combination of lower air temperatures and reduced food availability, and experimental manipulations of these two variables are needed to elucidate their respective roles as drivers of seasonal metabolic variation. A better understanding of these relationships could greatly benefit predictions of how bird populations might respond to climate change.

For natural selection to act on physiological traits, they must be repeatable and heritable. A few studies have addressed repeatability (reviewed by Nespolo and Franco, 2007) and heritability (Rønning et al., 2007; Tieleman et al., 2009b) of BMR in birds. These studies have typically found that BMR is repeatable and heritable, and, therefore, subject to natural selection. Because upper limits of metabolic output might be under greater selection pressure than BMR, at least under conditions of high energy demand, it might be expected that repeatabilities and heritabilities of M_{sum} and MMR might be higher than those for BMR. Alternatively, if these traits are highly flexible in response to environmental variability, then repeatabilities and heritabilities might be low. Swanson and Weinacht (1997) found that M_{sum} was not repeatable between seasons in outdoor-captive northern bobwhite *Colinus virginianus*, but Chappell et al. (1996; 1999) found that MMR during running or hop-flutter activity was repeatable for red junglefowl and house sparrows. Further studies examining repeatability and heritability of peak metabolic rates, and how repeatability and heritability are related to environmental variability, are needed to determine the degree to which these traits are subject to selection. Another avenue of research pertinent to these questions is study of the fitness consequences of M_{sum} and MMR. For example, is M_{sum} positively correlated with overwinter survival in birds inhabiting cold climates, and does this relationship change with severity of the winter? Research addressing such questions is needed to better understand the evolution of patterns of metabolic diversity in birds.

Finally, the influence of irreversible phenotypic variation resulting from developmental processes (developmental plasticity, Piersma and Drent, 2003) on avian metabolic rates remains almost entirely unknown. In view of the magnitude of reversible metabolic adjustments observed in acclimation and acclimatization studies, we would argue that future research should examine the contribution of developmental plasticity to metabolic variation within and among species. Partitioning avian physiological variation into genetic and plastic components is likely to be particularly important for developing mechanistic, process-based predictions of how birds will be affected by climate change.

Acknowledgements We thank Joe Williams and an anonymous reviewer for their constructive comments on the manuscript.

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Table 1 Allometric exponents derived from log M_{sum} or log MMR against log M_b regressions for interspecific avian studies

Metabolic Rate[a]	Taxa	n	OLS Exponent	PIC Exponent	Reference
M_{sum}	Variety (7 Orders)	8	0.615	---	Hinds et al. 1993
M_{sum}	Passerines	10	0.716	0.792[b]	Dutenhoffer and Swanson 1996
M_{sum}	Variety (10 Orders)		0.600	0.651	Rezende et al. 2002
M_{sum}	Passerines + Piciformes				
	Summer	21	0.699	0.700	Swanson and Liknes 2006
	Winter	11	0.559	0.503	Swanson and Liknes 2006
M_{sum}	Tropical Passerines + Columbiformes	19	0.814	0.615	Wiersma et al. 2007a, b
M_{sum}	Variety (6 Orders)	44	0.626	0.704	Swanson and Garland 2009
M_{sum}	Suboscine Passerines	16	0.832	0.767	Swanson and Bozinovic unpubl.
M_{sum}	Oscine Passerines	44	0.670	0.611	Swanson and Bozinovic unpubl.
MMR_F	Variety (6 Orders)	17	0.649	---	Hails 1979
MMR_F	Variety (8 Orders)	33	0.813	---	Norberg 1996
MMR_R	Variety (3 Orders)	7	0.80	---	Fedak et al. 1974
MMR_R	Variety (8 Orders)	14	0.754[c]	---	Taylor et al. 1982
MMR_{HF}	Tropical Passerines + Columbiformes	19	0.757	0.734	Wiersma et al. 2007a

Exponents for both ordinary least squares regression (OLS) or least squares regression of phylogenetically independent contrasts (PIC) mapped back onto the original data space (Garland and Ives 2000) are presented, if such exponents were reported.

[a] Maximum metabolic rates generated by cold exposure (M_{sum}), flight (MMR_F), running (MMR_R), and in a hop-flutter wheel (MMR_{HF})

[b] The PIC exponent for the data of Dutenhoffer and Swanson (1996) was calculated by Garland and Ives (2000).

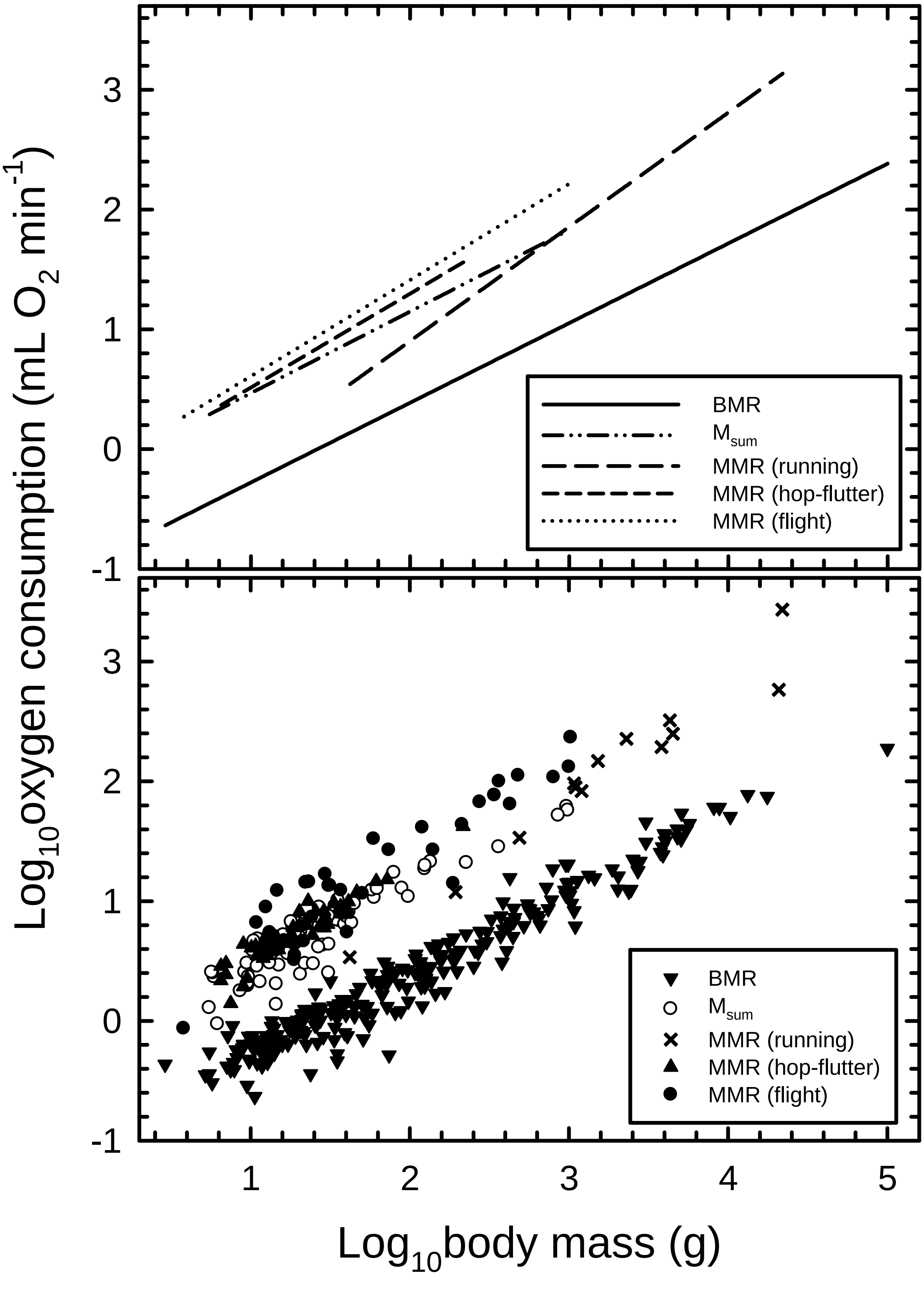
[c] Regression coefficient for M_b in multiple regression with the other independent variable being an allometric relationship with speed.

Figure legend

Fig. 1 Basal (BMR), summit (M_{sum}) and maximal (MMR) metabolic rates in birds, expressed as oxygen consumption

Maximal metabolic rates elicited in three different ways, namely running, hop-flutter chamber, and flight, are shown separately. The lower panel shows the actual data, and the upper panel shows the scaling relationship for each metabolic rate, based on a conventional (i.e., non-phylogenetically independent) linear regression model. Equations for the regressions are as follows: BMR: $\log_{10}BMR = 0.666 \log_{10}M_b - 0.944$, $R^2 = 0.949$; M_{sum}: $\log_{10} M_{sum} = 0.681 \log_{10}M_b - 0.214$, $R^2 = 0.843$; MMR (running): $\log_{10}MMR = 0.956 \log_{10}M_b - 1.006$, $R^2 = 0.956$; MMR (hop-flutter): $\log_{10}MMR = 0.783 \log_{10}M_b - 0.270$, $R^2 = 0.882$; MMR (flight): $\log_{10}MMR = 0.804 \log_{10}M_b - 0.196$, $R^2 = 0.860$. The original sources for the BMR data shown here can be found in McKechnie and Wolf (2004); all values that met these authors' criteria for BMR measurement conditions are included, irrespective of sample size. The M_{sum} data were obtained from Hinds et al. (1993), Rezende et al. (2002), Swanson and Liknes (2006), Wiersma et al. (2007a,b), and Swanson (unpublished data). MMR data for the different methods were obtained from the following sources: hop-flutter data were from Wiersma et al. (2007a); running data were from Fedak et al. (1974), Pinshow et al. (1976), Bamford and Maloiy (1980), Brackenbury and El-Sayed (1985), Bundle et al. (1999), Hammond et al. (2000), and Seymour et al. (2008); flight data were from Norberg (1996).

Figure 1.


3
2
1
0
-1
BMR
M$_{sum}$
MMR (running)
MMR (hop-flutter)
MMR (flight)
▼ BMR
○ M$_{sum}$
× MMR (running)
▲ MMR (hop-flutter)
● MMR (flight)
Log$_{10}$oxygen consumption (mL O$_2$ min^{-1})
1
2
3
4
5
Log$_{10}$body mass (g)