On the intraspecific variability in basal metabolism and the food habits hypothesis in birds

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Abstract The food habits hypothesis (FHH) stands as one of the most striking and often-cited interspecific patterns to emerge from comparative studies of endothermic energetics. The FHH identifies three components of diet that potentially produce variability in mass-independent BMR, i.e. food quality, food availability, and food predictability or environmental productivity. The hypothesis predicts that species with diets of low energy content and/or low digestibility should evolve low mass-independent BMRs. The effects of food habits on BMR have been widely investigated at the interspecific level, but the variation between individuals and populations has been largely ignored. Our focus is to compare predictions derived from interspecific studies with data collected from within-species studies to explore the mechanisms and functional significance of adaptive responses predicted by the food-habits hypothesis among birds. We conclude that if BMR is correlated with daily energy expenditure, then organisms that can lower BMR will reduce daily energy expenditure and hence, food requirements. Birds that lower BMR in stressful environments may increase survival. Nevertheless, the mechanism (s) by which birds eating a low quality diet reduce BMR and whether lower BMR affects fitness remain to be determined [*Current Zoology* 56 (6): 759–766, 2010].

Key words Intraspecific comparisons, Avian energetics, Food habits hypothesis, Diet, Basal metabolic rate

1 Introduction

Species-specific rates of energy metabolism among endotherms have been studied and correlated with biotic and abiotic factors. This has been used as evidence for metabolic adaptation to different environments (e.g., Gordon, 1977; Schmidt-Nielsen, 1997; Willmer et al., 2000; McNab, 2002). Energy metabolism is associated with the rate at which animals acquire and process energy to fuel activity. Since metabolic rates set the pace of life, assessment of their variability has been, and continues to be, of great importance to several contemporary ideas which attempt to link animal energetics to traits such as species richness, species distribution, reproductive effort, activity levels and life-history strategies (Kooijman, 2000; Brown et al., 2004; Cruz-Neto and Jones, 2005). McNab (1992a), Hulbert and Else (2004), and Speakman et al. (2004) provide historical overviews of the development of various metabolic measurements, and describe in detail the measurement that came to be known as basal metabolic rate (BMR).

Between-species comparisons assume that traits are fixed for any given species, with the variation between individuals being minimized. However, at least for BMR, within-species variability can be high and biologically significant (Bech et al., 1999; Nespolo et al., 2003), serving as the raw material upon which natural selection acts. Intraspecific analysis of BMR seems to be a useful approach for evaluating hypothesis about mechanisms and adaptation of energy metabolism in animals. Also, intraspecific studies can be used to test the predictions derived from between-species comparisons, and thus help to identify factors influencing energy metabolism in addition to those revealed by interspecific studies. Here, we attempt to show that interspecific analyses are oriented to the analysis of the ultimate factors responsible for the variability in BMR (Cruz-Neto and Jones, 2005), while intraspecific analyses can complement these interspecific studies, by giving insights into the proximate factors responsible for metabolic variability as well as the primary underlying mechanisms and functional significance.

Consequently, we analyzed intraspecific variations in BMR in birds. We hope to highlight current weaknesses in the study of the intraspecific variability in BMR among birds within the framework of the food habits

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hypothesis (see below), and to suggest avenues of future research. We focused our analysis on birds because they are one of the most diverse groups of terrestrial vertebrates. For example, birds exhibit a great diversity of feeding habits at both intra- and interspecific levels and inhabit nearly all geographical zones, with a concomitant diversity in life-history traits. Specifically regarding dietary diversity, the class Aves encompasses species with widely contrasting dietary habits in time and space, including ontogenetic shifts, and includes individuals, populations and species that feed only on grasses, leaves, seeds, invertebrates, fruits, meat or various mixtures of these food types (see Klasing, 1998). This variability provides an outstanding opportunity to test the effects of food habits and dietary shifts on BMR. Moreover, birds have the highest mass-independent metabolic rates among vertebrate animals (Schmidt-Nielsen, 1997), so energy metabolism should be under strong selective pressure.

2 Basal Metabolic Rate

Originally defined as a way to assess the minimum rate of energy use necessary to maintain homeostasis, BMR is by far the most widely measured energetic parameter in endothermic vertebrates. It has been used extensively to assess costs of the different components of organisms' energy budgets, to analyze species-specific variation in rates of energy expenditure during maximal and sustained activities, to evaluate scaling effects on rates of energy flux among species, and to understand metabolic performance and tolerance to temporal and spatial changes in environmental conditions (McNab, 2002). Consequently, understanding and explaining the selective pressures that underlie differences in BMR within and across species are pivotal to addressing major questions in evolution, ecology and physiology (van der Meer, 2006).

The dependence of metabolic rates (including BMR) on body mass has long been recognized, but functional explanations for this dependence are still subject to intense debate (e.g. Cruz-Neto and Jones, 2005; McNab, 2009; Glazier, 2008; Raichlen et al., 2010. Nevertheless, it is well known that differences in body mass alone are not sufficient to explain all variation in BMR (McNab, 1992b). There are several hypotheses that attempt to address how biotic and abiotic conditions affect mass-independent BMR (i.e., the deviation from allometrically expected BMR; see McNab, 2002). One of the most inclusive, albeit debatable hypotheses predicts that mass-independent BMR is associated with diet.

3 Patterns of Basal Metabolic Rate and the Food Habits Hypothesis

Originally proposed by McNab (1986 and references therein) for mammals, the food habits hypothesis identifies three components of diet which can produce variability in BMR: quality, availability and predictability (Cruz-Neto and Bozinovic, 2004). Specifically, the hypothesis posits that species or populations that exploit food with low energy content and/or low digestibility are likely to evolve low mass-independent BMRs (Cruz-Neto et al., 2001; McNab, 2002). Likewise, the evolution of a low mass-independent BMR is likely to occur in habitats where food availability is low and/or unpredictable (McNab, 2002; Cruz-Neto and Jones, 2005). However, the cause-effect relationships between metabolic rates and food quality and availability are still poorly understood. Indeed, Cruz-Neto and Bozinovic (2004) reviewed intraspecific studies which tested the food habits hypothesis and concluded that results from studies on the effects of diet quality provided mixed support for the hypothesis. The hypothesis is supported by data from interspecific comparisons, but only in certain taxa, such as carnivores, bats and some species of birds (McNab, 1969, 1988, 2003a; Muñoz-Garcia and Williams, 2005). Among birds, McNab (2003b) proposed that food habits have exerted a significant effect on energetics, but Schleucher and Withers (2002) found that BMR of pigeons and doves was not correlated with diet when phylogeny is explicitly incorporated in the analysis. Nevertheless, McNab (2009) recently analyzed data on BMR for of 537 bird species, concluding that after the effect of body mass was removed, there was a significant effect of diet. McNab concluded that species feeding on nectar/pollen or nuts had higher BMRs than omnivores, which had higher BMR than species eating only aquatic invertebrates, insects, or seeds, which in turn had higher BMRs than specialists that ate only fruit or vertebrates. These comparative studies have generally focused on the ultimate (evolutionary) rather than proximate (mechanistic) factors responsible for differences in the rate at which energy is acquired, processed and expended. Indeed, the FHH can, and perhaps must, be tested in both contexts. In this vein, Cruz-Neto and Bozinovic (2004) suggest that results from intraspecific studies revealed that the factors responsible for the association between diet quality and BMR might not be the same as those that favored the evolution of the correlation initially.

4 Birds, Basal Metabolic Rate and the Food Habits Hypothesis: Within Species Comparisons

Several problems have emerged from studies purporting to test the food habits hypothesis. One significant issue is the taxonomic level of analysis. For example, as pointed out before, intraspecific (or interpopulational) analyses of physiological traits have the potential to compensate for many of the pitfalls associated with interspecific studies (Dohm et al., 2001; Nespolo et al., 2003; 2005; Labocha et al., 2004; Konarzewski et al., 2005; Sadowska et al. 2005; Lovegrove, 2006; Bozinovic et al., 2007). In addition to the taxonomic level of analysis, several specific problems also plague the interpretation of tests of the food habits hypothesis. For example, ambiguities surrounding diet categorization can potentially confound interpretations from interspecific analyses of the relative importance of diet quality (Cruz-Neto et al., 2001; McNab, 2002; Muñoz-Garcia and Williams, 2005). Evidence for an association between mass-independent BMR and food availability and predictability comes from interspecific or interpopulation studies where factors such as latitude, temperature, rainfall and aridity of the species´ habitats of origin are used as a proxies for the effects of food availability and predictability on BMR (McNab, 2002; Tieleman and Williams, 2000; Tieleman et al., 2003a,b; Wikelski et al., 2003; Degen et al., 1998; Mueller and Diamond, 2001; Lovegrove, 2000; 2003; Cruz-Neto and Jones, 2005; Rezende et al., 2004; Williams et al., 2004). The degree to which these proxies provide an accurate assessment of food availability and productivity and their effect on BMR is unknown. With the exception of some interpopulational analyses where habitat productivity and/or variability were directly assessed (Mueller and Diamond, 2001; Speakman et al., 2004; Bozinovic et al., 2009), the precise effects of these two components cannot be separated, due to confounding effects from other features of the habitat where the species has evolved.

Several experimental studies have tested how diet quality and availability shape energy budgets in mammals, but few studies have evaluated the FHH at the intraspecific level in birds. Geluso and Hayes (1999) found no effect of chronic dietary acclimation (insects versus fruits) on BMR in *Sturnus vulgaris* while Piersma et al. (2004) found BMR declined in *Calidris canutus* when shifted from a soft (trout chow diet) to a

hard-texture (mussels, *Mytilus*) diet (see also Piersma et al., 1996). Bech et al. (2004) reported no effect of food quality on BMR during early development in zebra finches *Taeniopygia guttata*, whereas Moe et al. (2005) reported that after diet restriction, duckling *Anas platyrhynus* BMR significantly decreased. Recently, Maldonado (2009) found that rufous-collared sparrows *Zonotrichia capensis* respond to dietary acclimation. After seven weeks of acclimation, birds fed a diet of mealworms had decreased metabolic rates compared to birds fed seeds, supporting the FHH. Moreover, the BMR of birds on the seed diet did not differ between the pre- and post-acclimation period. Thus, these results suggest that sparrows consuming mealworms decreased BMR in comparison to wild birds. The FHH predicts a decrease in the energy expenditure when the energetic return from food is diminished. Because the digestibility of seeds by passerines is higher than that of insects (Novoa et al., 1996; Karasov, 1990; Weiser et al., 1997), such differences in digestibility may explain observed differences in BMR, thus supporting the FHH.

Maldonado's (2009) study also revealed differences in the response to dietary acclimation among different populations of sparrows. Only birds from a xeric site responded to dietary treatment, whereas birds from more mesic localities did not. This suggests that the climatic features of the habitats could influence the response of energetic traits to dietary acclimation, as has been demonstrated for the response to thermal acclimation (Cavieres and Sabat, 2008). This is consistent with the hypothesis of Williams and Tieleman (2000) which proposes that phenotypic flexibility in BMR among desert birds will be greater than that among similar birds from mesic areas. The rationale for this hypothesis is that birds dwelling in habitats with low predictability of rain pulses and hence resource abundance, will adjust organ sizes and then BMR. Nevertheless, Williams and Tieleman (2000) did not find intraspecific variation in metabolic response in birds from desert or non desert habitats, whereas Maldonado (2009) did. It is possible that the contrasting results may result from different experimental approaches. While Williams and Tieleman (2000) compared metabolic response to thermal environment, Maldonado (2009) tested the hypothesis by collecting data directly assessing the effect of diet quality on BMR.

Similarly, we (Sabat et al., 2009) also examined the relationship between intraspecific BMR, diet, and climate among populations of the omnivorous passerine

Zonotrichia capensis. We measured BMR on birds immediately following capture and used stable isotopes to estimate each individual's relative trophic level. Based on estimates of $\delta^{15}N$, close to 15% of the variability in mass-independent BMR was explained by trophic level after accounting for the effect of body mass, suggesting that birds at higher trophic levels exhibited lower BMR. These results support the food habits hypothesis. BMR in *Z. capensis* also varied among geographic localities. Thus, it is clear that differences in climatic conditions (e.g., aridity, air temperature, rainfall) can exert a significant effect on BMR, as demonstrated previously for this species (Sabat et al., 2006; Cavieres and Sabat, 2008).

Essential to these types of analyses is the assumption that climatic variability directly influences food availability and predictability. Sabat el al. (2009) suggested that the effect of climate had both a positive direct effect and a negative indirect effect (through trophic level) on BMR. However, whether either of these effects is the proximate mechanism for the dependence of BMR on dietary habits at the intraspecific level is unknown. The limited data (both from interspecific and intraspecific analyses) suggest that animals from lower trophic levels (consuming mainly nectar, fruits and seeds) have higher BMR than individuals from higher trophic levels (e.g., those preying on insects and invertebrates).

Given that plant tissues have high levels of secondary chemical compounds, animals consuming allelochemicals may increase BMR as a consequence of increased detoxification costs (Cork and Foley, 1991; Foley and McArthur, 1994). However, Cruz-Neto and Bozinovic (2004) noted that physiological responses to different food types will differ depending on whether species are dietary specialists or generalists. The effects of diet quality have also been extended to an ecological time scale. It has been hypothesized that within an individual's lifetime, organisms feeding on a low quality diet can lower BMR and thus reduce daily energy requirements (Cork, 1994). However, interspecific tests of the FHH among mammals have not always corroborated the expected patterns. Results differ with the experimental protocol used and/or the specific component of the hypothesis being tested (Mueller and Diamond, 2001; Cruz-Neto and Bozinovic, 2004; Speakman et al., 2004).

For intraspecific studies of mammals, reductions in diet quality are generally accompanied by correlated decreases in BMR, although not in all cases. For example, Veloso and Bozinovic (1993) found support for such a relationship, demonstrating that the herbivorous rodent, *Octodon degus* or degu, maintained on a low quality diet for six months had significantly lower BMRs than those fed a high quality diet (high lipid and protein diets). In addition, Fuglei and Oritsland (1999) found a reduction in resting metabolic rate of arctic foxes *Alopex lagopus* starved for 10 days in cold temperatures. Koteja (1996) reported that *Peromyscus maniculatus* decreased BMR after 10 days eating poor diets. Rosen and Trites (1999) assessed the metabolic effects of low-energy diets on sea lions, *Eumetopias jubatus*, and found that sea lions depressed BMR in response to decreases in energy intake and body mass. Choshniak and Yahav (1987) documented low metabolic rates in the vole *Microtus guenteri* after one month of acclimation to low food quality. However, they observed no effect of diet quality on BMR in the rodent *Meriones crassus*. Also conflicting with data suggesting a negative impact of diet quality on BMR in mammals, Bozinovic (1995) reported that after 10 days of acclimation to diets of different cellulose concentration, BMR of degus did not change. At the intraspecific level, we hypothesize that small birds, similar to most small mammals, should decrease BMR to survive on a low quality diet.

The relationship between BMR and diets with elevated levels of plant secondary compounds has been investigated in a few mammal species. Thomas et al (1988) documented increased BMR in voles feeding on plants with phenol gallic acid. However, both Bozinovic and Novoa (1997) and Bozinovic et al. (1997) found no effect of subchronic dietary cellulose and tannic acid on the BMR of degus or the mouse *Phyllotis darwini*. However the paucity of studies regarding the effect of plant secondary compounds on BMR and its apparent contradictory results, precludes any generalization. Whether the effect of reductions in diet quality due to elevated concentrations of plant secondary compounds may impact BMR differently than reductions in diet quality due to low energy content should be a matter of future studies.

Finally, If BMR is correlated with daily energy expenditure, then organisms that lower BMR should reduce daily energy expenditure and hence, food requirements. Lower BMR in stressful environments may enhance fitness through increased survival. However, the mechanisms by which animals lower BMR when fed low–quality diets and whether lower BMR affects fitness, remain unknown (Table 1).

Table 1 Resume of most relevant studies in birds testing the food habits hypothesis FHH, including the experimental approach, the possible ultimate (evolutionary) or proximate (mechanistic) causes explaining the differences in BMR among or within specie

Taxa	BMR change	Approach	Support for FHH	Causative explanation	Source
Zonotrichia capensis	Increased BMR with increased trophic level	Field and interpopulation data	Yes	Mechanistic	Sabat et al., 2009
Zonotrichia capensis	Higher BMR with seed diet than with insect diet in some but not all populations	Experimental studies and interpopulation data	Yes	Mechanistic	Maldonado, 2009
Pigeons and doves	No change in BMR with diet	Interspecies comparisons; phylogenetic approach	No	Evolutionary	Schleucher and Withers, 2002
Multi-species (537)	BMR: nectar/pollen eaters > omnivorous > insectivorous > frugivores/vertebrate eaters	Interspecies comparisons	Yes	Evolutionary	McNab, 2009
Paradisiae birds	BMR: Omnivores and insectivores > frugivores	Interspecies comparisons	Yes	Evolutionary	McNab, 2003b
Sturnus vulgaris	No change in BMR with insects versus fruits diets	Experimental studies	No	Mechanistic	Geluso and Hayes, 1999
Calidris *canutus*	Reduction in BMR when fed with mussels compared when fed with trout chow.	Experimental studies	Yes	Mechanistic	Piersma, 2004 et al.
Taeniopygia guttata	No change in BMR with diet quality	Experimental studies	No	Mechanistic	Bech et al., 2004
Anas platyrhynus	Decrease in BMR after diet restriction	Experimental studies	Yes	Mechanistic	Moe et al., 2005
Multi-species (139)	BMR and FMR were reduced in desert birds compared with mesic species	Interspecies comparisons; phylogenetic approach	Yes	Evolutionary	Tieleman and Williams, 2000
Alaudidae (12 species)	BMR decreased along a gradient of increasing aridity	Interspecies comparisons; phylogenetic approach	Yes	Evolutionary	Tieleman et al., 2003a
Taeniopygia Guttata	Low quality diet in growing birds produced an elevation of RMR in adults.	Experimental study	Yes	Mechanistic	Criscuolo et al., 2008

5 Future Directions

Studies seeking to unravel the adaptive nature of physiological traits have relied heavily on interspecific comparisons. One of the most significant conclusions to come from these studies is that most physiological traits are highly variable. In this sense, recent emphasis has been given to the analysis of intraspecific variation in physiological traits. Again, interspecific comparisons assume that for any given species all traits are fixed, with variation between individuals largely ignored (Bennett, 1987).

Many questions about how organisms adapt to different biotic and abiotic conditions remain unanswered. For example, we still do not understand the relative contributions of genetic and environmental factors in determining physiological responses at molecular and integrative levels in adults. To answer these questions, data about heritability of physiological traits are needed. In fact, the use of narrow-sense heritability and its magnitude allows determining the capacity of a trait to respond to current natural selection. Since natural selection reduces variation, this index represents the degree to which a trait has been under selection in the past. We suggest that comparative physiological ecologists should study not only how animals work, but also how

physiological systems evolve. The ecological and functional diversity of birds provide an ideal opportunity for using both quantitative genetic models and physiological traits to study such physiological systems from the cellular level to the whole organism, to populations and species.

While BMR is a consistent trait under steady-state conditions (although see Bozinovic, 2007), practically all studies have used adult, full-grown individuals. Thus, a related but rarely addressed question is the extent to which early (i.e., hatchling or fledgling periods) exposure to a given diet quality affects BMR during adulthood. As far as we know, only Verhults et al. (2006) and Criscuolo et al. (2008) have demonstrated lasting effects of rearing conditions (including diet quality) on adult BMR in zebra finches. Thus, a promising avenue of research is to test for: 1) the effect of feeding experience during ontogeny on mass-independent metabolic rates of adults; 2) the role of ontogenetic nutrition on BMR in adulthood; and 3) the effect of changes in metabolic efficiency through ontogenetic time.

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