



Comparative basal metabolic rate among passerines and the food habit hypothesis

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ABSTRACT

The food habit hypothesis (FHH) predicts that mass-independent BMR is associated with dietary traits. In spite of decades of research, the FHH remains controversial, in part because ambiguities surrounding diet categorization can potentially confound interpretations from interspecific analyses of the relative importance of diet quality. In this study, we investigated possible relationships between BMR and the percentage of nitrogen, and the percentage of various prey items in the gut content of 19 passerine species under an explicit phylogenetic context. There were no significant effects of the percentage of dietary nitrogen, invertebrates, or plants on mass-independent BMR using either conventional or phylogenetically corrected regressions. Consequently, our results do not support the FHH in passerine birds. The lack of a significant correlation between diet and BMR could be explained by generally similar levels of activity and similar body composition among species. In this sense, it is possible that the impact of food habits could depend mainly on body mass, which is also associated to the high cost of the endothermy at small sizes.

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1. Introduction

Metabolic rates set the tempo of life, thus, assessment of their variability has and continues to be, of great importance to several contemporary ideas which attempt to link animal energetics to traits such as species richness and distribution, reproductive effort, activity levels and life-history strategies (Kooijman, 2000; Brown et al., 2004; Cruz-Neto and Jones, 2005). 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 (Cruz-Neto and Jones, 2005; Labra et al., 2007; McNab, 2009; Raichlen et al., 2010; Swanson and Garland, 2009). Nevertheless, it is well known that differences in body mass alone do not explain variation in BMR (McNab, 1992). There are several hypotheses that attempt to explain how biotic and abiotic conditions affect mass-independent BMR (McNab, 2002).

One of the most inclusive, albeit debatable hypotheses, the food habit hypothesis (FHH) predicts that mass-independent BMR is associated with diet. Originally proposed by McNab (1986 and references therein) for mammals, the FHH identifies three components of diet which can produce BMR variability: 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).

The evidence of 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). 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 evolved. Cruz-Neto and Bozinovic (2004) reviewed studies which tested the food habit 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 taxa, such as, carnivores, bats and some species of birds (McNab, 1969, 1988, 2003a; Muñoz-García and Williams, 2005). Among bird species McNab (2003b, 2009) 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.

In spite of decades of research, McNab's (1986) FHH remains controversial. The controversy stems from the difficulty of teasing

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apart the multiple possible factors that impinge on BMR from comparative data sets that use species as data points (Cruz-Neto and Bozinovic, 2004). Cruz-Neto and Bozinovic (2004) have argued that interspecific comparative tests of FHH rely in broad categorical diet categories that ignore the potential variation in diets of a species. 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-García and Williams, 2005).

In this study, we examined the relationship between BMR and diet among 19 species of passerine birds from central Chile, under an explicit phylogenetic context. We measured BMR on freshly caught birds and took advantage of the previous results of the proportion of animal and vegetal prey in the gut content and the elemental chemical analysis (percentages of nitrogen and carbon) of bird's diet (Ramirez-Otarola, 2010) to estimate the proportion of protein consumption by each individual (Sturner and Elser, 2002). We focused our study on passerine birds because they are one of the most diverse groups of terrestrial birds (Sibley and Ahlquist, 1990). Our study included species that feed on insects, invertebrates, seeds, nectar, and fruit, or are omnivores (Lopez-Calleja, 1995; Sabat et al., 1998; Jaksic, 2001). Consequently, this dietary diversity provides an outstanding opportunity to look at the relationships between food habits on BMR. Moreover, birds have the highest mass-independent BMR's among vertebrates (McNab, 2002), consequently energy metabolism should be under strong selective pressure.

2. Materials and methods

2.1. Collection of individuals

Birds were captured at two localities of Central Chile: Quebrada de la Plata (33°30'S, 70°54'W) and San Carlos de Apoquindo (33°23'S, 70°30'W). Both sites have Mediterranean climate with cool and wet winters and relatively dry and hot summers. Sixteen species of songbirds were captured with mist nets from November 2008 to April 2009. We captured birds only in spring and summer, to avoid the putative seasonal variation in physiological parameters. Following capture, we transported them to a laboratory in Santiago, Chile (33°27'S, 70°42'W). Here, birds were held in individual plastic-mesh cages (50 × 50 × 50 cm) in a constant temperature room (22 ± 2 °C) on a 12 L:12D photoperiod.

2.2. Basal metabolic rate

Measurements of BMR were made in the same day of capture in post-absorptive (four hour fasted), resting birds during the inactive phase and within the thermoneutral zone of the species, using standard flow-through respirometry methods. Briefly, birds were weighed, placed in a dark metabolic chamber (1–5 L), and then placed in a controlled temperature cabinet (Sable Systems, Henderson, NV, USA) at a constant temperature (typically $T_a = 30 \pm 0.5$ °C). The metabolic chamber received dried air at 200–800 mL min⁻¹ from a mass flow controller and through Bev-A-Line tubing (Thermoplastic Processes Inc.). The excurrent air passed through columns of Driedite, CO₂-absorbent granules of Baralyme, and Drierite before passing through an O₂-analyzer, model Turbo Foxbox (Sable System) calibrated with a known mix of oxygen (20%) and nitrogen (80%) that was certified by chromatography (INDURA, Chile). The mass flow meter of the Turbo Foxbox was calibrated monthly with a volumetric (bubble) flow meter. The measurement and calibration protocols we followed were after Tieleman and Williams (2000). Because water vapor and CO₂ were scrubbed before entering the O₂ analyzer, oxygen consumption was calculated as [Withers (1977: p 122)]: $VO_2 = [FR * 60 * (F_i O_2 - F_e O_2)] / (1 - F_i O_2)$, where FR is the flow rate in mL/min after STP correction, and F_i and F_e are the fractional concentrations of O₂ entering and leaving the metabolic chamber, respectively. Body mass (M_b)

was measured before the metabolic measurements using an electronic balance (±0.1 g) and cloacal body temperature (T_b) was recorded at the end of each measurement with a Cole–Palmer copper-constantan thermocouple attached to a Digisense thermometer (Model 92800-15). We found that all animals were euthermic after the metabolic trials ($T_b = 40$ – 42 °C). Output from oxygen analyzer (%) and flow meter were digitalized using a Universal Interface II (Sable Systems) and recorded on a personal computer using EXPEDATA data acquisition software (Sable Systems). Our sampling interval was 5 s. Birds remained in the chamber until a visual inspection of the recorded data allowed us to determine when steady-state conditions had been achieved (see Tieleman and Williams, 2003b; Tieleman, 2007). This typically occurs after 4 h in most species. We averaged O₂ concentration of the excurrent air stream over a 20 min period after steady-state was reached (following Tieleman et al., 2002).

2.3. Data analysis

To test the hypothesis that dietary patterns affect the BMR, we investigated possible relationships between BMR and the percentage of nitrogen, and the percentage of prey items in the gut content of each species. Because we could not determine the dietary composition (percentage of prey items) and the BMR of each specimen simultaneously, dietary composition of bird species was taken from Ramirez-Otarola (2010). In that study, the volumetric percentage of insects and seeds found in each bird's gastrointestinal tract were determined in the same time and localities of capture of our sample animals. Besides, Ramirez-Otarola (2010) analyzed the percentage of nitrogen and carbon of food. To satisfy normality assumptions of parametric statistical tests (Zar, 1996), we arcsin square root transformed percentage data before analyses. In addition to our data set, we also included in a separate analysis the BMR of additional 3 species for which the BMR and the percentage of animal and plant items in diet were reported in the literature, and that dwell in the same habitat and captured in the same season (Table 1). For this data set, we only calculated the relationship between the BMR and the percentage of invertebrates and vegetal items.

To test the possible effect of phylogenetic inertia on BMR, M_b , the volumetric percentage of insects and seeds and the percentage of nitrogen food, we calculated the *K*-statistics (Blomberg et al., 2003). Because BMR is closely related with body mass, we transformed the values of BMR according Blomberg et al. (2003) method, and then we calculated the phylogenetic signal for mass-independent trait values. To do that we first log-transformed the original data and calculated the phylogenetic independent contrast for each response variable. Then we performed a least squares regression (LSR) (through the origin) and the slope of the model was used to standardize the original variable. With this new variable we calculated the *K*-statistics using the Independent Contrasts v2.18 programs (P. Withers, pers. Comm.). To examine correlations among variables we used both standard correlation and LSR methods, and correlation and regression on phylogenetically independent data (Felsenstein, 1985). Phylogenetically independent data were calculated using a constructed phylogenetic tree (Fig. 1) on the basis of Sibley and Ahlquist (1990). Although some species were not listed, we used another species within the same genus as equivalent to determine branch lengths in our phylogeny. In addition, we estimated the phylogenetic distance between *Asthenes humicola* and *Leptasthenura aegithaloides* from Gonzalez and Wink (2008), whereas the phylogeny of the Family Tyrannidae was obtained from Ohlson et al. (2007). Besides, the phylogenetic distance between *Cinclodes fuscus* and *Cinclodes oustaleti* was estimated from Chesser (2004). The distance between *Curaeus curaeus* and *Sturnella loyca* was derived from the phylogeny proposed by Lanyon and Omland (1999). Finally, an arbitrary phylogenetic distance of 0.1 was set between *Phrygilus fruticeti* and *Phrygilus laudinus*. In addition, we used phylogenetic autocorrelation to

Table 1Summary of ecological features and species mean (\pm SD) for body mass (M_b) and BMR of 19 passerine species from Central Chile.

Family	Species	Dietary category	M_b (g)	BMR (mL O ₂ h ⁻¹)	Source	BMR* (%)
Cotingidae	<i>Phytotoma rara</i>	Herbivore	42	89.46	1	108.2
Emberizidae	<i>Zonotrichia capensis</i>	Omnivorous	19.29 \pm 3.3	57.50 \pm 5.9	This study	115.6
	<i>Sicalis luteola</i>	Granivore	15.47 \pm 1.02	57.37 \pm 3.95	This study	133.2
	<i>Phrygilus fruticeti</i>	Granivore	36.15 \pm 4.73	80.76 \pm 12.6	This study	107.8
	<i>Phrygilus alaudinus</i>	Granivore	18.00 \pm 3.25	58.45 \pm 21.88	This study	123.0
	<i>Diuca diuca</i>	Granivore	34.63 \pm 3.28	73.81 \pm 15.24	This study	101.3
Fringillidae	<i>Carduelis barbata</i>	Granivore	14.30 \pm 2.22	49.19 \pm 6.23	This study	120.3
Furnariidae	<i>Asthenes humicola</i>	Insectivore	20.50 \pm 2.09	58.01 \pm 11.99	This study	112.1
	<i>Leptasthenura aegithaloides</i>	Insectivore	7.83 \pm 0.58	35.02 \pm 3.13	This study	126.9
	<i>Cinclodes oustaleti</i>	Insectivore	24.90 \pm 1.3	73.95 \pm 12.7	2	125.9
	<i>Cinclodes fuscus</i>	Insectivore	28.90 \pm 1.4	97.10 \pm 18.2	2	150.0
Icteridae	<i>Sturnella loyca</i>	Omnivorous	88.53 \pm 11.52	137.05 \pm 22.79	This study	101.9
	<i>Curaeus curaeus</i>	Omnivorous	90.09 \pm 10.26	161.66 \pm 27.15	This study	118.8
Mimidae	<i>Mimus thenca</i>	Omnivorous	65.97 \pm 6.25	128.80 \pm 20.09	This study	116.0
Troglodytidae	<i>Troglodytes aedon</i>	Insectivore	8.92 \pm 0.88	33.59 \pm 10.06	This study	111.8
Turdidae	<i>Turdus falcklandii</i>	Omnivorous	70.50 \pm 11.14	131.92 \pm 23.83	This study	113.8
Tyrannidae	<i>Anairetes palurus</i>	Insectivore	5.43 \pm 0.56	19.51 \pm 3.04	This study	89.8
	<i>Xolmys pirope</i>	Insectivore	32.55 \pm 2.53	73.12 \pm 2.62	This study	104.5
	<i>Elaenia albiceps</i>	Omnivorous	13.52 \pm 1.91	33.97 \pm 6.27	This study	86.1

1. Rezende et al (2001), 2. Sabat et al (2004).

* Deviation (%) from expected BMR ($=7.2M_b^{0.653}$) from "standard" birds, (McNab 2009).

address possible effects of phylogeny on the diet–BMR relationship (Cheverud and Dow, 1985; Rohlf, 2001). To calculate phylogenetically independent data, the Independent Contrasts v2.18 programs were used. The adequacy of branch lengths for standardizing contrasts was tested through correlation analyses between standardized contrasts and the square root of the sum of branch lengths for all variables (see

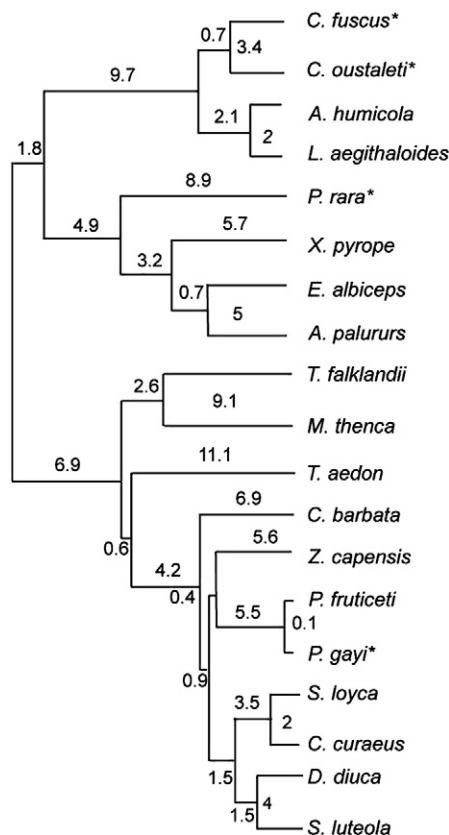


Fig. 1. Phylogenetic tree of passerine birds based on Sibley & Ahlquist (1990), used to obtain the phylogenetic independent contrast for basal metabolic rate (BMR) and percentage of plant material and invertebrate found in diet. Numbers represent the genetic distance between taxa according to DNA/DNA hybridization. Some branch lengths were chosen arbitrarily (see Materials and methods). Asterisks represent species that were not incorporated in the dietary nitrogen percentage tree.

Garland et al., 1992). The correlations were non-significant in all cases ($P>0.05$), finding that these branch lengths standardized the contrasts adequately. Because BMR was positively correlated with body mass (Fig. 2), we removed its effect calculating the residuals (thereafter mass-independent BMR) from least-squares linear regressions in both the conventional way and with phylogenetically independent contrasts (through the origin; see Garland et al., 1992). Data on BMR and body mass were log-transformed previous to analyzes. Finally, with the phylogenetic residuals obtained from the autocorrelation analysis we performed a Kruskal–Wallis Anova to test if dietary category affects the BMR.

Besides to the phylogenetic analyses we performed a Kruskal–Wallis Anova to test if diet affect the mass-independent-BMR. To do that we first computed the expected BMR values using the standard curve proposed by McNab (2009) – i.e. $BMR (mL O_2/h) = 7.2M_b^{0.653}$ – and then the observed/expected ratio was compared using dietary category as a factor. Finally, we performed a similar analysis using phylogenetic proximity (Family) as a factor. In this case we only used three categories (Emberizidae, Furnariidae and Tyrannidae), because the remainder Families had only one species. All statistical analyses were performed using the Statistica (StatSoft 2001) statistical package for Windows.

3. Results

BMR, M_b , percentage of dietary seed, insect and nitrogen exhibited significant phylogenetic signal (1000 randomizations, $P<0.001$ in all cases, Table 2). As expected, we observed a significant relationship between M_b and BMR (Fig. 2). The relationship was described by $BMR = 7.41M_b^{0.67 \pm 0.06}$ for the LSR ($r^2(LSR) = 0.91$, $P<0.05$) for 15 species. The analysis for the 19 species revealed that the relationship between body mass and BMR was described by $BMR = 7.56M_b^{0.67 \pm 0.06}$ for the LSR ($r^2(LSR) = 0.90$, $P<0.05$). The

Table 2Phylogenetic signal (K) and associated probability (P) of basal metabolic rate body mass, percent of dietary nitrogen, percent of plant material and percent of invertebrate for 15 and 19 species (denoted by asterisk).

	K	P	K^*	P^*
Basal metabolic rate	0.38	<0.01		
Body mass	0.61	<0.01	0.19	<0.01
% Dietary nitrogen	0.64	<0.01	0.21	<0.01
% Plants	0.99	<0.01	1.01	<0.01
% Invertebrates	1.06	<0.01	1.19	<0.01

results of phylogenetically independent contrasts were very similar to those of standard regression analysis. The model described by the PIC analysis was $BMR = M_b^{0.63}$ ($r^2(\text{PIC}) = 0.65$, $P < 0.05$) for 15 species and $BMR = M_b^{0.55}$ ($r^2(\text{PIC}) = 0.79$, $P < 0.05$) for 19 species.

There were no significant effects of the percentage of dietary nitrogen, invertebrates, or plants on mass-independent BMR using either conventional or phylogenetically corrected regressions (see Table 3, Fig. 3). Accordingly, the Kruskal–Wallis Anova on the mass-independent BMR values obtained from the phylogenetic autocorrelation method revealed that dietary category had no significant effect ($H_{(3,19)} = 0.65$, $P = 0.89$). The percentage of the deviation of expected BMR values according to the standard curve proposed by McNab (2009) are shown in Table 1. These results revealed that nearly all species have a higher than expected BMR (but see Rezende et al. 2002). Finally, the Kruskal–Wallis ANOVA on the mass-independent BMR values obtained from the McNab (2009) standard curve revealed that dietary categories had no effect on mass-independent BMR ($H_{(3,19)} = 0.89$, $P = 0.63$), but Family had a significant effect ($H_{(2, 12)} = 6.36$, $P = 0.041$). In this case, the multiple comparison test revealed that Tyrannids species had lower rates of mass-independent BMB than Furnarids species.

4. Discussion

Recently, McNab (2009) analyzed data on BMR for of 537 bird species, belonging from 26 Orders and spanning from 5 to 4000 g in body mass and 26 food habits, concluding that after the effect of body mass was removed, there was a significant effect of dietary habits on BMR. McNab (2009) 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 on fruit or vertebrates. In that study, the vast effect of behavior and life modes and M_b (almost three orders of magnitude of differences in mass), the climatic conditions (seasonal and geographic) among others ecological factors, along with methodological differences were statistically accounted for. Here we removed the effect of climate, seasonality, experimental differences and phylogeny using birds from the same area and season and measuring all specimens with a similar experimental setup. In addition, McNab study did not consider the ambiguity of dietary categories, which may confound the analysis. In this study we assessed the putative effect of and dietary preferences (i.e., percentage of nitrogen and animal prey in the gut) on BMR in recently capture birds. To the best of our knowledge, this is the first attempt to contrast the FHH in birds using a quantitative variable to characterize

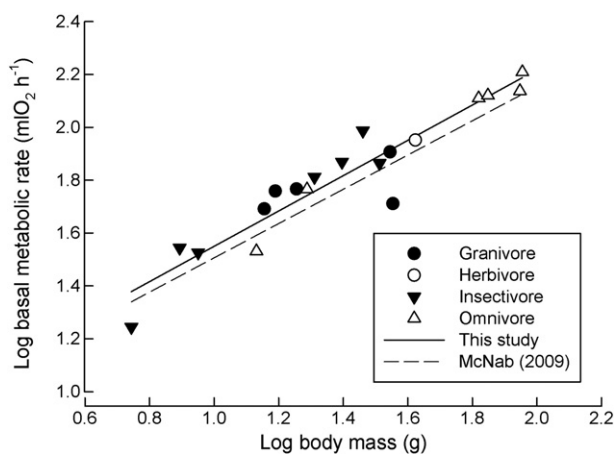


Fig. 2. Basal metabolic rate in freshly trapped birds as function of body mass in 19 species of passerines with contrasting dietary habits from central Chile.

Table 3

Correlations between mass-independent basal metabolic rate and dietary variables for 15 species of passerine birds. Results from the analysis including four additional species are denoted by asterisk.

	Contrast of mass-independent BMR		Mass-independent BMR	
	R	P	R	P
% Dietary nitrogen	-0.42	0.14	-0.05	0.87
% Plant	-0.12	0.70	0.01	0.96
% insect	0.12	0.67	-0.03	0.9
% Plant**	-0.18	0.47	-0.13	0.59
% insect**	0.20	0.44	0.13	0.59

dietary habits of bird species, and our results do not support the food habit hypothesis in passerines.

Specifically, the hypothesis posits that species or populations that exploit plant food are likely to evolve low mass-independent BMRs because plant material is poorly digestible, is more likely to have secondary compounds, and its availability in some cases may decay through the year (McNab, 1989; McNab, 2002; Cruz-Neto and Jones, 2005; 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. On the other hand, carnivore species might evolved higher rates of energy expenditure because animal prey are more digestible, without secondary compounds, and its availability may be less variable through the year (McNab, 1986, 1989). In this sense, the diet *per se* should be the variable affecting the rates of energy expenditure that in turns affect the BMR.

The use of quantitative variables as proxy of food habit is not new as a covariable in physiological studies (e.g., Shondube and Martinez Del Rio, 2004; Bozinovic et al., 2007). However, studies focusing on the effects of diet quality upon BMR at the intra and interspecific level in birds and mammals have revealed a mixed support for the hypothesis. Recently, we (Sabat et al., 2009) have examined the relationship between intraspecific BMR and diet among populations of the omnivorous passerine, *Zonotrichia capensis*, finding that after the effect of body mass and climate was accounted for, individuals at higher trophic levels exhibited lower values of BMR.

Why might intraspecific studies in passerine birds lead to different results than those achieved at the interspecific level? As pointed out by Cruz-Neto and Bozinovic (2004), the food-habit hypothesis, only took the effects of a reduction in intake and digestibility of dietary items, but has ignored the putative effect that the presence of

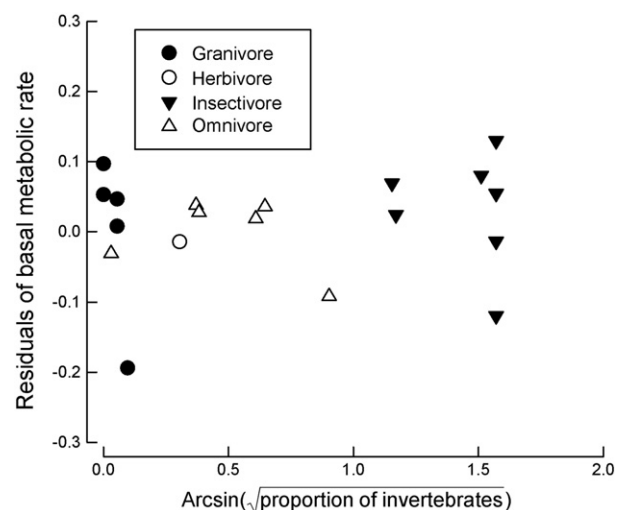


Fig. 3. Residuals of BMR against body mass as function of the proportion of invertebrate in their natural diet.

allelochemicals could exert on BMR. In this sense Cruz-Neto and Bozinovic (2004), suggested that the effect of the consumption of prey of vegetal origin might be different if measured on species that are evolutionarily committed to foods with high levels of secondary plant compounds (i.e., specialists) and in species that are forced to feed on such food by environmental constraints (i.e., generalists). We have found (Sabat et al., 2009) that the generalist *Z. capensis* consuming at lower trophic levels (and probably consuming more allelochemicals) had higher BMR than those sparrows consuming more animal prey. In this sense, the effect on the BMR may be a combined effect of the more digestible food (mainly seeds) and the higher BMR due to the effect of detoxification pathways of plant secondary compounds (Cork and Foley, 1991; Silva et al., 2004). At the interspecific level in this study, the absence of an effect of diet on BMR may be due to the differential evolutionary response to the natural diets, e.g., the presence of physiological mechanisms to detoxify the allelochemicals without a measurable increase in metabolic rate (Foley and McArthur, 1994). Also, as pointed out by Spicer and Gaston (1999), reported variations between species in physiological traits may result from methodological differences, allometric problems, species-specific or phylogenetic differences, and specific habitat conditions experienced by species and populations. The phylogenetic methods we used accounted for both allometric and phylogenetic differences, so these factors are not likely driving the results in the current study.

Nevertheless, our results contrast with that found by Muñoz-Garcia and Williams (2006) who found that among mammals of the order Carnivora the percentage of meat in the natural diet of species affected the BMR. Species that eat meat have also larger home ranges and higher BMR than species that eat vegetable matter. They proposed that higher metabolic rates would be related to higher levels of activity of animals having larger home range size. They called this hypothesis the “activity hypothesis” which states that the correlation between mass-independent BMR and diet would be a byproduct of the relationship between activity and diet. In this regard, the previous results in birds at the interspecific level that have demonstrated a correlation between levels BMR and diet, could be a consequence of different lifestyles associated to different dietary habits (McNab, 2003a,b, 2009), but not to differences in the quality of diet *per se*. In fact, as pointed out before, factors other than mass that have been suggested to influence mass-independent BMR have included – in addition to diet – climate, latitude, altitude, life-modes, existence on islands or continents, reproductive modes, and activity levels among others. Interestingly, many times these factors are frequently correlated with each other, so that their individual effects are difficult to delineate. (McNab, 1980, 1983, 1988, 2000; Lovegrove, 2000; Rezende et al., 2004; White et al., 2007). For example, Raichlen et al. (2010) demonstrated that among mammal species body composition explains differences in BMR after the body mass were accounted for. Consequently, the lack of significant correlation between diet and BMR among passerines in this study could be explained by comparable levels of activity, body size or body composition. Indeed, all species in this study were similar flying species with generally alike lifestyles and inhabiting similar habitat types.

4.1. Limitations of our study

The use of phylogenetically independent analyses has been profusely used in the last two decades in the attempt of inferring adaptation (Felsenstein 1985, Garland et al. 1992, Rezende et al. 2004). However, some authors have criticized the indiscriminate use of these methods. Among them, McNab (2003a, 2009) discussed two major problems with the phylogenetic analysis. The first one was related to the concept of independent character. McNab (2009) mentioned that if we only considered the evolution of a trait, then the species are non-independent, but if physiological rates are considered, the important issue is that such a physiological trait must match with the environmental conditions, in this case diet, to allow the survival,

irrespective if they were attained by ancestry or convergence. In this sense when a high colinearity exist between diet and phylogeny (see Cruz-Neto et al. 2001, 2003) it seems difficult to differentiate between phylogeny and diet as a predictor of physiology (e.g., BMR).

In our case, the comparisons between dietary categories using the residuals from phylogenetic autocorrelation analysis could be affected by colinearity between both factors. However, when non phylogenetically corrected data were analyzed some interesting patterns occur. For example the three Tyrannid flycatchers have slightly lower mass-independent BMR (see Table 1), which are in average 93% of the values expected from body mass, whereas species that feed on insects trapped from a surface, as our Furnarid species, have BMRs near 30% above the expected values. This difference may well reflect the unreliability of the capture of flying, as distinct from crawling, insects. Similar results have been reported for many bird species which depend on the capture of flying insects (see Dawson and Fisher 1969, Lasiewski et al. 1970, McNab and Bonaccorso, 1995). However, because our limited data do not allow generalizing beyond our species model, its variation must be considered as a hypothesis to be tested rather than a well-established pattern.

The second problem pointed out by McNab (2009) was related to the lack of complete and consensus cladograms. This is a major problem because the phylogenetic analysis assumes a well-known phylogeny (i.e. the topology as well as branch lengths must be known) which in most cases are unidentified or are subject of controversy. Regarding Sibley and Ahlquist (1990) phylogenetic hypothesis, some authors indicated that this cladogram is inaccurate (see Barker et al. 2004; Hackett et al., 2008). Unfortunately, to date no alternative phylogenetic hypothesis counting a significant number of our studied species is available, so our phylogenetic results should be taken with caution. In spite of that, the results of our LSR between diet quality and BMR revealed almost indistinguishable values, and then at least for this analysis, the results seem to indicate a lack of relationships between basal energy expenditure and dietary inclusion of insects and seeds.

Finally, the main assumption for the existence of a significant relationship between BMR and diet is that dietary quality affects the rates of consumption, digestion and absorption of energy and nutrients which in turn might affect the rates of energy intake. In our case we are confident that variations in insects and seeds consumption are probably related to differences in protein intake. However how other features and composition of the food, – e.g., digestibility (the presence of insect cuticles), presence of toxic compounds, along with the temporal variation of the availability of food, as in flying insects, or modifications of body composition in association with the means of food capture, are unknown. Besides, our model species do not represent the whole avian class. Indeed, our data set only represents the lower spectrum of body mass distribution in birds. In this sense, it is possible that the impact of food habits could depend mainly on body mass which is also associated to the high cost of the endothermy at small sizes as observed among Sigmodontine rodents (Bozinovic & Rosenmann 1988). Also, such effect could be higher among larger species, whereas at small masses, which imply lower total energy requirements, the effect of diet on BMR could be reduced. Thus, additional studies involving a more fine analysis of food composition along with the inclusion of a more representative group of birds could help the understanding of how different types of food affect the rates of energy expenditure in birds.

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