



Phenotypic flexibility in basal metabolic rate is associated with rainfall variability among populations of rufous-collared sparrow

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ABSTRACT

Phenotypic flexibility in metabolic rates allows organisms to reversibly adjust their energy flow to meet challenges imposed by a variable environment. In turn, the food habits hypothesis (FHH) predicts that species or populations adjust their basal metabolic rate (BMR) according to the diet attributes such as food abundance or predictability. Desert ecosystems represent a temporally heterogeneous environment because of low rain pulse predictability, which is also associated with temporal variation in food resources. In the present study, we investigated the relationship between the magnitude of BMR flexibility in response to dietary acclimation and the inter-annual rainfall variability in three populations of rufous-collared sparrows. Specifically we addressed the question of whether birds from a desert environment are more flexible in BMR than those from non-desert habitats. We found a positive trend between BMR flexibility and the inter-annual rainfall variability. In fact, dietary treatments had a significant effect only in desert birds, a result that also supported the FHH. Our study confirms the existence of phenotypic variation in response to environmental conditions among populations, and also highlights the importance of considering the circumstances in which phenotypic flexibility evolves and the specific environmental cues that induce their expression.

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1. Introduction

Metabolic rates set the pace of life, and the analysis of their plasticity in time and space is of vital importance for gaining insight about evolutionary and ecological theories (Kooijman, 2000; Brown et al., 2004). Metabolic rates in vertebrates are influenced by intrinsic factors such as body mass, phylogenetic relationships and activity levels; and ecological factors such as biotic and abiotic habitat conditions (McNab, 2002). Basal metabolic rate (BMR) represents the minimum rate of energy necessary to maintain homeostasis, and is the most widely measured energetic variable in endothermic vertebrates (McNab, 1992; Hulbert and Else, 2004; Speakman et al., 2004). Although the dependence of BMR on body mass has long been recognized (Kleiber, 1961), it is well known that

body mass alone does not fully explain variation in BMR (McNab, 1992).

There are several hypotheses that attempt to explain how biotic and abiotic conditions affect mass-independent BMR in vertebrates (McNab, 2002). One of the most comprehensive is the food habits hypothesis (FHH), which identifies three components of the diet that can produce variability in mass-independent BMR: food quality, food availability, and food predictability or productivity (Cruz-Neto and Bozinovic, 2004; Bozinovic et al., 2007). Specifically, the hypothesis predicts that species or populations that have to cope with diets of low energy content and/or low digestibility evolve low mass-independent BMRs (Cruz-Neto et al., 2001; McNab, 2002). Likewise, it is expected that during their lifetime organisms adjust their BMR according to diet attributes through reversible phenotypic changes in order to regulate their daily energy requirements (e.g., Veloso and Bozinovic, 1993; Cork, 1994; Fuglei and Øritsland, 1999). This phenotypic flexibility (sensu Piersma and Drent, 2003) in BMR is expected to be greater in individuals inhabiting variable environments (Schlichting and Pigliucci, 1998). In this regard, it has been argued that desert ecosystems are such variable environments, because of their low

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rain pulse predictability (Tieleman et al., 2003). In turn, primary productivity and hence food availability (seeds and arthropods) is directly associated with rainfalls (Phillipson, 1975; Del Grosso et al., 2008), above all in desert and semi-desert habitats (Yom-Tov and Geffen, 2006; Gutiérrez et al., 1993). Consequently, rainfall events in arid environments increase significantly the output of food, while dry years entail a shortage of resources (see Lima et al., 1999; Jaksic, 1998). These changes in the resource base can even influence the population dynamics (Meserve et al., 1995; Lima et al., 1999; Jaksic and Lazo, 1999). For instance, Jaksic and Lazo (1999) showed that rainfall events in arid environments increased bird species abundance, probably as a result of a rise in primary (vegetational resources) and secondary productivity (arthropod abundance), effects that may last even for six months after rains. In this context, a flexible BMR may be favorable if higher rates of energy processing are necessary in more rainy years. Thus, in accordance with the FHH, we predict that a reduction in the energy return from food will be associated with a decrease in mass-independent BMR and that the magnitude of this response (*i.e.*, physiological flexibility) will be larger in individuals from desert regions that deal with a greater inter-annual rainfall variability than those from mesic sites.

So far, there are few comparative studies attempting to evaluate the match between the magnitude of temporal heterogeneity and the amount of BMR flexibility (but see Tieleman et al., 2003; Cavieres and Sabat, 2008; Bozinovic et al., 2010). This makes it difficult to understand to what extent the degree of environmental variability influences the attributes of BMR reaction norms (McKechnie, 2008; Bozinovic and Sabat, 2010; McKechnie and Swanson, 2010). Consequently, here we examined the magnitude of BMR flexibility in response to dietary acclimation in three populations of rufous-collared sparrows from ecosystems that differ in their inter-annual rainfall variability. Specifically we addressed the question of whether birds from a desert environment are more flexible in BMR than birds from non-desert habitats. We also evaluated the effect of diet quality on the BMR of birds in order to test the predictions of the FHH. The FHH has been mostly tested in mammals, and the limited data used for evaluating its predictions in birds have shown uncertain results (*e.g.*, Geluso and Hayes, 1999; Bech et al., 2004; Piersma et al., 2004; Moe et al., 2005).

2. Materials and methods

2.1. Animals and study sites

The rufous-collared sparrow (*Zonotrichia capensis*) is distributed from southeast Mexico to Cabo de Hornos in southern South America (Goodall et al., 1951); in Chile, it inhabits both deserts and rain forests (Araya and Millie, 2005). *Z. capensis* is omnivorous, feeding on mixed diets based on seeds and insects (López-Calleja, 1995; Sabat et al., 1998). Moreover, it has been reported that the sparrow populations included in this study differ in their natural diets (Sabat et al., 2009; Maldonado et al., 2011).

Non-reproductive adult birds were captured with mist nets during the austral fall (April–June) in 2008. Birds were captured in three localities separated by more than 1800 km, which were chosen to reflect different levels of rainfall variability (see Fig. 1). The localities of capture were: Copiapó (27°18'S, 70°25'W; average annual rainfall = 11.2 mm; *n* = 20 animals), a typical desert scrubland; Quebrada de la Plata (33°31'S, 70°50'W; average annual rainfall = 337.2 mm; *n* = 16 animals), which is characterized by a Mediterranean climate; and Llanquihue (41°16'S, 73°00'W; average annual rainfall = 1971.2 mm, *n* = 17 animals), a southern cold-temperate forest. All study sites were rural areas.

In order to quantify rainfall heterogeneity, we calculated the coefficient of variation of annual rainfall using historical data

Table 1

Nutritional values of the experimental diets used in this study, as obtained from the literature (Jones et al., 1972; Abdel-Aal et al., 1997; Barker et al., 1998). All data are based on dry matter.

	Canary seeds	Mealworms
Proteins (%)	18.7	48.75
Crude fat (%)	8.7	31.1
Carbohydrates (%)	62.7	1.35
Fiber (%)	5.19	14.5 ^a
Ash (%)	2.1	4.3
Energy content (kcal)	21.2	27.4

^a Corresponds to neutral detergent fiber (NDF), a measure of dietary fiber that includes chitin (Barker et al., 1998).

from 1980 to 2008 from weather stations localized in the same geographic region as the study sites. These data were obtained from national meteorological institutes (Dirección Meteorológica de Chile and Dirección General de Aguas).

Following capture, birds were weighed (to the nearest 0.1 g) and then transported to the laboratory in Santiago, Chile (33°27'S, 70°42'W). They were kept in individual plastic-mesh cages (35 cm × 35 cm × 35 cm) and maintained at constant room temperature (22 ± 2 °C) and photoperiod (12L:12D). During a 1-day habituation period, sparrows were fed with mealworms (larvae of *Tenebrio molitor*), bird seeds and water *ad libitum*. After that, BMR was determined in order to obtain a pre-acclimation baseline (for specific procedures see Section 2.2 below). Once BMR measurements were completed, sparrows were weighed and randomly divided into two dietary treatments. One group was acclimated to an insect-based diet of mealworms and the second to a seed-based diet containing commercial bird seeds (*Phalaris canariensis*). Food and water enriched with a vitamin complex was provided *ad libitum* during an acclimation period of 7 weeks. We chose these diets in order to simulate the natural food types of the birds (López-Calleja, 1995). The insect-based diet represents a high protein and low carbohydrate diet while the seed-based diet represents a high carbohydrate and low protein diet (Table 1). After the acclimation period, measurements of oxygen consumption (BMR) were performed once again.

2.2. Basal metabolic rate

The rates of oxygen consumption were measured in post-absorptive resting birds during their inactive phase at a temperature of 30 °C, which is within the thermoneutral zone for this species (Sabat et al., 2006). The oxygen consumption was recorded in a computerized open-flow respirometry system (Sable Systems Int., Las Vegas, NV, USA). Birds were weighed using an electronic balance (to ±0.05 g) and placed in a dark metabolic chamber (1000 ml). The chamber was then placed in a controlled temperature cabinet (Sable Systems) at a constant temperature of 30 ± 0.5 °C. The metabolic chamber received dried air at 500 ml min⁻¹ provided by a gas pump located at the end of the system (*i.e.*, negative pressure) and controlled by a Sierra mass flow meter and controller (Sierra Instruments, Monterey, CA, USA). This flow ensured adequate mixing in the chamber. The mass flow meter was calibrated monthly with a volumetric (bubble) flow meter. The excurrent air passed through columns of Driedite, CO₂-absorbent granules of Baralyme, and Drierite before passing through an O₂-analyzer (model FC-10A; Sable Systems Int., Las Vegas, NV, USA). The open-flow respirometry system was calibrated with a known mix of oxygen (20%) and nitrogen (80%) certified by chromatography (INDURA, Chile). The measurement and calibration protocols followed Williams and Tieleman (2000).

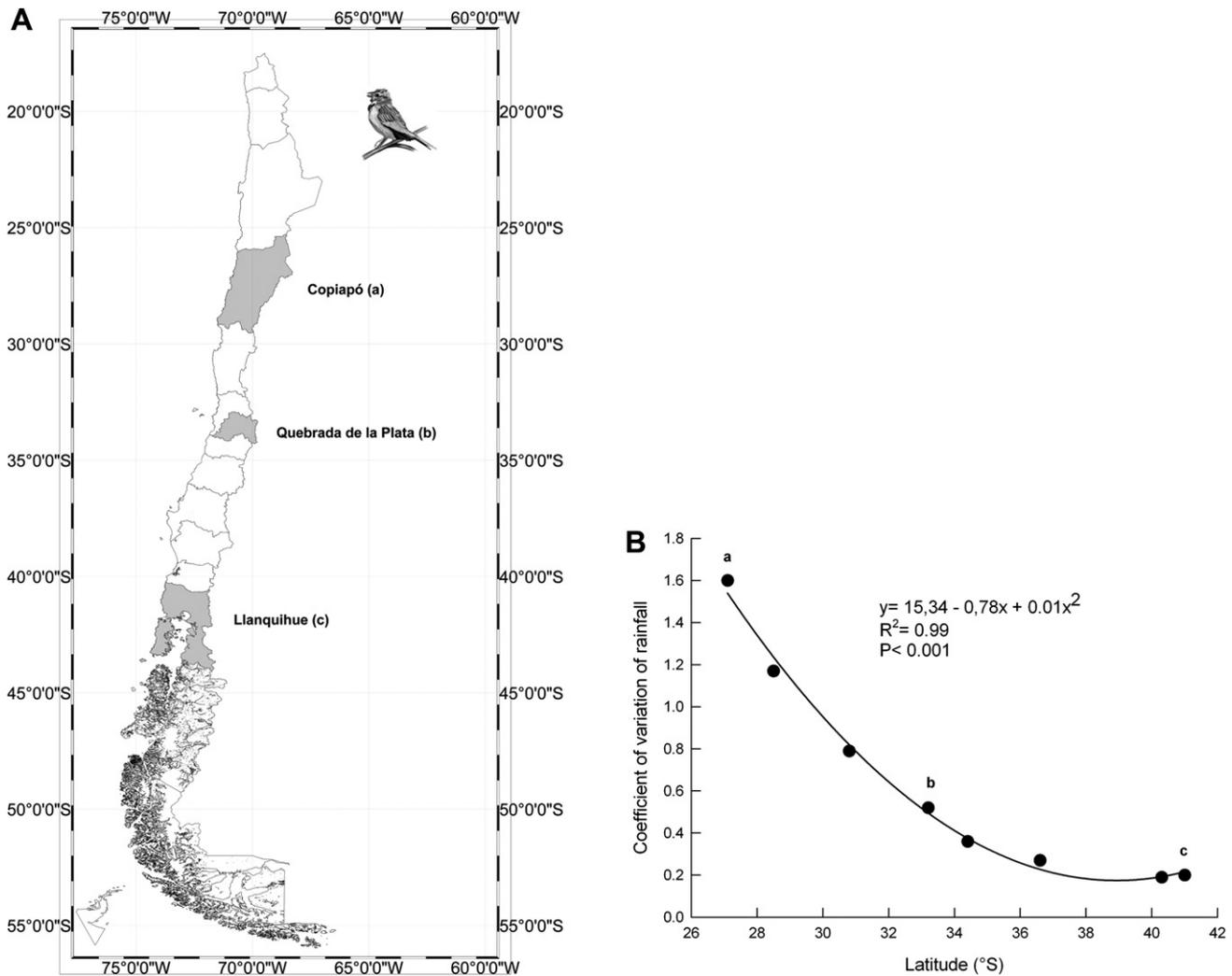


Fig. 1. (A) Geographic location of *Zonotrichia capensis* study sites. (B) Quadratic regression analysis between inter-annual rainfall variability and latitude in Chile. Letters a–c in the graph denote the *Z. capensis* study sites in (A).

Because CO₂ was removed before entering the O₂ analyzer, oxygen consumption was calculated according to Withers (1977):

$$VO_2 = \frac{FR \times 60 \times (F_iO_2 - F_eO_2)}{1 - F_iO_2},$$

where FR is the flow rate in ml min⁻¹, and F_i and F_e are the fractional concentrations of O₂ entering and leaving the metabolic chamber, respectively. Output from the oxygen analyzers (%) was digitized using Universal Interface II (Sable Systems) and recorded on a personal computer using the data acquisition software ExpeData (Sable Systems). Our sampling interval was 5 s. Birds remained in the chamber for at least 4 h, the time necessary to reach the steady state of these animals (Maldonado et al., 2009). We averaged O₂ concentration of the excurrent airstream over a 30 min period after steady state was reached. At the end of each measurement cloacal body temperature (T_b) was recorded with a copper-constantan thermocouple attached to a Digisense thermometer (Model 92800-15; Cole-Parmer Instrument Co., Vernon Hills, IL, USA) in order to corroborate that animals were euthermic after the metabolic trials (T_b = 40–42 °C).

2.3. Data analysis

To determine the relationship between inter-annual rainfall variability and latitude, we performed a regression analysis using

data of annual rainfall from 1980 to 2008 from weather stations located at altitudes that range between 80 and 512 m above sea level (Fig. 1).

Because metabolic rate is a power function of body mass (Kleiber, 1961; Lasiewski and Dawson, 1967), data were log₁₀ transformed before statistical analysis. To test differences in the BMR obtained in the pre-acclimation measurements, we performed an ANCOVA analysis using body mass as covariate. For the effect of diet acclimation and locality of origin on BMR of birds, a factorial ANCOVA was performed. In this analysis we used locality of origin and diet as factors, BMR as the dependent variable and body mass as covariate. We then used the Fisher *a posteriori* test for multiple comparisons. The effect of diet acclimation, *i.e.*, the magnitude of the BMR flexibility, was compared among populations through *a posteriori* estimation of the standardized effect size (SES). SES was estimated using the unbiased estimator of Hedges' *g* and its asymptotic standard error (Kline, 2004; Kampenes et al., 2007). The overlap level among asymptotic standard errors of populations was used to contrast the magnitude of digestive flexibility (Bozinovic et al., 2010).

Prior to all statistical analyses, data were tested for normality and homogeneity of variance using the Kolmogorov–Smirnov and Levene tests, respectively. The data analyses were performed using Statistica 7.0 (Statsoft Inc., Tulsa, OK, USA).

3. Results

We found no significant effect of locality of origin on BMR in the pre-acclimation period (ANCOVA: $F_{2,49} = 2.11$, $P = 0.13$). After acclimation, a factorial ANCOVA showed a significant effect of the interaction between locality and diet on birds' BMR (factorial ANCOVA: $F_{2,46} = 5.94$, $P = 0.005$; Fig. 2), but separately, neither diet nor locality significantly affected BMR (factorial ANCOVA: diet: $F_{1,46} = 0.79$, $P = 0.38$; locality: $F_{2,40} = 0.45$, $P = 0.64$). The *a posteriori* analysis revealed that only desert-dwelling birds changed their BMR in response to diet (*a posteriori* Fisher test: $P = 0.007$; Fig. 2). The desert group acclimated to an insect-based diet had a 15% lower BMR than the group acclimated to a seed-based diet (Fig. 2), whose BMR did not differ from the pre-acclimation BMR (ANCOVA, $F_{1,13} = 0.08$, $P = 0.77$). Consequently, birds from the desert site, which is characterized by a higher inter-annual variability in rainfall (Fig. 1), showed the highest flexibility in BMR (SES), followed by birds from the Mediterranean and cold-temperate environments (Fig. 3).

4. Discussion

The study of phenotypic flexibility has been a central issue in ecological and evolutionary physiology since it is recognized as an important component of the adaptive repertoire of animals inhabiting temporally heterogeneous environments (Scheiner, 1993; Schlichting and Pigliucci, 1998). This is well exemplified by desert-dwelling vertebrates, which besides dealing with the problem of water supply are faced with temporal shortages of food resources (Williams and Tieleman, 2005; Tirado et al., 2008). In the present study, diet acclimation experiments were performed in order to evaluate the effect of inter-annual rainfall variability on the magnitude of BMR flexibility. We found a positive association between BMR flexibility and the inter-annual variability in rainfall (Fig. 3). Moreover, the dietary treatments had a significant effect on desert birds' BMR, whereas neither sparrows from the Mediterranean nor the cold-temperate ecosystem showed differences between diet treatments (Fig. 2).

Desert-dwelling birds had a BMR at 102.5% (seed-based diet) and 96.9% (insect-based diet) of the value expected from the avian allometric equation proposed by Tieleman and Williams (2000). Although BMR in birds feeding on a seed-based diet was higher than in those with an insect based-diet, it did not differ from the pre-acclimation BMR. These results suggest that after seven weeks of dietary acclimation, the desert sparrows decreased their BMR in response to an insect-based diet. In addition, the variation around \log_{10} BMR vs. \log_{10} body mass regressions for the two diets appears to be smaller for the desert population, which suggests that the BMR is more tightly constrained in those birds. This fact could also support the FHH in that BMR more closely matches diet resources in the desert population than in the Mediterranean and cold-temperate sites.

In response to dietary changes, animals may adjust their digestive tract characteristics (e.g., intestine mass/length, digestive enzymes and organ mass; Karasov, 1996; Karasov and Hume, 1997; Sabat et al., 1998) or their metabolic expenditure in order to maintain the energy balance. In this regard, *Z. capensis* from different environments have been shown to vary in their ability to modify their digestive tract characteristics in response to diet. Indeed, sparrows from Mediterranean and cold-temperate environments have shown digestive tract flexibility in response to the same dietary treatments as used in the present study, i.e., seed and insects, but desert birds did not (Maldonado et al., 2011). Thus, we argue that the BMR reduction in desert birds is mediated by the differences in seed and insect digestibility. It has been reported that

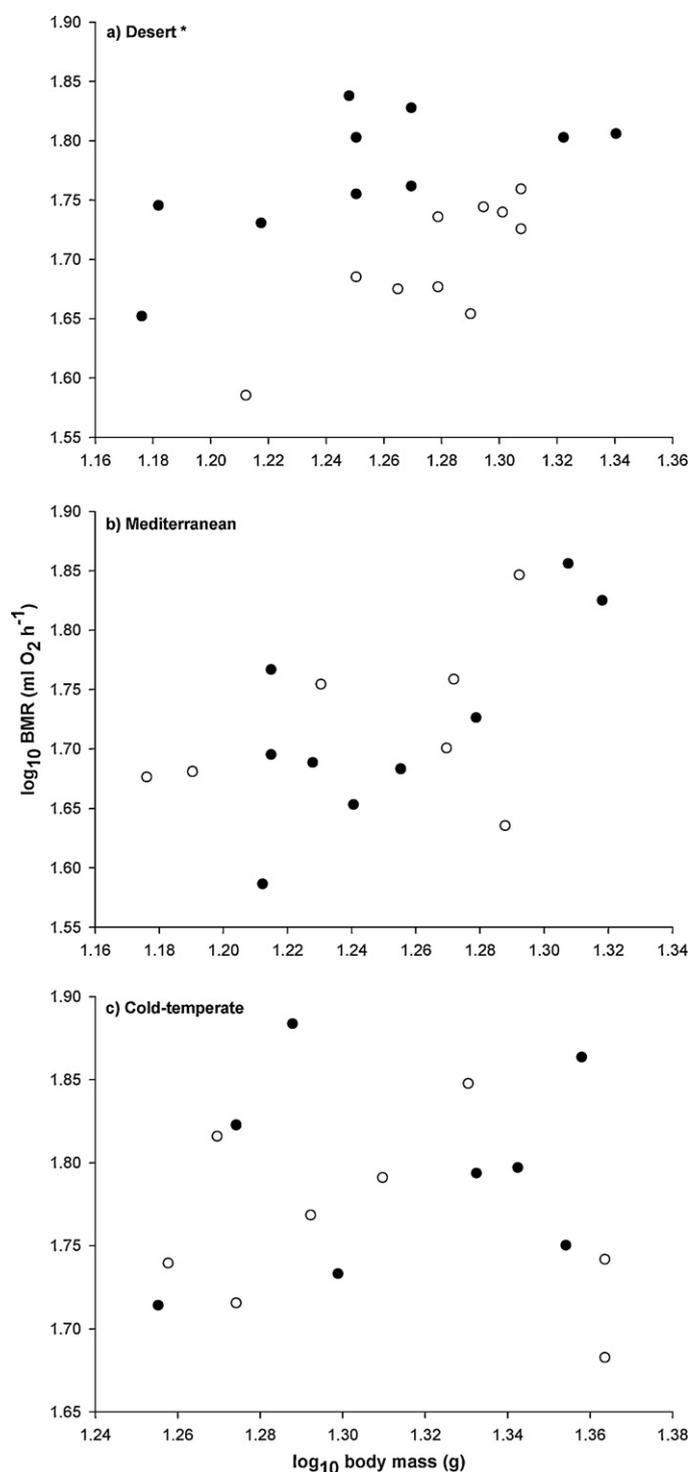


Fig. 2. Basal metabolic rate as a function of body mass for *Zonotrichia capensis* individuals from (A) desert environments, (B) Mediterranean environments, and (C) cold-temperate environments. Filled circles indicate birds acclimated to a seed-based diet and unfilled circles represent those acclimated to an insect-based diet. The asterisk in (A) denotes significant differences between diets revealed by a factorial ANCOVA analysis ($P < 0.05$).

seed digestibility by passerines is about 75%, and in *Z. capensis* reaches values of almost 80% (Novoa et al., 1996). Moreover, in this species assimilation efficiency experiments have shown that seed (*P. canariensis*) digestibility is higher in comparison to insect (*T. molitor*) digestibility (Novoa et al., 1996). Similarly, Sabat et al. (2009) found that freshly caught *Z. capensis* from higher trophic

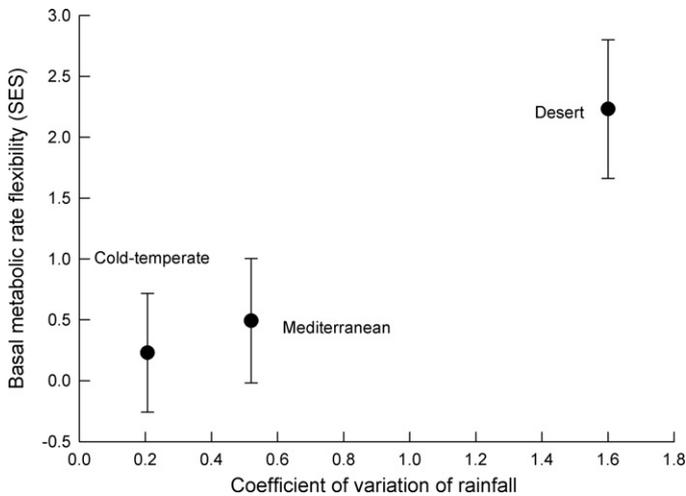


Fig. 3. Effect of dietary acclimation on basal metabolic rate among three populations of *Zonotrichia capensis* along a latitudinal gradient in Chile. The standardized effect size (SES) or magnitude of BMR flexibility is indicated as a function of the coefficient of variation of rainfall. Error bars represent the asymptotic standard error calculated for the effect size.

levels (i.e., birds that prey on invertebrates) exhibited lower BMRs than those at lower trophic levels. It is possible that insects represent a low-quality diet for *Z. capensis* from desert environments that lead to the observed BMR reduction. In addition, our results for the desert population are consistent with the FHH, which predicts a decrease in BMR when animals deal with nutritional bottlenecks or low-quality diets (McNab, 1986, 1988; Cruz-Neto and Bozinovic, 2004; Veloso and Bozinovic, 1993).

Does the inter-annual variability in rainfall explain differences in BMR flexibility? Tieleman et al. (2003) proposed that desert birds have greater BMR flexibility in comparison to those from mesic areas. This hypothesis is based on the fact that birds have evolved in sites in which rainfall pulses and thus resource abundance vary notably. Nevertheless, in some lark species this hypothesis was not supported by thermal acclimation experiments (Tieleman et al., 2003). We argue that since rainfall variability causes differences in resource abundance, changes in diet may act as a better environmental cue than temperature in order to predict the relationship between BMR flexibility and rainfall variability. The present study showed the expected pattern: desert dwelling birds, which experience the largest inter-annual variability in rainfall, showed the greatest BMR flexibility in response to dietary acclimation.

The high rainfall variability in the Atacama Desert has been associated with the El Niño Southern Oscillations (ENSO). According to the Southern Oscillation Index and following Jaksic (2001), relevant ENSO events have occurred at least nine times in the 28 years of data recording considered in the present study. “El Niño” is caused by coastal waters warming up during the winter months, thereby breaking down thermal inversion and allowing the intrusion of moist Pacific air masses (Aceituno, 1992; Trenberth, 1997). Thus, in Chile “El Niño” is correlated with an increase in rainfall (Aceituno and Montecinos, 1993; Ortlieb, 1994; Lima et al., 1999). The ecological effects of ENSO on terrestrial ecosystems of western South America are intense (Jaksic, 2001; Meserve et al., 2003). Indeed, “El Niño” episodes dramatically enhance primary productivity in arid regions (Armesto et al., 1993; Holmgren et al., 2006; Squeo et al., 2006), in which the seed bank has been shown to increase up to six-fold (Gutiérrez et al., 1993, 2000). These changes in environmental conditions have shown to influence ecological processes and patterns, both at population (Lima et al., 1999, 2002) and community levels (Meserve et al., 1995, 2003; Jaksic, 2001). Accordingly, food availability for desert animals in general and for rufous-collared

sparrows in particular may change dramatically according to the presence/absence of “El Niño”.

The environmental variation experienced by animals must have some degree of predictability to favor the evolution and maintenance of phenotypic flexibility (Scheiner, 1993). In this vein, an ENSO event has been considered a quasi-periodic phenomenon, with a return period of about 3.3 years (Houston, 2006). Consequently, desert sparrows which have a lifetime of about 6–9 years (Egli, 1995; Lindstedt and Calder, 1981) will experience during their lifetime both non-rainy years of low food availability, a condition that favors a reduction in BMR, and more rainy years, in which a higher BMR may be favorable in order to deal with higher daily energy requirements.

The fact that only the desert population of *Z. capensis* exhibited BMR flexibility in response to dietary acclimation was a surprising result. Cavieres and Sabat (2008) showed a positive relationship between climatic heterogeneity and BMR flexibility in response to environmental temperatures in three populations of *Z. capensis*. They found that sparrows inhabiting desert ecosystems showed an inflexible BMR reaction norm, whereas birds from the Mediterranean ecosystem showed the highest BMR variation after acclimation to different temperatures. Here we found that BMR is not an inflexible trait in birds from the desert ecosystem; however, its flexibility is in response to differences in diet quality rather than environmental temperature. Together, these results highlight the importance of considering the circumstances in which phenotypic flexibility evolves (de Jong, 1995; Pigliucci, 2005) and the specific environmental cues that induce their expression (Kingsolver and Huey, 1998). Nevertheless, a note of caution is necessary, since there is always a problem concerning the inability to control for developmental and parental effects on BMR. In essence, there is no way of controlling for these effects other than making the measurements in F1 generation animals that were raised under identical conditions and were swapped randomly between parents as eggs. In spite of this, we have shown that a large physiological diversity in receptiveness to different environmental conditions is observed between individuals from different populations, thus providing insights into the evolution of proximal metabolic capacities and flexibility.

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