Geographic Variation in the Association between Exploratory Behavior and Physiology in Rufous-Collared Sparrows[*]

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ABSTRACT

Increasing research has attempted to clarify the links between animal personality and physiology. However, the mechanisms driving this association remain largely unknown, and knowledge of how ecological factors may affect its direction and strength is scant. In this study, we quantified variation in the association between exploratory behavior, basal metabolic rate (BMR), and total evaporative water loss (TEWL) in rufous-collared sparrows (*Zonotrichia capensis*) inhabiting desert, Mediterranean, and cold-temperate climates. We found that the exploratory behavior score was highest in birds from the cold-temperate site, which was characterized by a moderate level of ecological variability (seasonality). Moreover, the association between exploratory behavior and physiological variables differed among localities. Only birds from the Mediterranean site showed a positive correlation between exploratory behavior and BMR. We found no association between exploration and TEWL at any study site. Our findings suggest that differences in the ecological conditions experienced by each sparrow population result in a particular combination of behavioral and physio-

logical traits. An understanding of this intraspecific variation along ecological gradients provides unique insights into how specific ecological conditions affect the coupling of behavioral and physiological traits and the mechanisms underlying that relationship.

Introduction

It has become clear that differences in behavior among individuals are not random. Instead, consistent interindividual behavioral variation, known as animal personality, may reveal important biological information (Sih et al. 2004; Bell 2007; Careau et al. 2008). In a physiological context, personalities have been linked to energy metabolism rates (Careau et al. 2008; Biro and Stamps 2010). From a theoretical perspective, two models have been proposed to explain the relationship between basal metabolic rate (BMR)—the minimum energy necessary to maintain the homeostasis in endotherms—and activity level or behavior (Levins 1968; Speakman 1997; Careau et al. 2008; Biro and Stamps 2010). First, the performance model assumes that the BMR reflects the total energy available to an individual, such that a higher BMR allows individuals to expend more energy on different behaviors. In contrast, the allocation model predicts that animals should allocate a fixed amount of energy between competing processes (i.e., between BMR and behavior), and thus a negative association between BMR and behavior is expected (Levins 1968; Speakman 1997; Careau et al. 2008; Biro and Stamps 2010). The performance model has received the most empirical support to date (for a review, see Biro and Stamps 2010), but past studies have focused mainly on aggressive behavior and success in competitive interactions (e.g., dominance status). To gain a more comprehensive understanding of the mechanisms driving the relationship between behavior and physiology, studies focusing on other behaviors are therefore clearly required.

An important component of animal personality is exploratory behavior, which allows an organism to acquire information about its surrounding environment (Dingemanse et al. 2002; Careau et al. 2009). In birds, exploratory behavior is often positively correlated with boldness toward novel objects and with risk-taking behavior and aggressiveness (Verbeek et al. 1994, 1996; van Oers et al. 2004; Groothuis and Carere 2005) and is related to a proactive copying style (sensu Koolhaas et al. 1999). Due to these characteristics, a link between energetic physiology and exploratory behavior may be expected, although this idea has received little empirical attention (but see Careau

et al. 2009). On the other hand, despite recent efforts to characterize the relationship between behavior, physiological traits, and ecological factors (e.g., Careau et al. 2009), a consensus on the direction and strength of these associations has yet to emerge (Réale et al. 2010). Exploratory behavior and BMR may be adaptive, heritable (e.g., Dingemanse et al. 2002; Nilsson et al. 2009), and specific to some bird populations (e.g., Cavieres and Sabat 2008; van Dongen et al. 2010). Given these findings, it may be expected that ecological conditions may also affect the evolution of particular combinations of behavior and physiological traits (see Réale et al. 2010).

In this study, we examined variation in the association between exploratory behavior and physiology in rufous-collared sparrows (*Zonotrichia capensis*) along a latitudinal gradient of precipitation, temperature, and primary productivity in Chile. In addition to BMR, we also examined total evaporative water loss (TEWL), which is another physiological trait considered of vital importance in passerine species (Williams 1996, 1999; Wolf and Walsberg 1996; Tieleman and Williams 2002; Sabat et al. 2006). Passerine birds are characterized by diurnal habits, high mass-specific metabolic rates, and high body temperatures, which result in high rates of water flux (Williams 1996). Because it is assumed that higher activity levels would result in higher rates of evaporative water loss, we hypothesized that animals that better resist dehydration conditions (lower TEWL) could spend more time exploring their surroundings, which results in a negative association between exploratory behavior and TEWL.

Material and Methods

Studies Species and Study Sites

Rufous-collared sparrows were collected from three Chilean localities—Copiapó, Quebrada de la Plata, and Llanquihue. Copiapó (27°18′S, 70°25′W) is situated in the Atacama Desert, with mean temperature 15.2°C, maximum mean temperature 23.9°C, and total annual precipitation 12 mm (di Castri and Hajek 1976; http://www.meteochile.cl). Quebrada de la Plata (33°31′S, 70°50′W) has a typical Mediterranean climate, with mean temperature 14.4°C, maximum mean temperature 22.5°C, and total annual precipitation 312.5 mm (di Castri and Hajek 1976; http://www.meteochile.cl/). In sharp contrast, Llanquihue (41°16′S, 73°00′W), the southernmost study site, has a cold-temperate climate, with mean annual temperature 9.4°C, maximum mean temperature 13.6°C, and total annual precipitation 3,112 mm (Centro de Informacion de Recursos Naturales, Chile). The three sites cover a latitudinal range of more than 1,800 km. Moreover, a large north-south increase in primary productivity exists (estimated from the Martone aridity index) from Copiapó through Quebrada de la Plata and Llanquihue (see van Dongen et al. 2010). Finally, regarding both rainfall and the natural diet of *Zonotrichia capensis* (measured by isotopes stables, $\delta^{15}N$), the Mediterranean site has been shown to be the most variable across seasons, followed by the cold-temperate and desert study sites (Maldonado et al. 2011).

Nonreproductive adult birds were captured with mist nets from the three study sites and housed under laboratory conditions at a constant temperature of $22° \pm 2°C$ and photoperiod of 12L : 12D at the Facultad de Ciencias, Universidad de Chile in Santiago. The sparrows were housed together in plastic mesh cages measuring 100 cm × 100 cm × 100 cm (up to four individuals per cage) and provided with seed, mealworms, and water ad lib.

Metabolism and Total Evaporative Water Loss

Measurements of BMR and TEWL were made in postabsorptive, resting birds between 2100 and 0300 hours, using standard flow-through respirometry and hygrometry methods. Birds were weighed using an electronic balance (± 0.05 g) and then placed in a 1,000-mL metabolic chamber. The metabolic chamber was positioned in a controlled temperature cabinet (Sable Systems, Las Vegas, NV) at a constant temperature of $30° \pm 0.5°C$, within the thermoneutral zone of *Z. capensis* (see Sabat et al. 2006). External air (500 mL min^{-1}) was drawn into the metabolic chamber by negative pressure created by a downstream vacuum pump controlled by a Sierra mass flowmeter/controller (Sierra Instruments, Monterey, CA), which was calibrated monthly with a volumetric flowmeter. The flow rate we used ensured adequate mixing of air relative to chamber volume. Before arriving in the chamber, the air was dried using Drierite desiccant and passed through Bev-A-Line tubing (Thermoplastic Processes) toward an RH-200 relative humidity/dew point hygrometer (Sable Systems), which allowed us to ensure that the pressure of water vapor was low in the incurrent air (<0.05 kPa). The excurrent air from the metabolic chamber passed through the RH-200 hygrometer and through columns of Drierite, Baralyme, and Drierite to remove all water vapor and CO_2 gas before being passed through the O_2 analyzer (model FC-10A, Sable Systems). The open-flow respirometry system was calibrated with a known mixture of oxygen (20%) and nitrogen (80%) that was certified by chromatography (INDURA, Chile). The measurement and calibration protocols followed Williams and Tieleman (2000). Because CO_2 was scrubbed before entering the O_2 analyzer, oxygen consumption was calculated according to Withers (1977, p. 122): $\dot{V}O_2 = [FR \times 60 \times (F_{i_{O_2}} - F_{e_{O_2}})]/(1 - F_{i_{O_2}})$, where FR is the flow rate (mL min^{-1}) and F_i and F_e are the fractional concentrations of O_2 entering and leaving the metabolic chamber, respectively.

TEWL (mg mL^{-1}) was calculated as TEWL $= (V_e \rho_{out} - V_i \rho_{in})$, where ρ_{in} and ρ_{out} are the absolute humidity (kg m^{-3}) of the inlet air and the outlet air, respectively. V_i is the flow rate of the air entering the chamber as given by the mass flow controller (500 mL min^{-1}), and V_e is the flow of exiting air. V_e was calculated following Williams and Tieleman (2000) as $V_e = V_i - [\dot{V}O_2(1 - RQ)] + \dot{V}H_2O$; V_i and $\dot{V}O_2$ (mL min^{-1}) are known. We assumed a respiratory quotient (RQ) of 0.71. Absolute humidity was calculated as $\rho = P/(T \times Rw)$, where P is the water vapor pressure of the air (Pa), T is the temperature of the dew point hygrometer (K), and Rw is the gas constant for water vapor (461.5 J kg^{-1} K^{-1}; Lide 2001). The P to calculate ρ_{in} was determined using the average value of the vapor pressure

Table 1: Exploratory behavior and physiological features of *Zonotrichia capensis* from desert, Mediterranean, and cold-temperate climates

	Desert (*n* = 19)		Mediterranean (*n* = 19)		Cold-temperate (*n* = 24)	
Exploratory behavior	.68 $\pm$	.40[A]	.85 $\pm$	.43[A]	2.87 $\pm$	4.94[A]
Body mass (g)	17.95 $\pm$	1.03[A]	17.72 $\pm$	1.31[A]	19.65 $\pm$	2.04[B]
BMR (mL O$_2$ h^{-1})	53.78 $\pm$	5.37[A]	49.45 $\pm$	7.9[A]	56.59 $\pm$	11.48[A]
TEWL (mg h^{-1})	67.19 $\pm$	16.13[A]	73.12 $\pm$	25.61[A]	103.97 $\pm$	38.45[B]

Note. BMR, basal metabolic rate; TEWL, total evaporative water loss; *n*, number of animals. Different letters denote significant differences ($P < 0.05$) between locations. Data are reported as means $\pm$ SD.

of the air entering the empty chamber before and after each experiment (i.e., the baseline period of 15 min). In order to confirm that animals were euthermic after the metabolic trials ($T_b = 40°$–$42°C$), we recorded their cloacal body temperature (T_b) with a Cole Palmer 24-gauge copper-constantan thermocouple attached to a Digisense thermometer (model 92800-15). Output from both H$_2$O (kPa) and oxygen (%) analyzers were digitized using a Universal Interface II (Sable Systems) and recorded on a personal computer using data acquisition software (EXPEDATA, Sable Systems). Our sampling interval was 5 s. Birds remained in the chamber for at least 6 h, the time necessary to reach the steady state of these animals (Maldonado et al. 2009). We averaged water vapor pressure and O$_2$ concentration of the excurrent air stream over an entire record period of 30 min after the steady state was reached (following Tieleman et al. 2002).

Exploratory Behavior

Exploratory behavior in rufous-collared sparrow populations appears to be a complex, multicomponent behavior (van Dongen et al. 2010). Exploration diversity, measured via Shannon's diversity index, has been considered a reliable indicator of true exploratory tendency in this species because an individual in an unknown environment would benefit from exploring a greater diversity of areas rather than exploring only a subset of the available area (van Dongen et al. 2010). In order to quantify the exploratory diversity, after physiological measurements, individuals were placed in a large cage (270 cm [length] × 150 cm [width] × 150 cm [height]) constructed of PVC poles and semitransparent black shading cloth. Five wooden perches (80 cm long, 2 cm in diameter) were hung throughout the cage at varying heights (between 50 and 110 cm above ground). One perch was placed diagonally in the opposite corner at each far end of the cage, and the remaining three were spaced at regular intervals (70 cm apart) along the long axis of the cage. The cage was placed in a fixed position within the laboratory. Before each trial, the subject was placed in a small holding cage (30 cm [length] × 25 cm [width] × 39 cm [height]) in a corner of the experimental cage and covered with a cloth during a 5-min habituation period. Each experimental trial lasted 10 min. At the beginning of the experimental period, the cloth was removed and the door of the holding cage was opened. An observer, hidden from view but with full sight of the cage, dictated the number and destination of all movements (flights and hops) by the subjects onto a digital voice recorder. Movement destinations included both the perches and the walls of the cage. We also distinguished between cases where the birds landed on the front and back ends of the two side walls. This resulted in 11 areas of the cage where the birds regularly perched (five wooden perches and six wall regions). At the termination of each trial, sparrows were recaptured within the cage using a butterfly net and returned to the housing. Exploration diversity was quantified via the Shannon's diversity index, via $H = -\sum \rho_l \ln \rho_i$, where ρ_i represents the total number of times perch *i* was visited, expressed as a proportion of the total number of perch visits throughout the trial. Individuals were assumed to be more thorough explorers when they visited a higher diversity of perches during the trial.

Data Analysis

All data were tested for normality and homoscedasticity via the Shapiro-Wilk test and Levene's test, respectively. To test the effect of location of origin on dependent variables (i.e., BMR, TEWL, and exploratory behavior), we used ANOVA or ANCOVA using body mass (M_b) as a covariate when the data were correlated with M_b. A posteriori Tukey's tests were performed for pairwise comparisons. Because exploratory behavior did not meet the assumptions of normality for some populations, even after $\ln(x + 1)$ transformations, P values were obtained from bootstrap randomizations (10,000 iterations) using the statistical software BioEstat 5.0 (Ayres et al. 2007). In both cases, the null hypothesis was rejected when $P \leq 0.05$. In addition, Pearson correlation coefficients were calculated, and linear regression analyses (LRA) were used to test for associations between variables. The analyses were carried out using STATISTICA 7.0 (StatSoft, 2004).

Results

We found significant variation in M_b among populations. M_b for birds from the cold-temperate region was significantly higher than that for sparrows from both Mediterranean and desert study sites (ANOVA; $F_{2,59} = 9.9$, $P < 0.001$; table 1). An

analysis of the pooled data indicated that BMR values were positively correlated with M_b ($r^2 = 0.45$, $P < 0.001$). An ANCOVA analysis using M_b as a covariate revealed that BMR did not differ among localities ($F_{2,58} = 1.6$, $P = 0.2$; table 1). In contrast, TEWL did not correlate with M_b ($r^2 = 0.01$, $P = 0.3$) but differed significantly among populations (ANOVA; $F_{2,59} = 10$, $P < 0.001$; table 1). TEWL values were higher in birds from the cold-temperate site in comparison to the desert and Mediterranean populations, even when using M_b as a covariate (ANCOVA; M_b: $F_{2,58} = 10.3$, $P < 0.001$). For exploratory behavior, birds from the cold-temperate site showed the highest exploration scores, although differences among groups were marginally insignificant (bootstrap; $P = 0.053$; table 1).

We also tested for within-population relationships between exploratory behavior, M_b, and physiological variables (TEWL and BMR). Sparrows from the Mediterranean study site displayed a significant positive relationship between exploratory behavior and BMR (LRA; $r^2 = 0.22$, $P = 0.04$; fig. 1). In contrast, exploratory behavior did not correlate with M_b (LRA; $r^2 = 0.17$, $P = 0.08$) or TEWL (LRA; $r^2 = 0.2$, $P = 0.054$) in this study site. This marginally insignificant correlation between exploratory behavior and TEWL disappears when considering the effect of BMR on TEWL (LRA between residuals of TEWL vs. BMR and exploratory behavior; $r^2 = 0.07$, $P = 0.25$). In addition, exploratory behavior was not significantly correlated with M_b or with BMR and TEWL in birds from the desert (LRA; M_b: $r^2 = 0.03$, $P = 0.5$; BMR: $r^2 = 0.17$, $P = 0.14$; TEWL: $r^2 = 0.02$, $P = 0.55$; fig. 1) and cold-temperate (bootstrapping Pearson correlations; M_b: $r^2 = 0.05$, $P = 0.15$; BMR: $r^2 = 0.09$, $P = 0.09$; TEWL: $r^2 = 0.02$, $P = 0.28$; fig. 1) populations.

Discussion

It is well known that interpopulation variation exists in both behavioral and physiological traits (e.g., Foster 1999; Bell 2005; Cavieres and Sabat 2008; Bozinovic et al. 2009; Quispe et al. 2009; van Dongen et al. 2010). However, the possibility that ecological conditions may affect the degree of association between behavior and physiology has been largely ignored. Our findings suggest that differences in the environmental conditions can lead to particular combinations of behavioral and physiological traits in *Zonotrichia capensis*.

To understand the function of exploration in animals, knowledge of the information value and payoffs of this behavior is required. Mettke-Hofmann et al. (2002) argued that, in a completely stable environment, exploratory behavior would not be advantageous because there are no environmental changes requiring organisms to constantly acquire new information. Similarly, in extremely variable environments, the extremely rapid value loss of previously acquired information would result in individuals not properly acquiring information. Therefore, in only moderately variable environments would exploration behavior lead to a significant increase in knowledge (Winkler and Leisler 1999; Vásquez et al. 2006). In our study, the most eco-

logically variable site (in terms of seasonality) was the Mediterranean site, followed by the cold-temperate and the desert sites (Maldonado et al. 2011). In accordance with the Mettke-Hofmann et al. (2002) hypothesis, we found that subjects from the cold-temperate population with a moderate level of climatic variability showed the highest values of exploratory behavior (see table 1).

Previously, Careau et al. (2009) analyzed published data on exploratory behavior of muroid rodents that inhabit deserts and open steppes and agricultural lands. The authors found that rodent species from the desert zone had the highest exploration score, while hamsters that lived in open steppes and agricultural areas displayed the lowest exploration score. The authors argued that an important selection pressure may be food availability and predictability. Thus, alternatively to Mettke-Hofmann et al. (2002), they proposed that arid zones, characterized by unproductive and unpredictable environments, should favor higher exploration behavior in order to increase the possibility of finding resources pulses (Mueller and Diamond 2001; Careau et al. 2009). However, in our study, sparrows from the desert study site did not exhibit higher values of exploratory behavior. It is possible that in arid zones, highly exploratory birds could incur a greater amount of water loss, which, in environments where fresh water is scarce or unavailable, may be crucial for survival. This would be particularly true for diurnal animals, such as birds, in contrast to nocturnal animals, such as most rodent species (Schmidt-Nielsen 1964; Walsberg 2000). The importance of water budgets for desert sparrows is supported by the low TEWL values measured from the desert population (table 1). Lower TEWL has been proposed to be a physiological adjustment to deal with the high temperatures and low relative humidity of arid environments (Tieleman et al. 2002, 2003; Cavieres and Sabat 2008). Thus, we suggest that the variation observed in the exploratory response to ecological conditions among mammals and birds could also be a consequence of among-taxa physiological and behavioral differences.

Animal personality may be considered an important factor explaining a component of the interindividual variation in physiological measurements (Careau et al. 2008; Biro and Stamps 2010). Exploratory behavior in birds from the Mediterranean site was positively correlated with BMR (fig. 1). It has been suggested that high exploratory behavior is part of a proactive coping style that involves energetically costly behaviors (Sih et al. 2004; Careau et al. 2008, 2009). Thus, individuals with a higher BMR could more likely engage in energetically costly behaviors, such as exploration. Alternatively, more exploratory birds could have a higher BMR because of higher general levels of activity and subsequent higher maintenance costs. In both cases, the positive relationship found between BMR and exploratory levels in the Mediterranean sparrows was in accordance with the performance model.

The relationship between physiological and behavioral traits could be a consequence of correlational selection, genetic correlation, or a shared regulation pathway (e.g., hormonal regulation; Careau et al. 2008; Biro and Stamps 2010). If traits are
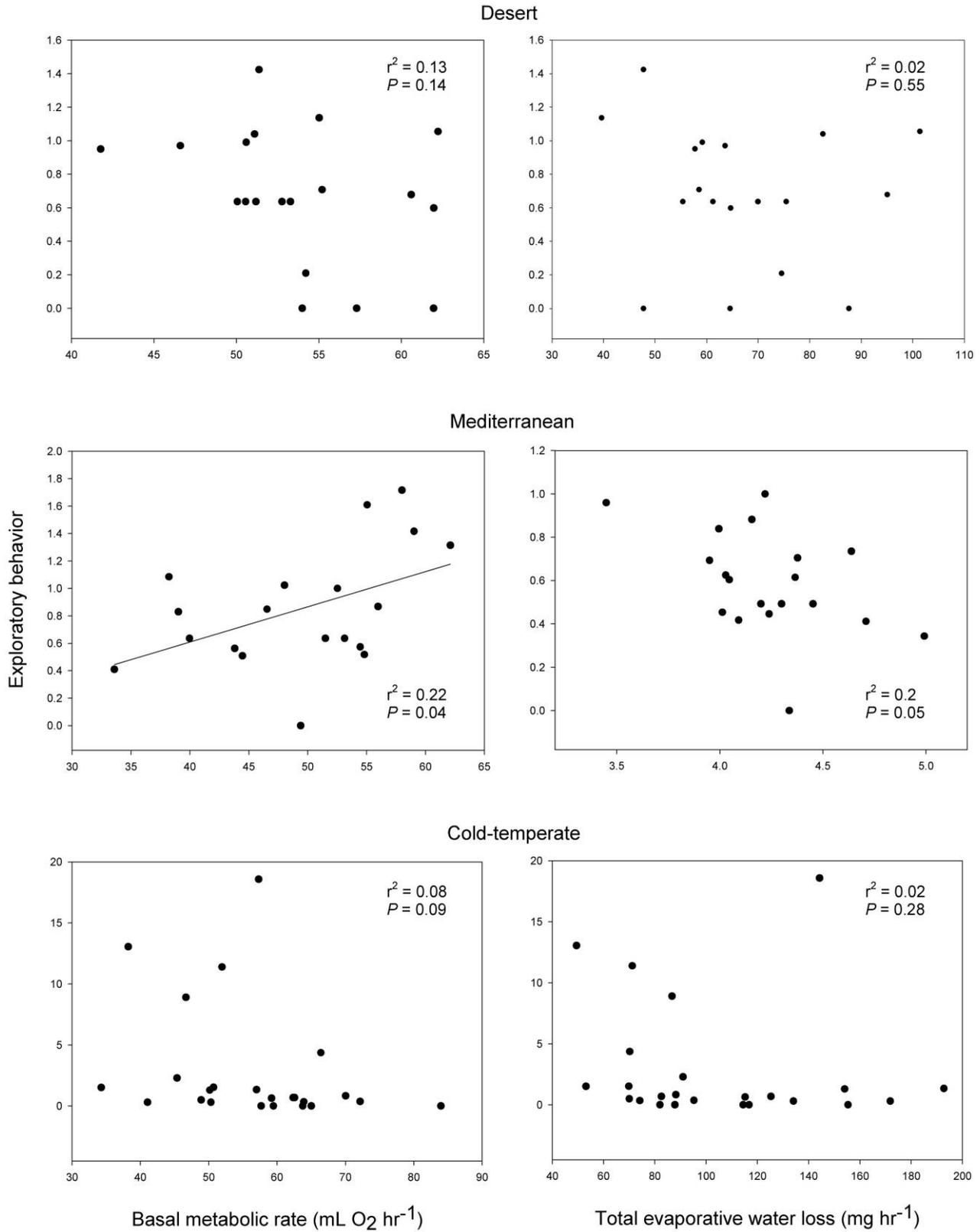
Figure 1. Exploratory behavior as a function of basal metabolic rate and total evaporative water loss in *Zonotrichia capensis* from desert, Mediterranean, and cold-temperate study sites. Regression line indicates significant relationship between variables at $P < 0.05$.

not genetically correlated and do not share a regulatory pathway, some population differences could be found in the relationship among those traits (Foster 1999; Bell 2005; Réale et al. 2010). Here, we found that exploratory behavior and physiological traits (and the association between the two) differed among study sites, which suggests that personality and physiology have evolved in different ways in order to adjust the phenotype to specific environmental pressures. Within-population differences in trait combinations with both a heritable basis and different fitness payoffs would lead to the stable coexistence of different phenotypes within populations (Dall et al. 2004). Nevertheless, although we explained this variation in terms of selective pressures that favor specific combinations of traits, there are several proximate and ultimate factors that could maintain the variability within a population. For example, variable responses may exist between individuals that differ in experience because of factors such as phenotypic plasticity or flexibility (Semlitsch et al. 1990; Houston and McNamara 1992; Piersma and Drent 2003). For instance, behavioral responses toward novel situations can be strongly affected by experiences during early stages of ontogeny, which could be maintained into adulthood (Winkler and Leisler 1999). Consequently, it is clear that studies examining the phenotypic and genetic basis of the inheritance of the combination of personality and physiological traits are needed in order to gain a better understanding of the proximal mechanisms that shape this relationship.

Finally, an understanding of this intraspecific variation along ecological gradients may provide valuable information on how ecological conditions may couple or decouple behavioral and physiological traits and on the possible consequence of this coupling at the population and biogeographic level (Réale et al. 2010). Studies elucidating the mechanisms underlying the putative behavioral and physiological coupling are necessary to better understand how these traits are related.

Acknowledgments

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