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ORIGINAL PAPER

Energy expenditure and personality in wild chipmunks

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Abstract According to the "pace-of-life syndrome" concept, slow-fast life-history strategies favored under different ecological conditions should lead to co-adaptations between metabolic rate and personality traits such as activity, exploration, and boldness. Although the relationships between resting metabolic rate (RMR) and personality traits have been recently tested several times, we still do not know whether personality is related to the daily energy expenditure (DEE) of free-living individuals in their natural habitat. The objectives of this study were to assess the links between RMR, DEE, and two personality traits (exploration in an open-field and docility during handling) in wild eastern chipmunks (*Tamias striatus*). Using a multivariate mixed model, we found that exploration and docility were significantly correlated at the among-individual level, confirming the presence of a behavioral syndrome within our population. We also found that exploration, but not docility, was negatively correlated with DEE. Hence, fast explorers show lower DEE levels than slow explorers, independently of RMR and docility. This result adds to an increasingly large (and complex) literature reporting the impacts of personality traits on the biology, ecology, and physiology of animals in their natural environment.

Keywords Doubly-labeled water · FMR · Pace of life · Repeatability · Temperament

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Introduction

The "pace-of-life syndrome" (POLS) concept postulates that closely related species or populations should differ in a suite of physiological traits as parts of co-adaptations with the life-history strategies favored under different ecological conditions (Ricklefs and Wikelski 2002). For example, "fast" species that grow quickly, mature early, have large litters, and die young have higher basal metabolic rate (BMR) than "slow" species, characterized by opposite suites of phenotypes (Careau et al. 2009; Williams et al. 2010). Although the POLS concept is potentially applicable across multiple levels of biological organization (i.e., species, populations, individuals), its relevance at the individual level remains poorly explored (Réale et al. 2010). Moreover, studies on the POLS concept have largely neglected behavioral traits, most likely due to the challenge associated with measuring behavior in a comparable manner across species (but see Careau et al. 2009).

One of the key predictions of the POLS concept is that active, bold, aggressive, and fast explorers should have higher daily energy expenditure (DEE) than less active, shy, unaggressive, and slow explorers. Studies conducted so far on the POLS have solely focused on BMR, resting metabolic rate (RMR), or standard metabolic rate (SMR), which are important metabolic measures of the "minimum cost of living" (Hulbert and Else 2004). Moreover, BMR, RMR, and SMR have been shown to be heritable, linked to fitness, and correlate positively with DEE during reproduction (Boratyński et al. 2010, 2013; Boratyński and Koteja 2010; Careau et al. 2011, 2013b; Mathot et al. 2013). However, BMR, RMR, and SMR are all measured on resting animals in an enclosed chamber, such that they cannot fully capture the diverse and complex energetic impacts of behaviors of animals as they go about their natural environment (Speakman 1998). Yet, our understanding of the energetic aspects of the POLS depends on reliable and accurate measurements of DEE in free-living subjects (Speakman 1997). An animal's DEE is an ecologically significant measure because it provides quantitative information on (*i*) how much food it needs, (*ii*) the total activity of all its physiological and behavioral mechanisms, and (*iii*) the share of energy it drains from its ecosystem (Speakman 2000).

Our objective was to estimate the among-individual correlations (Dingemanse and Dochtermann 2013) among two metabolic traits (i.e., DEE and RMR) and two personality traits (i.e., docility and exploration) in wild eastern chipmunks (*Tamias striatus*). In our study population, DEE tends to decline with age (Careau et al. 2013b) and is positively correlated with body temperature (Careau et al. 2012b), growth rate (Careau et al. 2013a), and litter size (Bergeron et al. 2011). Individuals also display consistent individual differences in their exploration patterns in the open-field test, ranging from "fast and superficial explorers" (start the test with a high level of exploration but decrease substantially their exploration during the following seconds) to "slow and thorough explorers" (display more moderate but constant exploration levels throughout the test; Montiglio et al. 2010). A fast exploration pattern in the open-field test is associated with (*i*) low docility, (*ii*) higher trappability [trapped more often (males) or farther from their burrows (females)], and (*iii*) lower hypothalamo-pituitary-adrenal reactivity (Montiglio et al. 2012). Moreover, individual differences in open-field exploratory pattern seem related to life-history strategies, with fast and slow explorers having their highest reproductive success at a younger and older age, respectively (Montiglio et al. 2014a) (see also Bergeron et al. 2013). Hence, individual differences in open-field exploration should have physiological implications in natural settings, which we expected to detect in DEE measurements.

Methods

Study area

The eastern chipmunk is a burrowing rodent that specializes on mast seed produced by oak (*Quercus* spp.), American beech (*Fagus grandifolia*), and maple (*Acer* spp.) trees (Elliot 1978). From 2004 to 2010, we monitored individually marked, free-ranging, eastern chipmunks on a 25-ha study site in the Ruiter Valley Land Trust (Sutton Mountains, Québec; 45° 05' N, 72° 26' W). Trapping sessions were conducted from early May until early October in all years, which we divided into three seasons: spring (May and June), summer (July and August), and autumn (September and October). Chipmunks were live-trapped daily between 08:00 hours and sunset using Longworth traps baited with peanut butter and visited every 2 h. At first capture, individuals were permanently marked with numbered ear tags (National Band and Tag Company 1005–1) and a Trovan®PIT-tag inserted in the inter-scapular region. At each capture, we noted trap location, body mass, sex, and reproductive status (males during mating had a developed scrotum and females during lactation had clearly visible mammae). We also recorded the minimum known age according to year of first capture and whether it was first captured as a juvenile (age=0) or as an adult (assumed to be one year old), as in Careau et al. (2010). We differentiated juvenile chipmunks from adults based either on an initial capture within a month following emergence when body mass was <80 g or, for individuals >80 g when first captured, on the absence of a darkened scrotum or developed mammae. All measurements were taken from 2004 to 2010 on individuals of known-age that were first captured between 2004 and 2009.

DEE

We measured DEE using the doubly-labeled water (DLW) technique (Speakman 1997). This technique provides an accurate measure of DEE over periods of several days in small mammals (Speakman et al. 1994) and has been used successfully on eastern chipmunks (Humphries et al. 2002). All manipulations were made in the field by the lead author to minimize variation. Briefly, we injected chipmunks intraperitoneally with 240 μl of DLW (37.78 and 4.57 % enriched ^{18}O and ^{2}H, respectively) after which subjects were held in the trap for a 1-h equilibration period (Speakman and Król 2005). Then, an initial blood sample was collected via a clipped toenail for isotope analysis (for further details, see Careau et al. 2012b, 2013b). Chipmunks were then released at the site of capture and recaptured, weighed and bled 1 to 3 days later, at as close as feasible to multiples of 24 h, and a final blood sample was taken to estimate isotope elimination rates. Taking samples over multiples of 24-h periods minimizes the influence of circadian variation in DEE (Speakman et al. 1994; Berteaux and Thomas 1999). The range of absolute deviation from multiples of 24 h was 0–180 min (25th percentile=20 min; median=38 min, 75th percentile=62 min). From 2007 to 2009, a total of 10 animals were blood sampled without prior injection to estimate background isotope enrichments of ^{2}H and ^{18}O (method C in Speakman and Racey 1987). The dataset used in this study is the same as the one used in Bergeron et al. (2011) and includes 53, 8, and 3 individuals measured once, twice, and three times, respectively. See Table 1 for sample size and descriptive statistics.

RMR

We measured RMR using a computerized open-circuit respirometry system that allowed us to measure two chambers sequentially for each of two oxygen analyzers, as described in Careau et al. (2010, 2013b). Each year, all respirometry runs were conducted by the lead author, helped by one or two assistants to minimize observer effects. For a given metabolic run, four individuals were weighed on a digital balance (±0.1 g) and then placed individually in a 650- or 850-ml Plexiglass cylindrical metabolic chamber. Chambers were placed in a constant-temperature cabinet regulated at 30 °C, which lies within the thermoneutral zone for chipmunks (Wang and Hudson 1971). A manifold and four mass-flowmeters provided a constant flow of 450 mL min^{-1} of dry, CO$_2$-free air to each chamber, as well as to two baseline airflows. The outflows of each chamber and the two baselines were directed to a computer-controlled multiplexor, which allowed us to sequentially sample baselines and the chambers using two oxygen analyzers. A 100 mL min^{-1} sub-sample of baseline air or chamber outflow was dried and pulled through the oxygen analyzer, alternating between baseline (5 min) and the two chambers (25 min each) over a 3.5-h period (each animal was monitored about 45 % of the time). By running two cycles between 20:00 and 05:00 hours, we were able to measure RMR during the resting phase for up to eight animals each night. RMR was not influenced by size of chamber, and whether the run was conducted early or late at night (results not shown). We calculated individual O$_2$ consumption according to eq. 4a of Withers (1977). We did not scrub the chamber outflows of CO$_2$, and we assumed a RQ of 0.8 to calculate O$_2$ consumption and convert data from mL O$_2$min^{-1} to mW (Koteja 1996; Speakman 2000). RMR was calculated from the lowest baseline level of O$_2$ consumption recorded for 5 min during a 3.5-h run. Resting state of individuals was confirmed by visual inspection of oxygen consumption rates and of the animals themselves, and most of them (96 %) were clearly resting (or even sleeping) at the end of a trial (Careau et al. 2013b). See Table 1 for sample size and descriptive statistics.

We avoided forcing chipmunks to be absent from their territory during daylight hours to minimize impacts on survival and reproductive success (e.g., loosing mating opportunities, or having their food hoards being pilfered). We therefore captured chipmunks as late as possible in the afternoon, transported them to the nearby (~10 km) laboratory facility, measured their metabolism overnight, and released them at their original trap location the following morning, just before sunrise. The limited amount of time animals were kept in captivity reduced their probability of being all post-absorptive during respirometry measurements. Therefore, all animals were provided with apple and peanut butter at all times except when in metabolic chambers. Because animals were probably not post-absorptive during the measurement, we classified metabolic measurements as RMR rather than BMR. Thus, like many recent metabolic studies on small, wild-caught endotherms (Speakman et al. 2004; Larivée et al. 2010; Timonin et al. 2011), our RMR measures include a non-quantified metabolic contribution from the heat increment of feeding. The average RMR in our population (2.34 kJ h^{-1} for a mean body mass of 90.8 g; Careau et al. 2013b) is 11 % higher than BMR measured in captive eastern chipmunks captured at a similar latitude (2.11 kJ h^{-1}; Levesque and Tattersall 2010), which is in agreement with the fact that RMR typically exceeds BMR by 5–15 % in small granivorous rodents (Nespolo et al. 2003).

Handling-bag test

We quantified docility by using the handling-bag test, which is increasingly used in behavioral ecology and captures an

Table 1 Descriptive statistics for resting metabolic rate (RMR), daily energy expenditure (DEE), docility during a handling-nag test, and open-field exploration in wild eastern chipmunks (*Tamias striatus*), including units of measurements, number of individuals measured, total number of samples, range of years with measurements, simple mean, variance, range (min and max), and coefficient of variation (CV)

	RMR	DEE	Docility	Exploration
Units	mW	mW	Seconds	Lines crossed
Individuals measured	296	64	299	228
Total number of samples	569	78	5273	386
Year range	2006–2009	2007–2009	2004–2010	2006–2009
Mean	0.646	2.131	11.814	96.184
Variance	0.009	0.558	246.95	3015.9
Min	0.254	0.730	0.000	2.000
Max	1.019	4.610	62.000	400.00
CV	0.151	0.351	1.330	0.571

individual's behavioral response to human presence (Martin and Réale 2008b). Upon releasing the chipmunk from the trap and putting into a mesh handling bag, it was suspended for 1 min, and the number of seconds spent immobile was used as a measure of docility (Martin and Réale 2008b; Montiglio et al. 2012). Thus, this test potentially captures aspects of freezing behavior in the wild. The handling bag test was performed on most captures by a total of 51 different field researchers. See Table 1 for sample size and descriptive statistics.

Open-field measurements

We quantified exploratory behavior using the open-field test (Hall 1934; Archer 1973; Walsh and Cummins 1976). Once captured and identified from the PIT-tag number, the chipmunk was immediately put back into the trap, carried to the open-field arena (distance ranging from 15 to 250 m), and transferred without direct manipulation to a PVC tunnel where they were gently pushed into the arena. The open-field arena consisted of one of two rectangular white plastic boxes of different dimensions (small, 80 L×40 W×40H cm; large, 100 L×100 W×50H cm) with a Plexiglas lid. Behavior was recorded for 3 min using a Sony Camcorder. After testing, the chipmunk was released at its capture location, and the arena was cleaned with 70 % alcohol. As the response of individuals may decrease across repeated trials, a minimum interval of 15 days was kept between successive open-field tests on any individual. Using The Observer 5.0 (Noldus Inc.) program, we superimposed a grid on the open-field floor (3×6 squares) and counted the number of times chipmunks crossed lines. This was entirely done by the second author to minimize variation. We calculated the total number of line crosses, providing a proxy of the level of exploratory behavior displayed by an individual (Réale et al. 2007). Individuals who scored high and low were assumed to be fast and slow explorers, respectively (for details, see Montiglio et al. 2010, 2012). See Table 1 for sample size and descriptive statistics.

Data analysis

We estimated the among-individual correlations (r_{ind}) between metabolic and personality traits using a Markov-chain Monte-Carlo multivariate mixed model in the R package MCMCglmm (Hadfield 2010), which allowed us to test each relationship in a one-step process instead of using best linear unbiased predictors (BLUPs) in a two-step approach (Hadfield et al. 2010). It is possible to partition a phenotypic correlation (r_{P}) into an among-individual correlation (r_{ind}) and residual correlation (r_e) whenever two traits are repeatedly assayed simultaneously in a set of individuals (Dingemanse and Dochtermann 2013). When the two traits are assayed repeatedly, but at different times, it is still possible to estimate r_{ind}, but not r_e. Unfortunately, it was impossible for us to measure personality and metabolism within the same hour, as RMR was measured at night in the laboratory and the open-field tests were conducted in the field during the day. In fact, most of our metabolic and behavioral measurements on a given individual were taken over varying time periods, ranging from the same day, month, season, and year. In principle, extending the time interval between two measurements makes it possible to estimate the r_e during this specific time interval, but this comes at the cost of potentially underestimating r_e (i.e., a long time interval will increase the likelihood of environmental effects acting on the error term of one of the trait independently of the other). Therefore, we did not attempt to estimate r_e in this study (i.e., we assumed that all r_e were equal to zero). A recent study on wild alpine marmots (*Marmota marmota*) reported that the r_es between physiological and personality traits were negligible compared to the r_{ind} observed (Ferrari et al. 2013; but see Dosmann et al. 2014).

We estimated the r_{ind} between DEE, RMR, docility, and exploration in a single four-trait multivariate mixed model that included all the data. For the purpose of this study, we only analyzed docility and exploration data for individuals whose DEE or RMR was quantified. All dependent variables were z standardized. The multivariate mixed model included a random effect variance of individual identity fitted to dependent variables in an unstructured variance-covariance matrix, such that an estimate of the among-individual variance (V_{ind}) was obtained for each trait in addition to covariances (COV_{ind}) between all the traits. The model was run for 6,500,000 iterations, with a thinning interval of 5,000 (i.e., only one iteration from every 5,000 in the Markov chain was used to estimate the posterior distribution of the parameters to reduce the occurrence of autocorrelation between successive iterations), and a burn-in of 1,500,000 (i.e., we discarded the first 1,500,000 models of the simulation to avoid autocorrelation problems). This yielded effective sample sizes of 1000 for all (co)variances. We visually inspected plots of the traces and posterior distributions as well as calculating the autocorrelation between samples to make sure that all models properly converged. Autocorrelations were less than 0.05 for all (co)variance components.

Before running a Bayesian model, one needs to set "priors" which are the prior distribution of the parameters before the data are analysed and can vary from non-informative to highly informative. As our knowledge about the relationship between metabolism and personality is relatively low, we ran the multivariate model with different priors and checked whether these different priors provide different posterior distributions (Hadfield 2010). We ran the models using inverse Wishart priors and parameter expanded priors, but only present results from the former priors as it yielded the lowest deviance information criteria and the conclusions did not qualitatively change according to prior specifications.

We calculated repeatability for each trait as the ratio of V_{ind} over the sum of V_{ind} and the residual variance (V_e). We calculated r_{ind} by dividing the $\mathrm{COV}_{\mathrm{ind}}$ term of a given pair of traits by the square root of the product of their V_{ind}. We inspected the 95 % highest posterior density (HPD) associated with each r_{ind} to check whether they overlapped with zero. A 95 % HPD interval contains most of the posterior distribution and is analogous to a confidence interval in the frequentist approach; a 95 % HPD that overlaps 0 indicates that the effect does not differ significantly from zero. Thus, for r_{ind} among each pair of trait, we determined whether the 95 % HPDs included or excluded zero, which, along with the estimate of correlation, provides good information on the importance of the correlation.

Previous analyses of the entire dataset thoroughly assessed how DEE, RMR, exploration, and docility were influenced by several extrinsic and intrinsic variables (Careau et al. 2010, 2013b; Montiglio et al. 2010). Using this prior knowledge, we fitted a fixed effect of age (continuous), sex, and reproductive status (reproductive or non-reproductive) to all variables. We also fitted a fixed effect of body mass to DEE and RMR, such that our r_{ind} estimates are conditioned on body mass. Fixed effects specifically fitted to RMR were season, number of parasites (botfly larvae), timing of measurement, and whether it was a mast year or not. Ambient temperature (hourly average between initial and final blood samples) was fitted as a fixed effect for DEE. Fixed effects specifically fitted to docility were season, field researcher identity, cohort, and whether it was a mast year or not. Fixed effects specifically fitted to exploration were season, cohort, ambient temperature, apparatus size, and test sequence. However, our main objective here was to test the r_{ind} after accounting for these significant covariates. Details on the effects of those variables are available in previous publications (Careau et al. 2010, 2012a, 2013a, b; Bergeron et al. 2011; Montiglio et al. 2012, 2014a).

Results

The multivariate mixed model revealed that RMR, DEE, docility, and exploration all showed significant V_{ind} (Table 2). Note, however, that V_{ind} in RMR was less than half that of other traits (Table 2). Repeatability (95 % HPD interval) was 0.14 (0.08–0.20), 0.59 (0.25–0.72), 0.26 (0.22–0.32), and 0.40 (0.32–0.46) for RMR, DEE, docility, and exploration, respectively. RMR was not significantly correlated with DEE, docility, or exploration, as the r_{ind}s were relatively low (range: −0.14 to 0.18) and not statistically different from zero (i.e., the 95 % HPD intervals overlap with zero; Table 3). Note, however, the negative (but non-significant) r_{ind} between RMR and exploration (r_{ind}=−0.14, 95 % HPD interval=−0.45–0.14). DEE was not significantly correlated with docility (r_{ind}=0.18, 95 % HPD interval=−0.12–0.47; Table 3, Fig. 1a). However, the r_{ind} between DEE and exploration was negative (r_{ind}=−0.32; Fig. 1b), and the 95 % HPD intervals did not overlap with zero (−0.71–−0.03; Table 3). Finally, exploration and docility were significantly and negatively correlated at the among-individual level (r_{ind}=−0.48, 95 % HPD interval=−0.60–−0.26; Fig. 1c; Table 3).

Discussion

Several recent empirical studies have explicitly looked at the r_{P} between personality traits and maintenance metabolism in insects (Krams et al. 2013), fish (Huntingford et al. 2010; Killen et al. 2012; D'Silva 2013), amphibians (Gifford et al. 2014), lizards (Le Galliard et al. 2013), birds (Maldonado et al. 2012; Bouwhuis et al. 2013; Mathot et al. 2014), mammals (Lantová et al. 2011; Timonin et al. 2011; Guenther et al. 2014; Šíchová et al. 2014), and humans (Terracciano et al. 2013). Results from these studies are remarkably variable, showing that the relationship between personality and metabolism is different across developmental stages (age), measurement trials, sex, reproductive status, and environments. Yet, none of these studies included a measure of energy expenditure in unrestrained, wild animals. As a result, our understanding of the energetic impacts of personality differences is limited to metabolism measured under highly artificial circumstances (i.e., restrained in a metabolic chamber). Hence, our most important result is that of a significant and negative r_{ind} between DEE—but not RMR—and open-field exploration. This correlation at the among-individual level could be due to environmental effects that simultaneously and permanently affect DEE and exploration (and potentially life-history traits, see Montiglio et al. 2014a). Alternatively, this association may reflect a genetic correlation between DEE and exploration (see also Careau et al. 2011).

We also found a significant and negative r_{ind} between exploration and docility, such that individuals who crossed more lines during the open-field test also struggled more during the handling-bag test (see also Montiglio et al. 2012). Dingemanse et al. (2012) recently clarified that behavioral syndromes are defined at the among-individual level as opposed to raw phenotypic correlations (which incorporate sources of within-individual variation, correlated measurement errors, and other confounding factors). In fact, studies on behavioral syndromes using a phenotypic correlation approach may not be able to detect important patterns as differences between the r_{ind} and r_e may lead to a null r_{P}. This could explain why, in another chipmunk population, the correlation between exploration and docility was not significant (Martin and Réale 2008a). Despite the fact that exploration and docility are part of a behavioral syndrome in our population,

Table 2 Among-individual variance (V_{ind}), within-individual variance (V_e), and repeatability in resting metabolic rate (RMR), daily energy expenditure (DEE), docility during a handling-bag test, and exploration behavior in an open-field test in free-ranging eastern chipmunks

Trait	V_{ind}			V_e			Repeatability		
	Mode	95 % HPD interval		Mode	95 % HPD interval		Mode	95 % HPD interval	
		Lower	Upper		Lower	Upper		Lower	Upper
RMR	0.102	0.058	0.145	0.624	0.545	0.714	0.136	0.081	0.197
DEE	0.244	0.120	0.483	0.284	0.163	0.474	0.509	0.246	0.715
Docility	0.231	0.189	0.284	0.683	0.659	0.712	0.258	0.223	0.319
Exploration	0.287	0.184	0.384	0.382	0.307	0.456	0.397	0.320	0.559

Variance components were estimated from the posterior modes of a four-trait multivariate mixed model, using a Bayesian approach (i.e., MCMCglmm procedure in R). Highest posterior densities (95 % HPD) provide lower and upper credibility intervals associated with each variance and repeatability estimate. See Table 3 for the correlations estimates from the same model

among-individual variation in docility was not correlated with variation in DEE. Hence, slow and thorough explorers show higher levels of DEE, independently of their docility.

Measurements of multiple metabolic traits are usually required to better understand the impacts of energy-demanding processes, such as reproduction, parasitism, and physical activity (Speakman 1997; Careau et al. 2012a; Careau and Garland 2012). Current conceptual models on the “energetics of personality” make different predictions on how RMR and DEE should relate to physical activity (Careau and Garland 2012). However, none of these models predict a negative correlation with DEE (i.e., that fast explorers have *lower* DEE than slow explorers). For example, the allocation model assumes a fixed energy budget and predicts a nil relationship between activity and DEE, but a negative relationship between activity and RMR because more active, fast explorers should reduce their maintenance costs to afford higher levels of activity (or *vice versa*). At first sight, the negative trend between RMR and exploration could lend support to the allocation model (see also Bouwhuis et al. 2013; Gifford et al. 2014; Guenther et al. 2014), but r_{ind} was not significant. Note that repeatability was low for RMR, which may be due to greater measurement error and/or phenotypic flexibility in RMR compared with other traits.

Table 3 Among-individual correlations (r_{ind}) between resting metabolic rate (RMR), daily energy expenditure (DEE), docility during a handling-bag test, and exploration behavior in an open-field test in free-ranging eastern chipmunks

Trait 1	Trait 2	r_{ind}	95 % HPD interval	
			lower	upper
RMR	DEE	0.154	−0.276	0.410
RMR	Docility	0.041	−0.254	0.230
RMR	Exploration	−0.143	−0.447	0.136
DEE	Docility	0.177	−0.119	0.473
DEE	Exploration	*−0.316*	*−0.709*	*−0.026*
Exploration	Docility	*−0.477*	*−0.599*	*−0.262*

Correlations were estimated from the posterior modes of a four-trait multivariate mixed model, using a Bayesian approach (i.e., MCMCglmm procedure in R). Highest posterior densities (95 % HPD) provide lower and upper credibility intervals associated with each correlation. Italic values indicate significant correlations. See Table 2 for the variance estimates from the same model

A negative relationship between open-field exploration and BMR was found across 17 muroid rodent species (Careau et al. 2009). This inter-specific study was based on an open-field test that lasted 10 min (Wilson et al. 1976; Webster et al. 1979) during which “slow and thorough” individuals should have spent more time active overall (see Fig. 1a, b in Montiglio et al. 2010). By contrast, “fast and superficial” individuals may be highly active in the first minutes of the test, but the activity rate will rapidly decline such that it yields a low exploration score over the whole 10-min testing period (see Fig. 1a, b in Montiglio et al. 2010). Hence, a negative inter-specific correlation between activity during the open-field test and BMR in muroid rodents is in accordance with the POLS concept because “fast and superficial” species (which scored low on the open-field test) had high BMR whereas “slow and thorough” species had low BMR. Since we have used a much shorter open-field test here (3 min), this scenario would imply that individuals scoring high in the open-field test would be those that are “fast and superficial” explorers (see Fig. 1c, d in Montiglio et al. 2010). This leaves us with counterintuitive result that “fast and superficial” individuals have lower DEE, which is opposite to what is predicted by the POLS concept and warrants further investigation.

One potential explanation for this counterintuitive result is that our open-field test quantified aspects of escape behavior and/or short-term response to stress, rather than long-term exploratory behavior in the wild. Slow explorers usually have higher hypothalamic-pituitary-adrenal reactivity than fast explorers (reviewed in: Carere et al. 2005; Øverli et al. 2007), which could make them more prone to stress in their natural

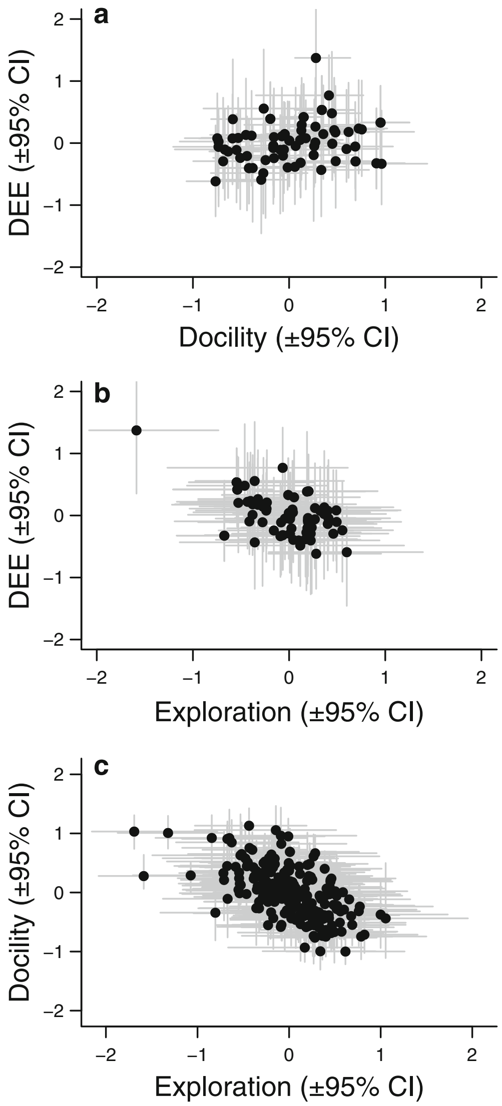

Fig. 1 Representation of the among-individual correlations between **a** daily energy expenditure (DEE) and docility during a handling-bag test (*n*=64), **b** DEE and open-field exploration (*n*=64), and **c** docility and exploration (*n*=226) in free-ranging eastern chipmunks (*Tamias striatus*). Shown are posterior modes of the best linear unbiased predictors (*black circles*) associated with the random effect of individual identity for each individual with both measurements, along with the 95 % highest posterior density (*gray lines*) providing credible intervals (CI)

environment. As a result, slow explorers would exhibit higher DEE despite their lower activity than fast explorers. In our study population, slow explorers have more temporally variable fecal cortisol metabolites (Montiglio et al. 2014b). If this is the reflection of higher or more frequent stress responses, then it could lead to higher DEE through conversion of energy from storage to useable forms.

An association between open-field exploration and DEE could also reflect the specific way an individual react to the stressful situations imposed by the DLW method, instead of natural stressors (Careau et al. 2008; Martins et al. 2011). For example, a link between DEE and exploration might arise if slow explorers, which spent more time freezing in the open-field test, had their DEE spuriously elevated by the DLW procedures. However, previous field studies on mammals have been unable to detect any negative effects of the DLW method on behavior and activity patterns of animals, indicating limited stress effects (Speakman 1997). The only study that showed an effect of the DLW method on birds actually reported a *decrease* in DEE in the most heavily manipulated individuals (Schultner et al. 2010). Moreover, if DEE levels are influenced by handling stress, then its relative importance should decrease over the number of days that DEE is monitored, which is not the case in our DEE measures (DEE levels were not significantly different between samples recorded over 1, 2, and 3 days, see Careau et al. 2013b). Finally, it is unclear why DEE would not be correlated with docility during the handling-bag test, because this behavioral measure is directly related to stress response to capture and manipulations.

Conclusion

We must remain cautious in our interpretations until empirical data exist in eastern chipmunks to support the view that the open-field test captures aspects of an individual's exploratory behavior in the natural habitat, such as shown in other rodent species (Boon et al. 2008; Boyer et al. 2010). However, some pieces of the puzzle are falling into place, as open-field exploration has been shown to relate to aspects of space use (trappability and distance trapped from burrows; Montiglio et al. 2012) and life-history strategies (Montiglio et al. 2014a) in our population. Here, we have showed the impacts of personality traits on a crucial aspect of the ecology and evolution of animals: the level energy expenditure that animals voluntarily sustain in their natural environment (Speakman 1997). The next step will be to relate RMR and DEE to measures of activity in the natural habitat and life-history strategies in our population.

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Ethical standards Animals were captured and handled following the protocol approved by the Animal Welfare Committee of Université de Sherbrooke and the Ministère des Ressources Naturelles et de la Faune du Québec.

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