

Exploration strategies map along fast–slow metabolic and life-history continua in muroid rodents

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Summary

1. Personality is highly relevant to ecology and the evolution of fast–slow metabolic and life-history strategies. One of the most important personality traits is exploratory behaviour, usually measured on an animal introduced to a novel environment (e.g. open-field test).

2. Here, we use a unique comparative dataset on open-field exploratory behaviour of muroid rodents to test a key assumption of a recent evolutionary model, i.e. that exploration thoroughness is positively correlated to age at first reproduction (AFR). We then examine how AFR and exploratory behaviour are related to basal metabolic rate (BMR).

3. Inter-specific variation in exploratory behaviour was positively correlated with AFR. Both AFR and exploration behaviour were negatively correlated with BMR. These results remained significant when taking phylogeny into account.

4. We suggest that species occupying unproductive and unpredictable environments simultaneously benefit from high exploration, low BMR and delayed AFR because exploration increases the likelihood of finding scarce resources, whereas low BMR and delayed reproduction enhance survival during frequent resources shortages.

5. This study provides the first empirical evidence for a link between personality, life-history, phylogeny and energy metabolism at the inter-specific level. The superficial-thorough exploration continuum can be mapped along the fast–slow metabolic and life-history continua.

Key-words: age at first reproduction, basal metabolic rate, fast–slow continuum, energetics, lifestyles, open field, personality, phylogeny

Introduction

Because many personality traits have important energetic consequences, there is reason to believe that behaviour and energy metabolism co-evolve as two facets of broad life-history syndromes (Biro & Stamps 2008; Careau *et al.* 2008). Information on daily energy expenditure (DEE) or basal metabolic rate (BMR) of individuals or species with different behavioural types will help us to understand how personality and life-history traits (co)evolve, an unresolved question of fundamental importance (Stamps 2007; Wolf *et al.* 2007). From a physiological perspective, personality represents an integrative factor that may explain some of the large inter-

and intra-specific variation in BMR, a physiological trait of high ecological and evolutionary significance (McNab 2002; Speakman, Krol & Johnson 2004).

It has been argued that vertebrates, including birds and eutherian mammals, can be placed along a fast–slow continuum for both life-history (Oli 2004) and metabolism (Lovegrove 2003). For a given body size, species at the ‘fast’ end of the continua mature earlier, have higher reproductive rates, shorter generation times and higher BMRs than those at the ‘slow’ end. Among life-history traits, age at first reproduction (AFR) is held to provide a reliable index of the ranking of mammal species along the fast–slow continuum (Gaillard *et al.* 2005; but see Oli 2004). There is also reason to expect that AFR is linked with personality, but little empirical support for such a link currently exists (reviewed in Biro & Stamps 2008). Nevertheless, an evolutionary trade-off between

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AFR and exploration thoroughness is key to a recent theoretical model that cogently explained the evolution and coexistence of personality traits (Wolf *et al.* 2007). The fundamental assumption of this model is that ‘fast’ individuals explore their environment superficially and reproduce earlier in life, whereas ‘slow’ individuals reproduce over a longer life span generated by later first reproduction and thorough exploration of their habitat. Wolf *et al.*'s (2007) model showed how exploration can co-evolve with boldness and aggressiveness: fast and superficial explorers are bold and aggressive, whereas slow and thorough explorers are shy and less aggressive. Their model offers an explanation for the widely observed phenomena called ‘behavioural syndromes’ or proactive/reactive coping styles (Koolhaas *et al.* 1999; Sih *et al.* 2004b; Groothuis & Carere 2005).

Although much of the theoretical and empirical work on personality is focused on consistent behavioural differences among individuals of the same species, species are also characterised by consistent behavioural traits that can be termed personality (Sih, Bell & Johnson 2004a; Réale *et al.* 2007). In parrots, for example, inter-specific differences in exploration behaviour seem to represent adaptations to different lifestyles that are set by differences in food habits, habitat complexity and predation risk (Mettke-Hofmann *et al.* 2005). Since one might expect personality to be closely related to life-history strategies (Biro & Stamps 2008) and metabolic traits (Careau *et al.* 2008), inter-specific analyses of personality correlates may reveal key axes of biological differentiation among species clades.

Whereas there is abundant literature on inter-specific variation in BMR and life-histories (e.g. Harvey, Pagel & Rees 1991; Symonds 1999; McNab 2002), systematic measures of personality traits across species are rare (Réale *et al.* 2007). We know of only one suitable mammalian comparative dataset to test the Wolf *et al.* (2007) model, that of Wilson *et al.* (1976) and Webster, Baumgardner & Dewsbury (1979), which quantified the exploration behaviour of 19 species of muroid rodent when introduced to a novel environment via the classic and widely used open-field test (Walsh & Cummins 1976). These muroid species can thus be placed along a superficial vs. thorough exploration continuum. This dataset in combination with analogous ones for life-history traits and BMR and the explosion of DNA sequence data, therefore, provide a unique opportunity to test inter-specific links between personality, metabolism and life-history in a phylogenetic context.

Here, we test the fundamental assumption of Wolf *et al.*'s (2007) model that exploration thoroughness is positively correlated with AFR and examine how these two traits are related to BMR. BMR is often viewed as the ‘idling cost’ of the metabolic machinery needed to sustain a given lifestyle or energy throughput (Mueller & Diamond 2001), a view supported by the fact that DEE and BMR are positively correlated at the inter-specific level (Ricklefs, Konarzewski & Daan 1996). A ‘fast’ lifestyle involving rapid growth, early AFR and above-average DEE should require above-average organ size for food and energy processing and hence above-average maintenance costs or BMR (Daan, Masman &

Groenewold 1990). Therefore, we expected AFR to be negatively correlated with BMR (McNab 1980, 2002), even when body-size effects are controlled for. Furthermore, we expected exploration thoroughness and BMR to also be negatively related (again, with corrections for body size) because, whereas exploration is not necessarily more energetically expensive than other behaviours, it is inversely related to boldness and aggressiveness, which are highly energy demanding (Lahti *et al.* 2002).

Methods

EXPLORATION BEHAVIOUR

Wilson *et al.* (1976) and Webster *et al.* (1979) introduced 10 males of 19 muroid species in an open-field and recorded the time spent in each of 10 behavioural categories over a period of 10 min (See Table S1 in Supplementary Material for categories and species). Wilson *et al.* (1976) defined locomotor-exploratory behaviour as ‘walking and running about the field’, which was the dominant behavioural category, averaging 50% (range 30–70%) of total time (Table 1). Therefore, activity in the open-field was used as a proxy for exploration although these behaviours are not mutually exclusive (e.g. an animal exploring its environment need not necessarily be truly ‘active’; Réale *et al.* 2007). Adding rearing and wall rearing behaviour in the analyses did not change our results. The open-field test was originally developed by psychologists to measure ‘emotionality’, albeit not without controversy (see Archer 1973; Walsh & Cummins 1976). Today, this test is gaining interest among ecologists because it provides a repeatable and heritable (Dingemanse *et al.* 2002) measure of exploration that has been found to be correlated with important behavioural, ecological and life-history parameters in the wild (Dingemanse *et al.* 2004; Boon, Réale & Boutin 2007).

LIFE-HISTORY AND PHYSIOLOGICAL DATA

We obtained estimates of AFR for all species from Duncan, Forsyth & Hone (2007) and Nowak (1999) (see Table 1). BMR and body mass data for 17 of these species were obtained from McNab (1992), Lovegrove (2000), White & Seymour (2003) and Mathias *et al.* (2004).

PHYLOGENY CONSTRUCTION

Because more closely related taxa share more of their evolutionary history in common, some of the variation in phenotypic traits may be correlated with phylogenetic relatedness (Harvey & Pagel 1991; Blomberg, Garland & Ives 2003). The phylogenetic tree used in this study (Fig. 1) was constructed and dated using a subset of six genes (*MT-CO3*, *MT-CYB*, *MT-ND3*, *MT-ND4L*, *MT-RNR1* and *RBP3*; names follow Wain *et al.* 2002) derived from the 68-gene dataset of Bininda-Emonds *et al.* (2007) that were informative for the set of species under examination here. *Sciurus vulgaris* and *Homo sapiens* were added as successive outgroups to obtain the final dataset.

The topology of the tree was obtained using a maximum-likelihood (ML) analysis of the concatenated supermatrix using RAXML v7.0.3 (Stamatakis 2006). Searches employed 100 replicates under a GTRMIX model, with ML parameters being free to vary between the six genes. The GTRMIX model uses the fast CAT approximation to the gamma distribution to account for rate heterogeneity during the branch-swapping phases, but derives the final likelihood score

Table 1. Percent of time spent exploring during a 10-min open-field test (% exploration), body mass, basal metabolic rate (BMR) and age at first reproduction (AFR) in 19 muroid rodents

Species	% exploration	Body mass (g)	BMR (mL O ₂ per h)	AFR (days)	References*
<i>Peromyscus gossypinus</i>	68.4	21.5	37.0	50	1,3
<i>Peromyscus leucopus</i>	54.6	20.0	33.2	70	1,3
<i>Peromyscus eremicus</i>	61.9	21.5	33.1	127	1,3
<i>Microtus montanus</i>	44.9	35.1	83.3	25	1,3
<i>Microtus ochrogaster</i>	31.1	46.7	79.1	47	1,3
<i>Microtus pennsylvanicus</i>	27.5	38.9	75.1	29	1,3
<i>Microtus californicus</i>	44.3	44.0	68.2	65	1,3
<i>Scotinomys teguina</i>	58.8	12.0	31.2	34	1,3
<i>Meriones tristrami</i>	59.4	112.0	98.6	84	2,3
<i>Baiomys taylori</i>	55.5	7.2	17.1	59	1,4
<i>Mesocricetus auratus</i>	30.9	98.0	147.0	46	1,3
<i>Ototylomys phyllotis</i>	45.4	100.9	–	26	1
<i>Peromyscus polionotus</i>	55.9	12.0	21.5	30	1,3
<i>Microtus canicaudus</i>	43.8	30.4	77.8	55	1,5
<i>Onychomys leucogaster</i>	65.4	40.0	–	122	1
<i>Mus musculus</i>	61.0	14.8	26.6	72	1,6
<i>Rhabdomys pumilio</i>	46.4	39.6	32.1	53	1,3
<i>Calomys callosus</i>	63.8	48.0	55.82	52	1,4
<i>Peromyscus maniculatus</i>	46.5	22.8	36.9	77	1,3

*1 = Duncan *et al.* (2007); 2 = Nowak (1999); 3 = White & Seymour (2003) 4 = Lovegrove (2000); 5 = McNab (1992); 6 = Mathias *et al.* (2004).

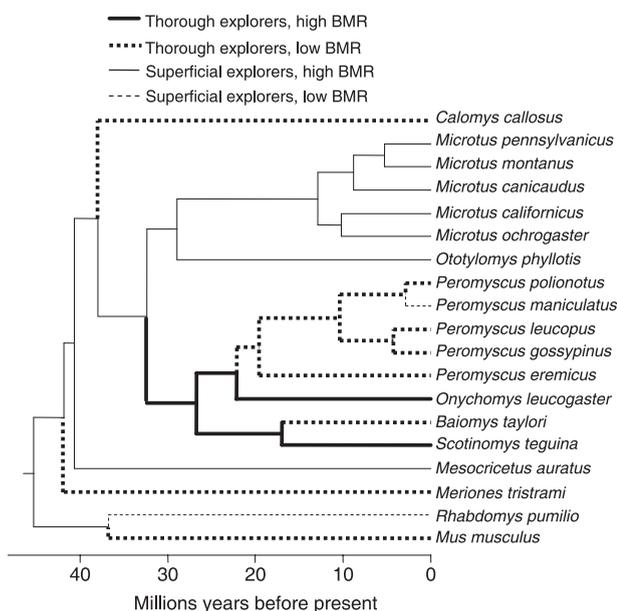


Fig. 1. The dated muroid phylogenetic tree with branch lengths used in this study. Thin vs. thick branches differentiate superficial vs. thorough explorers, respectively. Solid vs. dashed branches indicate species with higher vs. lower basal metabolic rate (BMR) than expected given their body mass, respectively.

under a true gamma distribution for comparability. Otherwise, default parameters in RAXML were used. Support for the final topology was determined using a nonparametric bootstrap (Felsenstein 1985) with 1000 replicates. Again, a GTRMIX model free to vary between genes was used.

Estimates of divergence time in the phylogeny were obtained using the relDate method (see Bininda-Emonds *et al.* 2007). For each

gene, gene trees with ML branch lengths were obtained by fitting the sequence data to the topology of the overall ML tree under the optimal model of evolution for that gene (including testing for the applicability of a strict molecular clock) as inferred using the AIC with ModelTEST v3.7 (Posada & Crandall 1998) and PAUP* v.4.0b10 (Swofford 2002) (see Table 2). The relative branch lengths for each gene tree obtained using relDate v2.3 (Bininda-Emonds *et al.* 2007) were then calibrated using the times for the Primates-Rodentia (91.8 million years ago) and Sciuridae-Muroidea (82.8) divergences presented by Bininda-Emonds *et al.* (2007). The date for each node was taken as the median of all estimates for it (up to five genes plus one calibration point). In general, the dates for most splits were derived from three or more estimates. The variation in date estimates between genes also enabled us to calculate 95% confidence intervals on the estimate. Finally, any negative branch lengths in any of the three sets of dates (best estimate and upper and lower 95% confidence intervals on that estimate) were corrected using chronoGrapher v1.4 (Bininda-Emonds *et al.* 2007). Both the supermatrix and the resulting phylogeny are available from TreeBASE (www.treebase.org; Sanderson *et al.* 1994) under the study accession number S2133 and matrix accession number M4035.

STATISTICAL ANALYSIS

BMR and many life-history traits are strongly correlated with body mass. Hence, many traits may be correlated with one another through their mutual link to body mass. To test whether the AFR was positively correlated with exploration thoroughness while controlling for the effect of body mass, we first used an ordinary least-squares (OLS) regression model that included exploration thoroughness as the independent variable and body mass as a covariate. We subsequently ran two other OLS models to test if AFR or exploration thoroughness could be negatively correlated with BMR with body mass as a covariate. We used the JMP 5.0.1 statistical package (SAS Institute, Cary, NC) to calculate studentized residuals and to check if outliers were present. Since the residuals from a

Table 2. Statistics relating to the five sequence data sets used for molecular dating, including the optimal model of evolution determined using ModelTEST. *P*-values for genes that were held to evolve in a strict clock-like fashion according to a likelihood-ratio test (LRT) are marked with an asterisk. All gene names follow Wain *et al.* (2002)

Gene	Number of taxa	Aligned length	Model of evolution	LnL (non-clock)	LnL (clock)	LRT χ^2	LRT <i>P</i> -value
<i>MT-CO3</i>	7	693	GTR + I + G	3050.19	3053.42	6.47	0.263*
<i>MT-CYB</i>	17	1123	GTR + I + G	9589.64	9628.61	77.94	1.66 × 10 ⁻¹⁰
<i>MT-ND3</i>	15	267	HKY + I + G	2420.80	2429.48	17.36	0.184*
<i>MT-ND4L</i>	15	297	HKY + G	2610.25	2617.90	15.31	0.288*
<i>MT-RNR1</i>	10	731	GTR + I + G	2979.67	2990.22	21.10	0.007
<i>RBP3</i>	10	666	TVM + G	2834.08	2845.31	22.46	0.004

regression will generally not be independently or identically distributed, it is advisable to weight the residuals by their standard deviations (i.e. studentization). Thus, outliers can be statistically identified using critical-value tables and the studentized residual of each data point (Lund 1975).

In a second set of analyses, we used the `ppls.lam` function developed by Duncan *et al.* (2007) in the statistical package R (R Development Core Team 2004) to fit phylogenetic generalised least-squares (PGLS) models that include a measure of the degree of phylogenetic signal (λ) in the data, having accounted for the adaptive hypothesis specified. The value of λ can range between 0 and 1, where 0 implies no phylogenetic signal (equivalent to the OLS model) and 1 implies a strong phylogenetic signal. In all PGLS models, the value of λ was estimated using ML to adjust the degree of phylogenetic correction optimally for each data set (Freckleton, Harvey & Pagel 2002). The significance of λ was tested using likelihood-ratio tests (LRTs) by examining twice the difference in negative log-likelihoods between the PGLS (full model with λ optimisation) and OLS models (one less parameter because λ was set to 0), which follows a χ^2 distribution with one degree of freedom.

Results

AFR was significantly correlated with exploration thoroughness ($F_{1,16} = 4.63, P < 0.05$), but not with body mass ($F_{1,16} = 0.11, P > 0.05$). In support of the assumption underlying Wolf *et al.*'s (2007) model, more explorative muroids start to reproduce at a later age (Fig. 2). AFR and BMR were negatively correlated in the full data set of 17 species (i.e. BMR data lacking for *Ototylomys phyllotis* and for *Onychomys leucogaster*), but the strength of the correlation was reduced remarkably by a single data point ($F_{1,14} = 3.33, P = 0.09$; Fig. 3a). This data point has a studentized residual of 2.89 and can thus be considered as an outlier because the critical value ($P < 0.05$) for $n = 17$ and $q = 3$ is 2.67. When this outlier was excluded, no further outliers were detected, and AFR was strongly negatively correlated with BMR ($F_{1,13} = 5.19, P < 0.05$; Fig. 3a) and positively correlated with the covariate body mass ($F_{1,13} = 6.03, P < 0.05$). Exploration thoroughness was significantly related with BMR ($F_{1,14} = 11.38, P < 0.01$), but not with body mass ($F_{1,14} = 3.85, P > 0.05$). More explorative species had lower mass-adjusted BMRs (Fig. 3b).

Table 3 shows that the phylogenetic signal in AFR was non-existent ($\lambda = 0$), moderate in exploration thoroughness ($\lambda = 0.65$), and maximal in all other traits considered in this study (body mass, BMR and mass-adjusted BMR; $\lambda = 1$).

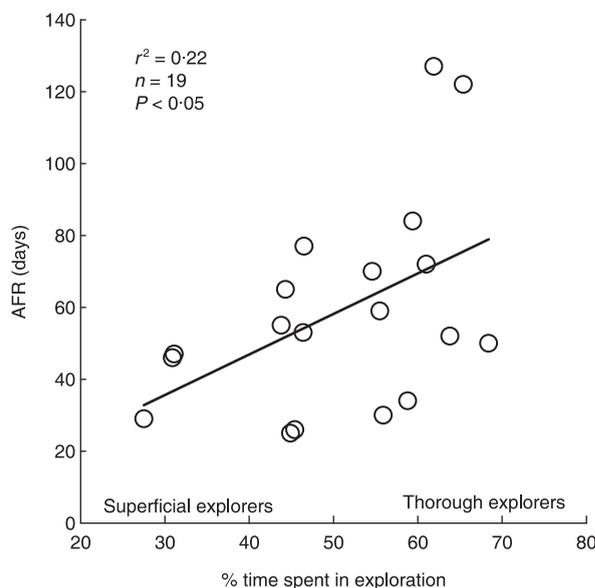


Fig. 2. Age at first reproduction (AFR, in days) as function of percent of time spent exploring a novel environment (in a 10-min open-field test) in 19 species of muroid rodents.

However, inclusion of phylogenetic information for each of the three models did not significantly increase the likelihood of these models (Table 3), and the value of λ was in fact optimised to 0 (no phylogenetic dependence) for each model. Therefore, relationships between AFR, exploration thoroughness and BMR remain significant when taking both body mass and phylogeny into account.

Discussion

We found that inter-specific variation in exploration thoroughness was positively correlated with AFR and that both of these traits were negatively correlated with BMR in muroids. That superficial explorers begin reproducing earlier than thorough explorers is consistent with a key assumption of Wolf *et al.*'s (2007) model that there is an evolutionary trade-off between exploration thoroughness and AFR. Empirical and theoretical studies on personality have shown that superficial and thorough exploration strategies are associated with proactive and reactive lifestyles, respectively (Sih *et al.*

Table 3. Analysis of phylogenetic signal in different traits (age at first reproduction = AFR, basal metabolic rate = BMR) and models considered in this study. Negative log-likelihood values ($-\ln L$) for fitted ordinary and phylogenetic least-squares (OLS and PGLS, respectively) are shown. PGLS models were set to optimise λ using maximum likelihood (ML λ), an indicator of phylogenetic signal. Twice the difference in the $-\ln L$ of both models follows a χ^2 distribution allowing testing of the significance of λ

Trait	$-\ln L$ OLS	$-\ln L$ PGLS	ML λ	χ^2	P value
Body mass	89.33	82.64	1	13.37	< 0.05
AFR	90.32	90.32	0	0.00	> 0.05
Exploration	76.88	72.07	0.65	9.60	< 0.05
BMR	83.73	77.42	1	12.62	< 0.05
Mass-adjusted BMR	72.90	67.47	1	10.86	< 0.05
Model					
AFR~mass + exploration	63.34	63.33	0	0.02	> 0.05
AFR~mass + BMR	76.38	76.38	0	0.00	> 0.05
Exploration~mass + BMR	60.19	60.19	0	0.00	> 0.05

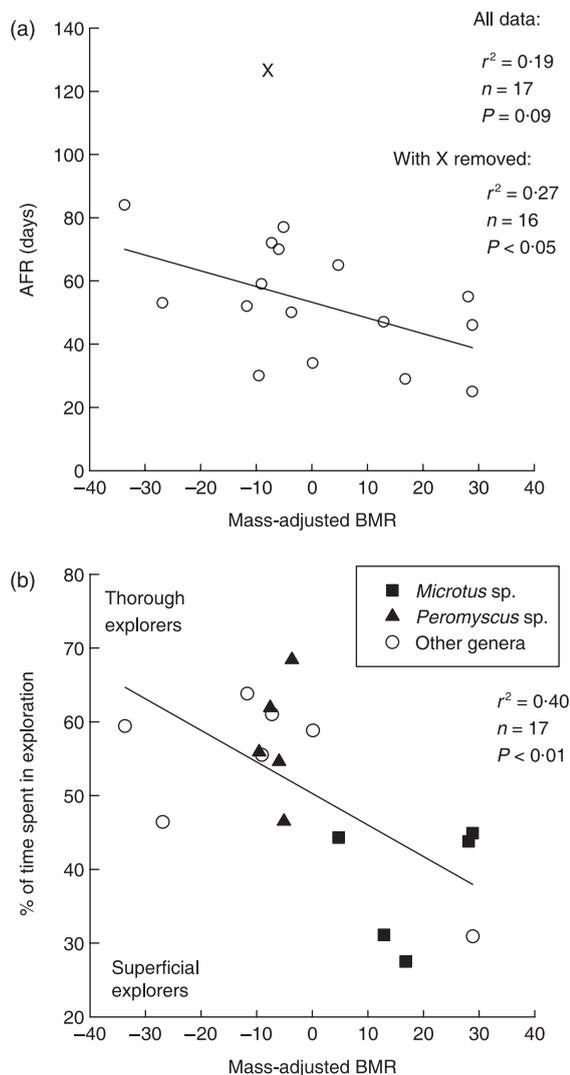


Fig. 3. (a) Age at first reproduction (AFR, in days) and (b) percent of time spent exploring a novel environment (in a 10-min open-field test) as function of residual variation in basal metabolic rate (mass-adjusted BMR), once the effect of body mass has been removed statistically in 17 species of murid rodents. In panel a, the species *Peromyscus eremicus* (X) is identified as an outlier and when removed the relation becomes significant.

2004b; Wolf *et al.* 2007). Because proactive individuals commonly express higher levels of energetically expensive behaviours such as boldness and aggressiveness, we expected this lifestyle to be associated with a higher BMR than the reactive lifestyle. This is what we found, a result that supports the performance model of Careau *et al.* (2008), where BMR represents the maintenance cost of the metabolic machinery necessary to sustain a given energy throughput (Daan *et al.* 1990).

If metabolic rate constrains reproductive rates as suggested by McNab (1980, 2002), then a high BMR should be necessary to sustain fast growth and to achieve early AFR. Our result for murid rodents is consistent with this view (Fig. 3a). However, when Harvey *et al.* (1991) re-analysed the relation between BMR and life-histories in an explicit phylogenetic framework, they found no evidence for McNab's (1980, 2002) claim across all mammals. Later, Symonds (1999) suggested that significant relationships between BMR and life-history traits in mammals are more likely to be restricted to specific taxonomic groups (especially small mammals, which face a metabolic challenge just by being small) rather than across mammals as a whole (as in Harvey *et al.* 1991). Thus, our result based on a small species assemblage supports the conjecture of Symonds (1999).

In this paper, we considered 'walking and running about the field' to be an index of exploration, but one could instead see these behaviours, strictly speaking, as merely an activity index related to locomotion. When (re)viewed from this latter perspective, our result shows more active species to have lower BMRs and to start reproducing later, which supports the allocation model postulating a trade-off between energy invested in maintenance (BMR), activity and reproduction (Careau *et al.* 2008). Identifying the physiological components that underlie a trade-off between activity and BMR has important evolutionary significance. One likely candidate is the immune system because numerous studies have detected large energetic costs tied to its maintenance (Martin, Weil & Nelson 2008a). Some hormones that promote activity (e.g. testosterone and cortisol) are also immunosuppressive (Adkins-Regan 2005) and multiple immunological patterns – which appear to be related to life-history strategies – exist

among *Peromyscus* species (Martin, Weil & Nelson 2008b). An apparent trade-off between activity and BMR may also arise from thermoregulatory constraints because activity can either completely or partially substitute for thermogenesis (Chappell *et al.* 2004; Lovvorn 2008). Therefore, personality traits that underlie activity may simultaneously relax the demand on the metabolic machinery associated with a strong thermogenic capacity, resulting in low BMRs within the thermoneutral zone.

Irrespective of physiological mechanisms, BMR, AFR and exploration thoroughness could be associated with one another simply because selection pressures have favoured particular combinations of traits (Hayes, Garland & Dohm 1992). One such important selection pressure may be food productivity and predictability. Unproductive and unpredictable environments might simultaneously favour high exploration, low BMR (see Lovegrove 2000; Mueller & Diamond 2001) and delayed AFR because exploration increases the likelihood of finding resources pulses, while low BMR and delayed reproduction increase longevity in general and, in particular, the odds of surviving food shortages in such habitats. In contrast, highly productive and predictable environments should favour reduced exploration, fast life-histories and elevated metabolism (Lovegrove 2000).

Small mammals such as muroids have a high mass-specific energy demand and are vulnerable to predation when exploring. Therefore, selection on BMR and exploratory behaviour may be strongly influenced by fluctuations in food abundance. All *Microtus* species examined herein are superficial explorers with high residual BMRs (Fig. 1) – these species all live in grasslands and feed on grass, which offers an abundant and highly predictable food source (Sera & Early 2003). In contrast, all but one of the *Peromyscus* species examined are thorough explorers with low residual BMR – they live in deserts (e.g. *P. eremicus*) or temperate forests and all are omnivorous with a large proportion of their diet consisting of unpredictable pulsed food sources (e.g. seeds; Whitaker 1966). Beyond the *Microtus* and *Peromyscus* clades – which comprise 10 of the 19 species included in our analyses – it is notable that the two lowest BMR values in our dataset are for *Meriones tristrami* and *Rhabdomys pumilio*, two desert rodents characterized by high exploration indices, whereas the highest BMR value is from the golden hamster *Mesocricetus auratus*, which lives in open steppes and agricultural lands and has a low exploration score. This study identifies how environmental conditions may simultaneously influence costs vs. benefits of exploration, life-history and metabolic strategies, all within an explicit phylogenetic framework.

We identified personality as an important integrative variable explaining inter-specific variation in BMR and AFR. Personality also offers promising explanatory power for intra-specific variation in BMR and AFR as well, although intra- and inter-specific relationships are not necessarily similar (Hayes *et al.* 1992). In this respect, it is interesting to note that Wolf *et al.*'s (2007) model and much of the literature on personality is focused on intra-specific variation. The results of this study suggest that species evolving towards a

fast lifestyle with earlier reproduction and a superficial exploration strategy face energetic challenges that are reflected in their high BMRs. Similarly, another study using the open-field test reported that more explorative rats (*Rattus norvegicus*) survived longer than less explorative individuals (Cavigelli & McClintock 2003), and in a recent meta-analysis Smith & Blumstein (2008) found a positive effect of exploration on survival. Therefore, a thorough exploration strategy seems to be associated with a slow pace of life because it is linked to low BMR, delayed reproduction and high survival.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Complete open-field data from Webster *et al.* (1979) and Wilson *et al.* (1976).

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