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# Behavior, metabolism, and size: phenotypic modularity or integration in *Acheta domesticus*?

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#### 1 Abstract

The pace-of-life hypothesis predicts that among-individual differences in behavior should 2 integrate with a wide variety of morphological, metabolic, and life-history traits along a 3 slow to fast pace-of-life continuum. Support for the pace-of-life hypothesis has been mixed, 4 5 in part because most empirical tests have been conducted strictly at the phenotypic level and have thus conflated genetic and environmental sources of covariance among traits. In 6 7 the present study, we tested the hypothesis that, according to the predictions of the paceof-life hypothesis, body-mass, routine metabolic rate, activity, and exploratory propensity 8 would be positively integrated in the house cricket *Acheta domesticus* (Orthoptera: 9 Gryllidae). Using modified open field behavioral tests and flow-through respirometry, we 10 determined whether among-individual differences correlate across morphology, behavior 11 and metabolism in 50 male house crickets. All traits were repeatable, but we found poor 12 evidence for overall integration across traits. Instead we found evidence for modularity, 13 with behavioral traits covarying independently from mass and routine metabolic rate. 14 Modularity, like that found here between activity and exploratory propensity, has been 15 suggested to facilitate adaptive evolutionary change by coupling functionally related traits 16 into suites on which selection can more rapidly act. 17

#### 19 Introduction

20 Phenotypic integration—correlations among phenotypic traits (Armbruster et al., 2014) — 21 can have numerous ecological and evolutionary impacts. For example, evolutionary 22 constraints are an expected product of phenotypic integration (Blows and Hoffmann, 2005), resulting from the inability of traits to respond independently to selection. These 23 correlations thereby generate fitness trade-offs (Careau et al., 2008; Roff, 2002; West-24 Eberhard, 2003). Such trade-offs are necessarily frequent, as the number of traits 25 expressed by organisms relative to the number of genes commonly present necessitates 26 pleiotropy (Walsh and Blows, 2009). Phenotypic integration can be contrasted with 27 modularity wherein traits are integrated within developmental (West-Eberhard, 2003) or 28 functional units (Araya-Ajoy and Dingemanse, 2014) independently from other traits or 29 30 groups of traits.

Recent interest in behavioral syndromes, which represent integration of behavioral 31 traits, is demonstrative of an increased appreciation for the importance of phenotypic 32 integration in behavioral ecology (Sih et al. 2004a, Sih et al. 2004b). Behavioral syndromes 33 elicit many of the same questions as phenotypic integration at large. For example, as with 34 other phenotypic traits, behavioral syndromes are of sufficient strength to have the ability 35 to constrain evolutionary responses available to populations (Dochtermann and 36 Dingemanse, 2013). Importantly our understanding of how behavioral responses integrate 37 with other phenotypic domains (e.g. with physiology and life-history) continues to lag 38 behind our understanding of integration within domains. 39

A variety of physiological and life-history traits are expected to covary with 40 behaviors. For example, Biro and Stamps (2010) and Careau et al. (2008) have suggested 41 that consistent individual differences in metabolic rate (and other physiological processes) 42 43 should promote consistent individual differences in behavior. These same differences in physiology are also expected to integrate consistent individual differences in growth, 44 reproduction, and other life-history processes into a "pace-of-life syndrome" (Biro and 45 Stamps, 2008, 2010; Careau and Garland, 2012; Careau et al., 2008; Reale et al., 2010). 46 Phenotypic integration will be modulated by physiology within a pace-of-life syndrome, as 47 argued by Ricklefs and Wikelski (2002), due to several underlying assumptions likely 48 general to animals (and, indeed, plants). In particular, integration should arise if: (1) 49 organisms respond to environmental variation; and (2) these responses are constrained by 50 limited resources (Ricklefs and Wikelski, 2002). Under the pace-of-life hypothesis 51 52 behavior, physiology and life-history are thus considered non-independent components of an integrated phenotype. 53

Within a pace-of-life syndrome, behavioral responses are expected to correlate with 54 several aspects of life-history and physiology in predictable ways (Reale et al., 2010). For 55 example, higher resting metabolic rates may allow individuals to more rapidly increase 56 57 energy expenditure (Reinhold, 1999). As a result, individuals with higher resting metabolic rates may be able to engage in more costly behaviors (Mathot et al., 2015). More generally, 58 59 under the pace-of-life hypothesis, metabolism is expected to positively correlate with activity, exploratory rate, dispersal, "boldness", and aggression (Reale et al., 2010 but see 60 Houston, 2010). 61

Current support for integration of behavior with metabolic rate according to the 62 pace-of-life hypothesis is mixed (Careau et al., 2015; Mathot and Dingemanse, 2015). 63 Supporting the pace-of-life hypothesis Careau et al. (2010) found that energy expenditure, 64 growth rate, and longevity were all positively correlated with "boldness" and aggression in 65 domestic dogs (Canis lupus familiaris); Mathot et al. (2015) found that metabolic rate and 66 risk-taking were correlated—albeit in a context dependent manner—in great tits (Parus 67 *major* (but see Bouwhuis et al., 2014 where a negative relationship was found between 68 metabolic rate and exploratory behavior in female great tits); Shearer and Pruitt (2014) 69 found that heart-rate, a purported proxy for metabolic rate, and "boldness" were positively 70 correlated; likewise heart-rate and social dominance were positively correlated in red deer 71 (Cervus elaphus; Turbill et al., 2013); growth rate and boldness were positively correlated 72 in crayfish (*Cherax destructor*; Biro et al., 2014); and fast and slow reproductive strategies 73 74 corresponded to fast and slow exploration in eastern chipmunks (*Tamias striatus*; Montiglio et al., 2014). In contrast to this support, Mathot et al. (2013) found that the 75 genetic correlation between metabolic rate and courtship was effectively zero in zebra 76 finches (*Taenipygia guttata*); in yellow mealworm beetles (*Tenebiro molitor*) metabolic rate 77 positively correlated with predator response latency and negatively correlated with time 78 79 immobile, supporting and contradicting the pace-of-life hypothesis respectively (Krams et 80 al., 2014); correlations between metabolic rate and behavior in viviparous lizards (Zootaca *vivipara*) did not differ from zero, although there were slight relationships between 81 behavior and locomotor performance (Le Galliard et al., 2013). Likewise, Gifford et al 82 (2014) found no relationship between metabolic rate and exploratory behavior in 83 salamanders (*Desmognathus brimleyorum*). This mixed support may stem, in part, from 84

difficulties in distinguishing differences among individuals in acquisition—the general
basis for pace-of-life relationships—and allocation trade-offs imposed by resource
availability (van Noordwijk and de Jong 1986; see also Careau et al. 2014).

Regardless of this mixed support, the majority of research into phenotypic 88 integration within a pace-of-life framework has focused on vertebrates. This discrepancy 89 reflects an overall vertebrate bias in the study of behavioral variation (Kralj-Fišer and 90 Schuett, 2014) and the study of behavior more broadly. Nonetheless, the assumptions of 91 the pace-of-life hypothesis will typically be met in invertebrate groups like arthropods. For 92 example, in *Acheta domesticus*, standard metabolic rate accounts for 78% of daily energetic 93 94 expenditure (Hack, 1997). A consequence of this relationship is that allocation of energy to 95 other purposes will be constrained, a necessary requirement for the pace-of-life hypothesis 96 (Ricklefs and Wikelski, 2002). Further, an important limitation of pace-of-life research is that empirical tests are often conducted strictly at the phenotypic level, thus conflating 97 genetic and environmental effects (Dingemanse and Dochtermann, 2013, 2014; 98 Dingemanse et al., 2012). This conflation means that phenotypic correlations can differ 99 substantially from, for example, among-individual or genetic correlations (Dingemanse and 100 Dochtermann, 2013, 2014; Dingemanse et al., 2012; Downs and Dochtermann, 2014 but 101 102 see Dochtermann, 2011) and thereby lead to inappropriate evolutionary or ecological inferences. 103

Within this framework of phenotypic integration and the pace-of-life hypothesis, we
 were interested in whether behaviors covary with physiology and morphology in house
 crickets (*Acheta domesticus*). We have previously demonstrated that *A. domesticus* exhibits

repeatable behavioral variation with respect to activity and exploratory propensity
(Dochtermann and Nelson, 2014), and Wilson et al. (2010) demonstrated that several
behaviors of *A. domesticus* were correlated at the phenotypic level. Here we sought to
determine whether individual differences in activity and exploration propensity were
correlated with adult mass and routine metabolic rate at the among-individual level.
Support for the pace-of-life hypothesis is expected to be confirmed if all traits are found to
be positively correlated.

#### 114 Methods

Male five-week old *Acheta domesticus* were commercially obtained (Fluker Farms) and
initially housed communally with shelter, *ad libitum* food (ground Purina chick starter),
and water. At least 7 days prior to any behavioral and metabolic testing subjects were
moved from communal to individual housing. Crickets were individually housed in 0.71
liter containers and provided with *ad libitum* food and water, as well as egg carton pieces
for shelter. All individuals were maintained under a 12:12 light/dark photoperiod.

#### 121 Behavioral tests

We measured behavioral responses using a modified open field test, in which individuals had to navigate around multiple obstacles to explore the entire arena (Figure 1). The arena was 60 cm × 60 cm × 10 cm, constructed of sealed and painted plywood with a Plexiglas lid. This obstacle course behavioral protocol was previously used with *A. domesticus* to evaluate exploratory behavior (Dochtermann and Nelson, 2014) and, here, is being used to assess exploratory propensity and activity levels.

Individuals were introduced into the lower right section of the arena (Z1, Figure 1) 128 and allowed to move throughout the arena for 180 seconds after introduction. Recording 129 started upon introduction for all individuals. We digitally recorded all behavioral trials and 130 131 used Noldus Ethovision (Noldus Information Technology) to track movements of these individuals from digital videos. Using Ethovision we superimposed a 5 × 5 grid on the arena 132 (Figure 1) and recorded the location and movement of individuals through the resulting 25 133 zones. As a measure of "exploratory propensity" we recorded the number of unique zones 134 visited. As a measure of "activity" we recorded the total distance moved by an individual. 135 Individual mass was measured immediately prior to behavioral tests. Arenas were cleaned 136 with alcohol wipes and allowed to air-dry between trials. 137

138 Exploratory propensity and activity as operationally defined here are expected to 139 exhibit some degree of structural correlation; i.e. individuals that visit more unique zones 140 necessarily move greater distances and individuals that move greater total distances might, but not necessarily, incidentally visit more unique zones. To address this issue, we 141 developed an individually-based simulation model described in greater detail in the 142 supplemental materials. In short, we modeled the movement of individuals through a 60 143  $cm \times 60$  cm area as a random walk and then calculated the correlation between activity 144 (total distance moved) and unique zones visited. Using this model, we estimated the null 145 structural correlation as 0.199. Unfortunately there is no *a priori* basis on which to 146 determine how this correlation is expected to be divided between the among- and within-147 individual levels. 148

149 Individuals were generally tested in the obstacle course twice, although due to 150 natural mortality some were only able to be tested once ( $N_{twice} = 42$ ,  $N_{once} = 10$ ).

We used CO<sub>2</sub> emission rate as an index of aerobic metabolic rate, as we have 152 previously done with other invertebrates (Yocum et al., 2011; Greenlee and Harrison, 2004, 153 154 2005; Owings et al. 2014). Crickets were weighed on an analytical balance to the nearest 0.01 mg (Mettler Toledo, Columbus, OH) just prior to and immediately following metabolic 155 measurements. Crickets (n = 42) were placed individually into 20 ml respirometry 156 157 chambers constructed from 50 ml syringes plumbed with Tygon tubing. Chambers were covered and the room was kept dark during recording to minimize activity. Using a 158 multiplexor (Intelligent Multiplexor V3, Sable Systems, Inc., Las Vegas, NV), seven crickets 159 160 plus a baseline chamber were run concurrently. Dry, CO<sub>2</sub> free air (Balston purge gas 161 generator, Haverhill, MA) was pushed through the measurement chamber and directed to 162 the CO<sub>2</sub> analyzer (LiCor 6252, Lincoln, NE) at a flow rate of 500 ml min<sup>-1</sup> using a mass flow 163 meter (Sierra Instruments, Monterey, CA) controlled by a mass flow controller (MFC-4; Sable Systems, Inc., LasVegas, NV). While not being measured, remaining chambers were 164 flushed with dry, CO<sub>2</sub> free air (140 ml min<sup>-1</sup>, Ametek R2 pump). We used Sable Systems 165 software (Expedata version 1.4.15) and hardware (UI2) to control switching between 166 chambers and to record data. One round of sampling from the multiplexed animals began 167 with recording from the baseline chamber (identical, but lacking a cricket) for 1 min. After 168 this time, the sample airstream was switched to chamber 1, and data were recorded for 5 169 min. The multiplexor was programmed to switch to the baseline chamber between each of 170 the subsequent animal chambers, which were sampled in series for 5 min each. Crickets 171 were each sampled four times for 5 min each. We calculated mass loss during the time 172 that animals were in the chambers. 173

174	We used Expedata to calculate the mean $\mathrm{CO}_2$ emission for each sampling period,
175	trimming the first and last 30 sec of each sampling period from each recording. Because
176	animals were not immobilized, we could not ensure a true resting metabolic rate. Instead
177	our measurement of metabolic rate represents an estimate of "routine metabolic rate"
178	(sensu Makarieva et al. 2008). We calculated routine metabolic rate (RMR) from baseline-
179	corrected $CO_2$ emission data as in Greenlee and Harrison (2004, 2005):
180	MCO <sub>2</sub> ( $\mu$ mol CO <sub>2</sub> h <sup>-1</sup> ) = Vin × ( <u>FECO<sub>2</sub> – FECO2</u> ) × <u>60</u> × <u>1000</u> × <u>22.4<sup>-1</sup></u>
181	where Vin is the upstream flow rate in ml min-1, FECO2 = 0. ml $g^{-1}$ ·min <sup>-1</sup> were converted to
182	$\mu mol \cdot g^{-1} \cdot h^{-1}$ using the following conversion factors: 1000 \cdot \mu l \cdot ml^{-1},
183	$60 \cdot \text{min} \cdot h^{-1}$ and $22.4 \cdot \mu l \cdot \mu \text{mol}^{-1}$ . MCO <sub>2</sub> was calculated for each of the four sampling periods
184	and these MCO <sub>2</sub> estimates used in subsequent analyses.
185	
186	Data analysis

To estimate the cross-domain relationships and overall phenotypic integration we 187 188 employed a two part analysis (see also Sprenger et al., 2012). First, we estimated the among-individual and within-individual variances and covariances for exploratory 189 190 propensity, activity, routine metabolic rate, and mass. Second, we used Structural Equation Modeling (SEM) to test a priori hypotheses about how morphological, physiological and 191 behavioral traits may be integrated. Among-individual and within-individual variances and 192 covariances were estimated using multiresponse mixed-effects models (Dingemanse and 193 Dochtermann, 2013, 2014; Dingemanse et al., 2012). We estimated among-individual and 194 within-individual components separately, because phenotypic correlations can be 195

misleading as to the direction and magnitude of trait relationships at the level ofindividuals when individuals can vary their own responses (Dingemanse and

198 Dochtermann, 2013; Downs and Dochtermann, 2014).

In our mixed-effects models we included individual as a random factor. Condition 199 (injured or not, four individuals had minor appendage injuries), time of testing and 200 temperature (centered within individuals; van de Pol and Wright, 2009) were included as 201 fixed effects to control for potential confounds and "pseudo-repeatability" or "pseudo-202 personality" (Nakagawa and Schielzeth, 2010; Westneat et al., 2011). Because we were only 203 interested in the variance components, we will not discuss the fixed effects results (see 204 Table S1). We modeled all variables according to a Gaussian distribution and scaled them 205 to standard deviation units. Mass and RMR were log<sub>10</sub>-transformed to linearize the 206 207 exponential relationship between these variables. Analyses were conducted using the MCMCglmm package (Hadfield, 2010) of R (R Development Core Team 2014) with  $1.3 \times 10^6$ 208 iterations, with a  $3 \times 10^5$  iteration burn-in and thinning intervals of 1000. We used a prior 209 that was flat and uninformative for the correlations. 210

From these mixed-effects models, we estimated behavioral, morphological, and 211 physiological repeatabilities and the among- and within-individual correlations across the 212 213 traits. Because they were assessed during separate testing events, we could not estimate the within-individual correlation of RMR with either activity or exploratory propensity. 214 215 Similarly, the within-individual correlation between mass and RMR could not be estimated. While our sample size for estimating among-individual correlations had low power to 216 distinguish estimates from zero, our correlation should have had relatively low bias (see 217 Figure 1 in Dingemanse and Dochtermann 2013) making these estimates useful in SEM 218

219	comparisons. The posterior modal estimates of the among- and within-individual
220	correlation matrices were used in the second part of the analysis.
221	For the second part of the analysis we used a structural equation model comparison
222	approach to assess how the different traits might be linked (Dingemanse et al., 2010a;
223	Dochtermann and Jenkins, 2007). We compared a priori models using Akaike's Information
224	Criterion (AIC). Eleven models of trait covariance were evaluated at the among-individual
225	level and four at the within-individual level (Figure 2):
226	model 1: all traits independent (evaluated for among- (A) and within-individual (W)
227	correlation matrices)
228	<i>model 2</i> : only behaviors correlated (A & W)
229	model 3: only mass and RMR correlated (A)
230	model 4: behaviors are correlated but independent from mass and RMR, which are also
231	correlated (A)
232	model 5: behaviors integrated with RMR via an underlying latent variable (A)
233	<i>model 6</i> : behaviors integrated with mass via an underlying latent variable (A & W)
234	model 7: all four traits integrated via an underlying latent variable (A)
235	<i>model 8</i> : both behaviors arise causally from the influence of RMR and mass (A)
236	model 9: both behaviors arise causally from the influence of RMR (A)
237	model 10: both behaviors arise causally from the influence of mass (A & W)

*model 11*: mass causally influences RMR and both behaviors arise causally from the
influence of RMR and mass (A)

Of these eleven models, model 1 represents null expectation, models 5-7 represent crossdomain trait integration, and models 8-11 represent causal influences of morphology and
physiology on behavior.

#### 243 **Results**

The four phenotypic measures showed repeatabilities (R) ranging from moderate to high 244 (Table 1), with mass showing the highest repeatability (R = 0.89) and behavior and routine 245 metabolic rate showing moderate repeatabilities (0.28 < R < 0.61, Table 1). At the among-246 247 individual level, activity (distance moved) and exploratory propensity (unique zones visited) were positively correlated while separately RMR and mass were positively 248 249 correlated (among-individual correlations: r = 0.56 and 0.53 respectively). Both of these correlations had 95% credibility intervals excluding 0 (Table 1). Remaining among-250 251 individual correlations did not differ from 0 (Table 1).

At the within-individual level only activity and exploratory propensity were correlated (r = 0.75, Table 1). In addition, the phenotypic correlation after controlling for fixed-effects and repeated measures between activity and exploratory propensity (calculated following Dingemanse et al. 2012) was substantially higher than the expected correlation derived from null expectations ( $r_P = 0.70 (0.57 : 0.79)$ ,  $r_{PNULL} = 0.19$ ; see Supplementary Information).

Consistent with the bivariate correlations, SEM model comparison results suggest
that model 4 (Figure 2) best explains the data at the among-individual level (Table 2). This

model suggests behavioral integration separate from the expected relationship between
RMR and mass. At the within-individual level, the model in which only behaviors covaried
(model 2) was best supported by the data (Table 2). However, since behavioral and
physiological measurements were not taken within the same time-spans, several of the
proposed models could not be fit to the within-individual correlation matrix.

#### 265 Discussion

266 We sought to determine whether A. domesticus exhibits phenotypic integration of behaviors, metabolic rate, and morphology as expected according to the pace-of-life 267 hypothesis. Ultimately, we did not find support for integration of behavior and metabolism 268 but found substantive correlations between activity and exploratory behaviors and, 269 270 separately, between routine metabolic rate and mass. The relationship between mass and metabolic rate has previously been observed in A. domesticus (Hack, 1997) and is expected 271 272 for allometric reasons (e.g. Downs et al., 2008). We also found that all four of the traits we measured exhibited considerable repeatable variation (Table 1), suggesting underlying 273 274 genetic variation is present in each (Boake, 1989). Meta-analyses suggest that, on average, about half of the repeatable variation present in behaviors corresponds to additive genetic 275 276 variation with the other half being attributable to permanent environmental differences (Dochtermann et al., 2015). How genetic variation and permanent environmental variation 277 278 might influence A. domesticus behavioral variation is unclear and future research should 279 address the heritability of and genetic correlations among these traits.

Our results also build on previous work by Wilson et al. (2010), who found that *A*.
 *domesticus* exhibited significant phenotypic correlations among several behavioral

measures. Specifically, our results extend those previous findings by demonstrating that
behavioral measures of presumably similar ecologically relevant behaviors demonstrate
repeatable variation. Our results therefore suggest that among-individual correlations
likely contribute to the phenotypic correlations reported by Wilson et al. (2010).

Importantly we did not find evidence for integration of behavior with metabolism. 286 Identifying correlations between behavior and metabolic rate is potentially problematic as 287 under most testing conditions the later cannot be measured independent of the former 288 (Mathot and Dingemanse, 2015). For example, activity in behavioral assays is expected to 289 positively correlate with routine metabolic rate simply because more active individuals will 290 also be more active during metabolic measurements. Such a correlation might be 291 incorrectly viewed as support for the pace-of-life hypothesis if routine metabolic rate is a 292 293 poor predictor of daily energy expenditure (Mathot and Dingemanse, 2015). This concern 294 is less valid for our results for two reasons. First, standard metabolic rate accounts for 78% of the daily energy expenditure of *A. domesticus* (Hack, 1997) and thus necessarily strongly 295 correlates with routine metabolic rate. Second, in our case the concern about RMR being a 296 poor predictor of daily energy expenditure is not likely to be valid, because the estimated 297 among-individual correlation between routine metabolic rate and activity did not differ 298 from zero (Table 1). Finally, because all individuals were provided with *ad libitum* food, we 299 also do not consider it likely this lack of a connection between behavior and physiology 300 reflects a balancing of allocation and acquisition trade-offs. 301

Our failure to detect phenotypic integration of behavior and physiology is
 particularly interesting given the considerable theoretical and conceptual literature that
 suggests such links are to be expected (Biro and Stamps, 2010; Careau et al., 2009; Careau

and Garland, 2012; Careau et al., 2008). In particular, pace-of-life models have posited that 305 among-individual differences in behavior, i.e. personality (sensu Dingemanse and 306 Dochtermann, 2013; Dingemanse et al., 2010b), might arise from underlying differences in 307 308 energy use (Careau et al., 2009; Careau and Garland, 2012; Reale et al., 2010). Such a connection with physiology might then integrate behavioral variation with aspects of life-309 history and slow versus fast-paced strategies (Reale et al., 2010). Here we found that 310 neither a causal relationship from metabolic rate to behavior nor general covariance of 311 behaviors and metabolic rate were supported. This lack of support for such cross-domain 312 connections does, however, fit with some recent failures to support pace-of-life predictions. 313 For example, in brown trout (Salmo trutta), behavioral variation was correlated to life-314 history variation opposite to the direction predicted (Adriaenssens and Johnsson, 2011). 315 Our results and corresponding findings elsewhere suggest that arguments such as a general 316 317 connection among behaviors and physiology due to "pace-of-life" and other conceptual constructs should be reevaluated. 318

Integration of traits exists on a continuum with "modularity", i.e. independence or 319 "discreteness" of traits (West-Eberhard, 2003). Integration may also exist within 320 modularity; specifically, traits that show integration due to shared developmental or causal 321 pathways (West-Eberhard, 2003) or that have been jointly shaped by selection for a 322 particular function (Araya-Ajoy and Dingemanse, 2014) may be integrated within modules 323 independent from other traits. Here, activity and exploratory propensity can be considered 324 as a module independent of metabolic rate and mass. Our observation of modularity rather 325 than integration across phenotypic domains is important to consider in terms of the 326 potential ecological and evolutionary implications of behavioral syndromes. While 327

328	behavioral syndromes might have direct effects on evolutionary outcomes for behavior
329	(Dochtermann and Dingemanse, 2013), our results here suggest that these evolutionary
330	consequences might not carry-over across phenotypic domains. Our findings here that
331	behavior often exists in an integrated module (e.g. as a behavioral syndrome) separate
332	from physiology affords populations with greater adaptive potential, allowing functionally
333	related traits to respond rapidly to changing evolutionary pressures (West-Eberhard,
334	2003).
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340	
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490	

491 Tables and Figures

Table 1. Trait repeatabilities (shaded diagonal), among-individual correlations (above
diagonal), and within-individual correlations (below diagonal, italicized). Values in bold
indicate correlations with 95% credibility intervals (in parentheses) that <u>do not</u> overlap

495 zero.

	Activity	Exploratory Propensity	RMR	Mass
Activity	0.28	<b>0.56</b>	0.02	0.16
	(0.20 : 0.51)	(0.17 : 0.77)	(-0.43 : 0.34)	(-0.26 : 0.51)
Exploratory	<b>0.75</b>	0.33	0.15	0.13
Propensity	(0.49 : 0.80)	(0.18; 0.48)	(-0.27 : 0.48)	(-0.24 : 0.52)
RMR	-0.04*	-0.16*	0.61	<b>0.53</b>
	(-0.49 : 0.45)	(-0.43 : 0.42)	(0.48 : 0.75)	(0.28 : 0.76)
Mass	0.05	-0.06	0.02	0.89
	(-0.08 : 0.22)	(-0.14 : 0.17)	(-0.22 : 0.29)	(0.84 : 0.93)

496 \*These values could not be estimated and, as reflected by their credibility intervals, roughly center on zero.

497 Variation around zero is due to stochasticity in the MCMC process.

ŀ	Among-individual			Within-individual		
Model	AIC	ΔΑΙC	Model	AIC	ΔΑΙϹ	
Model 4	540.07	0.00	Model 2	531.22	0.00	
Model 2	554.29	14.22	Model 6	535.09	3.87	
Model 6	556.80	16.72	Model 1	571.51	40.29	
Model 5	557.11	17.04	Model 10	575.21	43.99	
Model 3	557.29	17.22				
Model 7	557.83	17.75				
Model 11	562.21	22.14				
Model 1	571.51	31.44				
Model 10	573.23	33.15				
Model 9	574.31	34.24				
Model 8	576.43	36.35				

Table 2. Model comparison results at the among- and within-individual levels. For modeldescriptions see Figure 2.

504 Figures

Figure 1. Obstacle course arena. Individuals were introduced into zone 1 (Z1) and allowed
180 s to explore the arena. Shaded areas represent the placement and size of obstacles
within the arena.

508

509 Figure 2. A priori models of how the four traits might covary. In model 1, all traits are independent. In model 2 (path a active), the two behavioral measures covary. In model 3 510 511 (path b active), routine metabolic rate (RMR) and mass covary. In model 4 (paths a and b active), the two behavioral measures covary while separately RMR and mass covary. In 512 model 5 (path c active) the two behaviors covary with routine metabolic rate (RMR) while 513 mass varies independently. In model 6 (path d active), mass covaries with the two 514 515 behavioral measures while RMR varies independently. In model 7 (paths c & d active), RMR and mass covary with each other and with the two measured behaviors. In model 8 (paths 516 517 e through h active), the two behaviors are hypothesized to covary due to the joint effects of mass and RMR. In model 9 (paths e and f active), the two behaviors are hypothesized to 518 covary due to the effects of RMR. In model 10 (path g and h active), the two behaviors are 519 hypothesized to covary due to the effects of mass. In model 11 (paths e through i active), 520 the two behaviors covary due to the effects of both RMR and mass while variation in RMR 521 arises (in part) due to variation in mass. 522





524 525 Figure 1.



528 Figure 2.

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