



HAL
open science

The fast and the curious II: performance, personality, and metabolism in Karoo bush rats

Paul Agnani, Jennifer Thomson, Carsten Schradin, Vincent Careau

► **To cite this version:**

Paul Agnani, Jennifer Thomson, Carsten Schradin, Vincent Careau. The fast and the curious II: performance, personality, and metabolism in Karoo bush rats. *Behavioral Ecology and Sociobiology*, 2020, 74 (10), 10.1007/s00265-020-02908-y . hal-02966807

HAL Id: hal-02966807

<https://hal.science/hal-02966807>

Submitted on 14 Oct 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **The fast and the curious II:**
2 **performance, personality and metabolism**
3 **in Karoo bush rats**
4

5 Paul Agnani^{1*}, Jennifer Thomson², Carsten Schradin^{3,4}, and Vincent Careau¹

6
7 Published as

8 [Agnani, P., Thomson, J., Schradin, C. & Careau, V. 2020. The fast and the curious II: performance, personality, and](#)
9 [metabolism in Karoo bush rats. *Behavioral Ecology and Sociobiology*, 74, 123.](#)
10

11
12 ¹Department of Biology, University of Ottawa, ON, Canada.

13 ²University of St Andrews, Scottish Oceans Institute, Gatty Marine Laboratory, St Andrews
14 KY16 8LB, Scotland, UK.

15 ³CNRS, IPHC UMR 7178, Université de Strasbourg, F-67000 Strasbourg, France.

16 ⁴School of Animal, Plant and Environmental Sciences, University of the Witwatersrand,
17 Johannesburg, South Africa.

18 *Author for correspondence:

19 pagnani@uottawa.ca

20 ORCID: 0000-0002-1137-0774

21 Department of Biology

22 University of Ottawa

23 30 Marie Curie, Ottawa, ON, CANADA, K1N 6N5

24 Tel: (613) 562-5800 x6349

25 Fax: (613) 562-5486
26

27 **Running title:** Exploration and locomotor performance

28
29
30

31 **Abstract**

32 Personality traits (e.g., activity, exploration, boldness) are frequently correlated with each
33 other and with various other traits of biological importance. According to the performance,
34 allocation, and independent models of energy management, the relationship between
35 personality traits and resting metabolic rate (RMR) is predicted to be either positive,
36 negative, or nil. As for the relationship between personality traits and locomotor
37 performance, the trait compensation and co-specialisation hypotheses respectively predict a
38 positive and negative relationship. To test for associations between personality, metabolism,
39 and performance, we studied a wild population of Karoo bush rat (*Myotomys unisulcatus*) in
40 South Africa. During summer 2018 we captured 45 individuals (38 females and 7 males) a
41 total of 293 times and repeatedly measured docility (time spent immobile during a bag test),
42 exploration (distance moved in an open-field test), sprint speed, and RMR. We found a
43 behavioural syndrome in our population, as more docile individuals covered less distance in
44 the exploration test ($r \pm SE = -0.74 \pm 0.21$). RMR was not correlated with any trait; therefore, the
45 independent energy management model applies in this population. Fast sprinters were less
46 explorative in the novel environment than slow sprinters ($r \pm SE = -0.41 \pm 0.21$), going against
47 the prediction of the phenotypic compensation hypothesis and suggesting co-specialisation
48 of these traits. A similar result was previously observed in two other rodent species,
49 suggesting that exploratory behaviour and locomotor performance may interact in an
50 additive instead of compensatory way. Given the apparent complexity of the links between
51 performance, behaviour, and metabolism, more studies are needed in order to understand
52 their relationships.

53 **Keywords:** Among-individual correlations, basal metabolic rate, personality, running
54 performance, resting metabolic rate.

55

56 **Significance Statement**

57 In this study, we test alternative energy management models and hypotheses predicting
58 different relationships between behavioural, performance, and metabolic traits. Our results
59 support the independent model of energy management, since resting metabolic rate was
60 not correlated with either docility nor exploration. The negative relationship between
61 exploration and sprint speed is counter to the intuitive idea that more explorative individuals
62 should be better equipped to deal with the increased risks of predation, but instead
63 supports the co-specialisation hypothesis. Finally, we emphasize the importance of
64 partitioning the variance in raw measurements as a way to better appreciate variability in
65 measurements of metabolic rate and locomotor performance. Such multilevel analyses
66 provide an idea of the relative variability at among-individual level vs. other levels (tests,
67 trials, and residuals), which might have important implications for the understanding of how
68 factors like stress and motivation might potentially generate or obfuscate relationships
69 between behavioural, performance, and metabolic traits.

70

71 **Introduction**

72 The field of animal personality – defined as repeatable individual differences in activity,
73 exploration, boldness, aggressiveness, and sociability – has experienced a major surge in
74 interest over the last 20 years (Stamps 1991; Dingemanse and Réale 2005; Dingemanse et al.
75 2010; Stamps and Groothuis 2010; Carter et al. 2013). Salient features of animal personality
76 studies are 1) the focus on individual variation and 2) the use of standardised tests to
77 measure individual behavioural reactions to various situations (e.g., novel, familiar, and risky
78 situations). Although behavioural tests are sometimes conducted in an unnatural context
79 (e.g., the open-field test), individual differences captured in these tests are thought to relate
80 to behaviours exhibited in various natural situations such as habitat use, predation
81 avoidance, dispersal, or social behaviours (Dingemanse et al. 2003; Dall et al. 2004) and have
82 been validated in many cases (Fraser et al. 2001; Boon et al. 2008; Boyer et al. 2010; van
83 Overveld and Matthysen 2010; Yuen et al. 2016). As such, personality traits have been found
84 to affect fitness components (Dingemanse and Réale 2005; Moiron et al. 2020 but see Smith
85 and Blumstein 2008)

86 Personality traits are frequently correlated with each other, in which case they can
87 be referred to as behavioural syndromes (Sih et al. 2004). Behavioural syndromes imply
88 limited plasticity in behaviour (Sih et al. 2004). Although individuals may display different
89 levels of aggressiveness depending on contexts, more aggressive individuals typically remain
90 more aggressive in all contexts (i.e., rank order maintained) and are also generally bolder
91 than less aggressive individuals (Riechert and Hedrick 1993). Behavioural syndromes are
92 especially relevant to the field of animal behaviour as they may help us understand the
93 maintenance of inter-individual variation in behaviour. If personality traits are correlated

94 across different contexts, personality traits may not evolve independently from each other,
95 but instead as a suite of correlated traits (Price and Langen 1992). Furthermore, personality
96 traits may not only correlate with each other, but also with other traits of biological
97 importance such as circulating hormones levels (Chang et al. 2012), aspects of the immune
98 system (Butler et al. 2012; Monceau et al. 2017), locomotor performance (Careau and
99 Garland 2012) and metabolic rate (Careau et al. 2008).

100 All biological processes in an organism require energy, for which individuals must
101 match metabolic fuel supply (lipids, carbohydrates, and protein) to ever-changing energy
102 demands (Weber 2011). The rate at which an individual oxidizes substrates to produce
103 energy has been defined as the metabolic rate. Due to the highly variable nature of
104 metabolic rate in response to various factors (e.g., temperature, biosynthesis, activity), a
105 certain degree of standardisation is required to compare metabolic rate among individuals.
106 Basal metabolic rate (BMR) – the lowest rate at which substrates are oxidized by an
107 endotherm to stay alive – is often measured as the O₂ consumption of an animal that is alert
108 but resting, fasting (i.e., post-absorptive), not reproducing or growing, within its thermal
109 neutral zone, and is measured during the inactive part of the animal's daily cycle (Speakman
110 2013). Despite the highly standardised nature of BMR measurements, there usually remains
111 a large degree of inter-individual variation within populations (Speakman et al. 2004). In
112 many circumstances, especially in field studies, it is not possible to meet all of the criteria to
113 measure BMR, in which case measurements are referred to as resting metabolic rate (RMR).
114 BMR and RMR are nevertheless considered analogous traits (hereafter referred to as RMR).

115 The links between RMR and animal personality have been intensely explored over
116 the last decade (Careau et al. 2011; Killen et al. 2011; Le Galliard et al. 2013; Bouwhuis et al.

117 2014; Gifford et al. 2014; Krams et al. 2017; Chen et al. 2019; Cornwell et al. 2020).
118 According to the allocation model, which assumes that there is a finite amount of energy
119 that an animal can spend on competing processes, behaviours such as activity should be
120 negatively correlated with RMR, as a higher RMR will result in less energy available to spend
121 on activity, and *vice versa* (Speakman 1997; Careau et al. 2008). Alternatively, according to
122 the performance model, RMR and activity should be positively correlated because more
123 active individuals sustaining higher levels of energy expenditure should require a larger
124 “machinery” (larger organs) which, at rest, leads to a higher RMR (Daan et al. 1990; Careau
125 et al. 2008). Finally, the independent model recognizes that physical activity has a direct
126 impact on daily energy expenditure, but assumes that RMR and physical activity are
127 independent (Careau and Garland 2012).

128 The behavioural repertoire of an animal is, by definition, confined within a space set
129 by its performance abilities (Bennett 1989). Performance – the ability of an individual to
130 perform a task when maximally motivated – includes repeatable traits such as speed,
131 strength, and endurance (Garland and Losos 1994). Intuitively, an individual that can run fast
132 or has a strong bite could behave more boldly and aggressively than an individual that run
133 slow or has a weak bite (Herrel et al. 2009). This intuitive idea corresponds to the “trait
134 compensation” hypothesis developed in the context of co-adaptations between anti-
135 predator behaviour and morphological defence (Dewitt et al. 1999). With respect to
136 locomotor performance, the trait compensation hypothesis received some empirical
137 support. In zebrafish (*Danio rerio*), artificial selection for boldness resulted in the bold line
138 having higher locomotor performance than the shy line (Kern et al. 2016). In the delicate
139 skink (*Lampropholis delicata*), bolder individuals with a “hot thermal type” had faster sprint
140 speeds than shyer individuals with a “cold thermal type” (Michelangeli et al. 2018). In the

141 Asian agamid lizard (*Phrynocephalus vlangalii*), time spent moving during a novel
142 environment test was positively correlated with endurance (Chen et al. 2019).

143 According to the trait compensation hypothesis, a fast sprinter can take more risks
144 (e.g., forage farther from refuge) because it could potentially escape a predator more easily
145 than a slow sprinter. An alternative possibility is that both behaviour and performance
146 enhance overall protection from predation, which corresponds to the “trait co-
147 specialisation” hypothesis that predicts a negative relationship between boldness and
148 locomotor performance (Dewitt et al. 1999). We are aware of three studies that support the
149 trait co-specialisation hypothesis, all on rodents. In Barbary ground squirrels (*Atlantoxerus*
150 *getulus*), escape speed was negatively correlated with time of entrance into the open field
151 (i.e., faster sprinters were shyer; Piquet et al. 2018). Similarly, sprint speed was negatively
152 correlated with distance moved during a novel environment test in Eastern chipmunks
153 (*Tamias striatus*) (Newar and Careau 2018). In Yellow bellied marmots (*Marmota*
154 *flaviventris*), sprint speed was positively correlated with vigilance while foraging (i.e., faster
155 sprinters were more vigilant; Blumstein et al. 2004). Given the contrasting results supporting
156 both the trait compensation and co-specialisation hypotheses, further research is needed on
157 the links between personality and performance, and how these two aspects of the
158 phenotype covary with metabolic rate.

159 Here, we test for associations between behaviour, metabolism, and performance in a
160 wild population of Karoo bush rats (*Myotomys unisulcatus*) in South Africa. Karoo bush rats
161 are diurnal (crepuscular) central-place foragers for which locomotor performance abilities
162 such as sprint speed are important to rapidly travel across open spaces between bushes and
163 therefore play a functional role in survival. At our field site (see below), Karoo bush rats are

164 solitary living (JT and CS, unpublished data), which prevents an influence of social status on
165 personality. We repeatedly captured marked individuals and measured different aspects of
166 their personality (exploration and docility), energy metabolism (RMR), and locomotor
167 performance (sprint speed). Such repeated sets of measures of these traits also allowed us
168 to partition phenotypic correlations into the among-individual correlations (r_{ind} ; correlation
169 between individual means) and within-individual correlations (r_e ; correlation between
170 deviations from the individual means). Although we found no relationship between
171 personality and RMR (supporting the independent model), we found a negative r_{ind} between
172 exploration and sprint speed, thus supporting the trait co-specialisation hypothesis.

173

174 **Methods**

175 *Study site*

176 Karoo bush rats were monitored from February to April 2018 in an area surrounding the
177 Succulent Karoo Research Station in the Goegap Nature Reserve, Northern Cape Province,
178 South Africa (29°41'56"S, 18°1'60"E, altitude 912m). The Succulent Karoo is an arid
179 biodiversity hotspot with a mean annual rainfall of 160mm, our study took place during a
180 drought with ~76mm of rainfall for 2018. At our field site, the minimum night-time and
181 maximum daytime temperatures are respectively -1.5 and 24°C during winter and 4 and
182 42°C during summer (CS, unpublished data).

183

184 *Captures*

185 Sherman-like traps baited with a mix of bran flakes, oil, raisins, salt, and freshly cut apples
186 were used to trap individuals around their nests. Traps were set before the sun was
187 illuminating the valley (6:00-7:00) and checked at first after 45min and again after 90min.
188 For every capture done by one of two observers (PA or JT), individuals were removed from
189 the trap and a bag test was performed before any other handling occurred. The bag test
190 consisted of transferring the individual from the trap into a plastic handling bag, where it
191 was suspended at an arm's length for 1 min while the number of seconds spent immobile
192 was measured using two stopwatches (one for the duration of the test and another for the
193 time spent immobile). This test was previously used to capture aspects of docility and
194 freezing behaviour in the presence of humans (Martin and Réale 2008; Newar and Careau
195 2018). The bag test was not done when individuals were accidentally captured by members of
196 another research team working on striped mice (47 out of 292 captures), in which case the
197 individuals were identified and directly brought to the laboratory without bag test.

198 After the bag test, individuals were identified (or tagged if this was the first capture
199 of an individual, see below), sexed, and weighed using a digital scale (KERN EMB 500, 0.1g
200 precision). Upon first capture, individuals were permanently marked using ear-tags (National
201 Band and Tag Co., Newport, KY, USA) for individual recognition, and immediately released.
202 Ear tagging is a technique considered relatively harmless and more efficient than
203 alternatives techniques of marking, but that can increase tick load (Wood and Slade 1990;
204 Kuenzi et al. 2005; Ostfeld et al. 2017). After the bag test and standard manipulations were
205 done, individuals were either released because they were brought to the lab on the previous

206 day (107 out of 245 captures) or placed back into their traps and transported to an adjacent
207 on-site laboratory where aspects of their behaviour, performance, and metabolism were
208 measured. Up to 9 individuals per day were transported to the laboratory, but not all tests
209 were conducted on all individuals on a given day to avoid rapid habituation to the novel
210 environment and because our respirometry system allowed for measuring only 3 individuals
211 per day. Individuals were released at their nest of capture after completing, one, two or the
212 three tests, depending on their last capture date, and were never kept longer than 7 hours in
213 the laboratory. It was not possible to record data blind because our study involved focal
214 animals in the field.

215

216 *Behavioural test*

217 Once in the laboratory, the first test conducted was an open-field test (Archer 1973). All
218 open-field tests were done between 9:00 to 10:30. Karoo bush rats were released in a white-
219 painted rectangle test arena (80×95cm), where their behaviour was recorded with a camera
220 (Microsoft LifeCam Cinema H5D-00018) for 5 min. Black curtains were placed around the
221 arena to ensure that the individuals could not see the surroundings and were not disturbed.
222 The software EthoVision XT (Noldus Information Technology, Wagenigen) was used to track
223 the individual and extract the total distance moved.

224

225 *Performance test*

226 The second laboratory test, usually conducted between 10:30 to 11:30, was designed to
227 measure sprint speed on a 6m long by 12cm wide plastic racetrack with marks at 1, 2, 3, 4,
228 and 5m allowing to measure the sprint speed over 4m (starting at 1 and ending at 5).

229 Individuals were released at the beginning of the racetrack and allowed to explore shelters
230 (square metal box) at both ends of the racetrack where they could rest/hide in between
231 trials. The individual was then chased by an observer who ran and screamed behind the rat
232 using a piece of cardboard to scratch the surface of the racetrack behind the rat. Videos
233 were recorded using a wide-angle camera at 30 frame per second (DanCoTech A9-DCH-BA).
234 Trials in which the individuals did not run, stopped, or jumped out of the racetrack were
235 discarded. A total of three trials per test were conducted on each rat on a given day. The
236 status of the individual was closely monitored throughout the test to make sure the
237 procedures did not induce any adverse effects (such as injuries or complete exhaustion that
238 could lead to lasting effects after the test ended, which never occurred). Running speed was
239 determined by using the Tracker software (Open Source Physics) by counting frames in
240 between marks. For each test, we extracted the trial that yielded the fastest speed over one
241 meter, this value was retained as the maximum sprint speed for that individual on that day.

242

243 *Respirometry*

244 Respirometry tests were conducted after open-field and sprint speed tests, between 13:00
245 and 16:00. This period corresponds to the non-active phase of the diurnal cycle in Karoo
246 bush rats (they are considered crepuscular and therefore lower their activity in the
247 afternoon to avoid heat; du Plessis et al. 1991). Metabolic rate was measured using a flow-
248 through respirometry system with three chambers and one baseline channel. Ambient air
249 was pumped and directed into a manifold where it was split into 4 different streams. Each
250 individual air stream was directed through a mass-flow meter (FB8, Sables Systems) and sent
251 into one of the 4 chambers (three chambers containing individuals and one empty chamber

252 as baseline) at a flow rate of $\sim 700\text{mL}\cdot\text{min}^{-1}$. Outcoming air was directed through O_2 , CO_2 , and
253 water vapor sensors (FoxBox, RH-300; Sable systems). After monitoring the baseline channel
254 for 5 min, the system sequentially sampled the 3 chambers for 10 min each, after which
255 another baseline measurement was taken. This process was repeated 3 more times, yielding
256 a total of four 10 min samples for each individual on a given day. For each 10 min sample, we
257 extracted the lowest mean O_2 consumption over a period of 4:30 min. The lowest of these
258 four estimates was retained as the RMR of that individual on that day. While in the
259 chambers, individuals were monitored using a webcam (Microsoft Livecam HD-3000) to
260 ensure that they were resting (i.e., not moving). We did not discard any estimates as
261 individuals were always immobile for the timestamps corresponding to the lowest O_2
262 consumptions.

263

264 *Statistical analyses*

265 Statistical analyses were done using ASReml-R version 3 (Gilmour et al. 2009). All traits were
266 standardised to a mean of 0 and a variance of 1. Before analysing sprint speed and RMR, we
267 wanted to gain a better understanding of the variability in the raw measurements at various
268 levels. Indeed, variation in running speed occurs at four different levels; among individuals,
269 among tests within individuals, among trials within tests, and among successive meters
270 within trials. To capture variance at each of these levels, we used a multilevel approach,
271 where random effects of 1) individual identity (ID) captured among-individual variance (V_{ind}),
272 2) ID combined with test captured variance among tests within individuals (V_{test}), and 3) ID
273 combined with test and trial number captured variance among trials within tests (V_{trial}). After
274 accounting for these levels of variance, the residual variance (V_e) represented the variance in

275 running speed between successive meters within trials and measurement error. For
276 metabolic rate, we took 4 repeated measurements per respirometry test; therefore variation
277 in metabolic rate occurs at three different levels; among individuals (V_{ind}), among tests
278 within individuals (V_{test}), and among successive measurements within tests (V_e).

279 In a second step, we extracted daily maximum running speed (hereafter called sprint
280 speed) and the daily minimum metabolic rate (hereafter called RMR) that we used to
281 calculate repeatability and estimate among- and within-individual correlations. We first ran
282 univariate mixed models to assess the effects of Julian day, sex, and test sequence (i.e., the
283 number of times the individual passed the test) on body mass, docility, distance moved in
284 the open field, sprint speed, and RMR. All univariate mixed models included body mass as a
285 fixed effect (except the one in which body mass was the response variable) and included
286 individual identity as a random effect to partition the phenotypic variance (after
287 conditioning on the fixed effects above) into an among-individual variance (V_{ind}) and within-
288 individual variance (V_e ; residuals). Adjusted repeatability of sprint speed, RMR, time spent
289 immobile in the bag test, and distance moved in the open field were calculated as the ratio R
290 $= V_{ind}/(V_{ind}+V_e)$. The approximate standard errors (se) for R were calculated using the delta
291 method using the pin function in `nadiv` (Wolak 2012).

292 We then used a multivariate mixed model to assess the among-individual
293 correlations (r_{ind}) and the within-individual correlations (r_e) between docility, exploration,
294 sprint speed, and RMR. The multivariate model included the same fixed effects as above
295 (body mass, sex, test sequence, and Julian day) fitted to all traits. A 4×4 correlation matrix
296 ('corgh' structure in `ASReml-R`) was fitted at the among-individual level (ID) to estimate V_{ind}
297 and r_{ind} between traits. A 4×4 correlation matrix was also fitted at the residual level to

298 estimate V_e and r_e between traits. The 95% confidence intervals for r_{ind} and r_e were
299 calculated using profile likelihoods with the proLik function in nadiv (Wolak 2012). Best
300 linear unbiased predictors (BLUPs) were extracted from the multivariate mixed model to
301 obtain a graphic representation of r_{ind} and r_e .

302 ASReml-R uses a model-based missing data augmentation method (more specifically,
303 “full information maximum likelihood”) for the estimation of missing values in the response
304 variables of a multivariate mixed model, which allowed us to fully consider all observations
305 made on all individuals throughout the study in our multivariate mixed model. The missing
306 data procedures in ASReml-R can improve the estimation of among-individual correlations
307 and are preferable over “complete cases analyses” (Noble and Nakagawa 2018). Note that
308 although traits were not always all measured on a given day, there was enough overlap
309 between measurements to estimate r_e (e.g., sprint speed and RMR were measured 113
310 times on the same day, sprint speed and exploration were measured 110 times on the same
311 day, and RMR and exploration were measured 87 times on the same day). Our protocol also
312 means that individuals experienced different combinations of testing in the laboratory. We
313 tested the possibility of carry-over effects by creating a dummy variable indicating if the
314 individual was tested in the open field prior to the other measurements, but this variable
315 was not significant for sprint speed and RMR ($P > 0.05$ in both cases). Similarly, a dummy
316 variable indicating if the individual was tested in the race track prior to respirometry did not
317 have a significant effect on RMR ($P > 0.05$). Therefore, we are confident that carry-over
318 effects of sequential testing did not influence the results.

319 Finally, the multilevel analysis above revealed substantial variance in running speed
320 from one meter to the next within performance trials (see below). Therefore, we wanted to

321 explore if behaviour and running speed covary differently at different points along the race
322 track. We fitted a second multivariate model using the same fixed and random effects as
323 above (body mass, sex, test sequence, and Julian day, ID) in which the response variables
324 were the two behavioural traits and running speeds at each meter (speed 1, speed 2, speed
325 3 and speed 4) of the race track. A 6×6 correlation matrix was fitted at the among-
326 individual and residual levels to provide the r_{ind} and r_e between behavioural traits and
327 running speed at each meter of the race track.

328

329 **Results**

330 *Descriptive statistics*

331 We captured and tested a total of 45 individuals (38 females, 7 males), of which 37 were
332 repeatedly tested (8 individuals were only tested once). A total of 244 bag tests, 119 open-
333 field tests, 123 respirometry tests, and 177 sprint speed tests were performed with repeated
334 measures varying between 1 to 14 for each individual (see Table 1).

335 Time spent immobile during the bag test averaged 53.7 seconds (see Table 1 for
336 descriptive statistics). While many individuals remained “frozen” (immobile) for the whole
337 test, a few individuals were more active with the shortest time spent immobile being 5.8
338 seconds. During the open-field test, most rats moved around the walls of the arena, avoiding
339 the centre and moved over relatively short distances (13m) with some individuals showing
340 higher levels of exploration than others (range: 1-40 m). Sprint speed ranged between 1.5 to
341 $4.3 \text{ m}\cdot\text{s}^{-1}$ for an average of $3.2 \text{ m}\cdot\text{s}^{-1}$ which is within the range of the sprint speed recorded
342 on similar sized rodents (Djawdan and Garland 1988). RMR ranged from 0.62 to $2 \text{ mlO}_2\cdot\text{min}^{-1}$

343 with an overall mean of $1.2 \text{ mlO}_2 \cdot \text{min}^{-1}$, which is in accordance with values measured for
344 similar-sized grazing rodents (Bozinovic 1992).

345

346 *Variance in running speed and metabolic rate*

347 Considering all running speed tests and trials, we found that 35.1% of the variance was due
348 to differences between individuals (as estimated by the V_{ind} random effect), while 11.4% was
349 due to differences between days within individuals (as estimated by the V_{test} component)
350 (Table S1). Additionally, only 6.2% of the variance was due to differences between trials
351 within days (as estimated by V_{trial}). Finally, 52% of the variance in running speed occurred
352 among meters within trials (as estimated by V_e). The analysis of sprint speed below is based
353 on the fastest speed recorded over one meter on a given test (day).

354 Considering all respirometry tests, 31.7% of the variance in metabolic rate was due to
355 differences between individuals (V_{ind}), whereas 36.2% was due to differences between days
356 within individuals (V_{test}) (Table S1). Finally, 31.9% of the variance occurred among successive
357 measurements within trials, representing measurement error and variation in metabolic rate
358 (probably due to activity and stress) when rats were restrained within metabolic chambers.
359 The lowest metabolic rate value recorded over the four sampling periods on a given test
360 (day) was extracted as RMR, and which always corresponded periods of inactivity.

361

362 *Effect of mass, sex and test sequence*

363 Males were heavier than females (Table 2A; Fig. 1A). Sex also had a significant effect on
364 sprint speed with males showing slower sprint speed than females (Table 2D; Fig. 1B). Body

365 mass did not affect docility, exploration, and sprint speed (Table 2), but as expected there
366 was a positive effect on RMR (Table 2E; Fig. 1C). Test sequence had a negative effect on
367 distance moved in the open field (Table 2C), especially between the first and second
368 measurements (Fig. 1D), suggesting an habituation effect. Test sequence also had a positive
369 effect on sprint speed (Table 2D; Fig. 1E), suggesting that individuals would perform better
370 as they repeated the sprint speed test. Finally, Julian day had a positive effect on RMR (Table
371 2E).

372

373 *Among- and within-individual correlations*

374 After taking the above-mentioned fixed effects into account, all traits were significantly
375 repeatable, with estimates ranging from $R \pm SE = 0.903 \pm 0.021$ for body mass to $R \pm SE =$
376 0.203 ± 0.115 for RMR (Fig. 2). None of the within-individual correlations were significant
377 (Table 3). At the among-individual level, however, there were two significant correlations
378 (Table 3). There was a strong negative correlation between docility and exploration ($r_{ind} \pm$
379 $SE = -0.740 \pm 0.216$) indicating that individuals who spent more time immobile during the bag
380 test moved over shorter distances during the open-field test (Fig. 3A). There was also a
381 negative correlation between sprint speed and exploration ($r_{ind} \pm SE = -0.399 \pm 0.213$),
382 indicating that the fastest sprinters moved over shorter distances during the open-field test
383 (Fig. 3B).

384

385 *Behaviour vs running speed*

386 Here, we consider all speed measurements from the trial for which sprint speed was
387 extracted and look at the covariance with behaviour. As can be expected, consecutive

388 speeds at each meters were correlated with each other with estimates ranging from 0.999 to
389 0.854 at the among-individual level and 0.563 to 0.230 at the within-individual level (Table
390 S2). At the among-individual level, exploration was negatively correlated with running speed
391 at all positions of the race track, with significant relationships at 3 of the 4 positions (first,
392 second and fourth meter; Table S2; Fig. 4). None of the within-individual correlations were
393 significant between exploration and running speed (Table S2; Fig. 4). By contrast, docility
394 was not correlated with running speed at the among-individual level, but the within-
395 individual correlations changed as function of the position of the race track; the only
396 significant within-individual correlation was with running speed recorded over the first
397 meter of the race track (Table S2; Fig. 4).

398

399 **Discussion**

400 Our objective was to test for correlations between personality, performance, and metabolic
401 rate at the among- and within-individual levels. As previously found in many studies on
402 rodents, we found a behavioural syndrome in our population in which docility and
403 exploration were negatively correlated at the among-individual level. We did not find
404 correlations between RMR and any other traits, including docility and exploration.
405 Therefore, our results support the independent model (Careau and Garland 2012). We found
406 a negative correlation between exploration and sprint speed at the among-individual level.
407 Altogether, our results and those from three other studies on rodents (Blumstein et al. 2004;
408 Newar and Careau 2018; Piquet et al. 2018) provide empirical support for the idea that
409 personality and performance traits are co-specialised.

410

411 *The fast and the curious*

412 If performance determines what individuals can do behaviourally, higher sprinting abilities
413 should allow individuals to take more risks, because those individuals are better equipped to
414 escape potentially dangerous situations (Careau and Garland 2012). Interestingly, however,
415 we found that the individuals with the highest locomotor performance (fastest sprinters)
416 were also less explorative in the open-field test. This is the opposite result to what is
417 predicted from the trait compensation hypothesis (Dewitt et al. 1999). Instead, the negative
418 correlation between sprint speed and exploratory behaviour lends support to the trait co-
419 specialisation hypothesis (see Dewitt et al. 1999), where both traits additively reinforce
420 protection from predators. Although trait compensation seems to be one of the most
421 commonly observed pattern among species between behavioural and morphological
422 defenses, whereby species with larger defenses (e.g., shells) are bolder and/or more
423 explorative (Mikolajewski and Johansson 2004; but see Hossie et al. 2017), studies
424 conducted so far on the functional relationship between behaviour and performance at the
425 individual level suggest that the prevailing pattern is trait co-specialisation in mammals (this
426 study; Blumstein et al. 2004; Newar and Careau 2018; Piquet et al. 2018). In other words,
427 shy or less explorative individuals are less prone to encounter a predator, and in the event of
428 an encounter, their higher sprinting abilities further increase chance of successful escape,
429 and therefore survival.

430 An alternative explanation for the negative relationship between sprint speed and
431 exploratory behaviour could be that the stress response of the individuals covary with
432 individual variation in motivation during the performance tests. For example, if shy
433 individuals are more fearful and anxious than bold individuals, they might be less motivated

434 to explore the arena during the novel environment test, but more motivated to run down
435 the race track at their fastest when being chased. For that scenario to be true, however,
436 there has to be individual variation in motivation, while performance protocols are typically
437 designed to eliminate such variation. Nevertheless, Losos et al. (2002) identified motivation
438 as “the major problem bedeviling studies of performance”, as previous studies showed that
439 some individuals do not use their maximal capacities during the tests (Pough 1989; Garland
440 and Losos 1994). Sub-maximal trials – when animals are judged as not having performed to
441 their maximum – are usually excluded from performance studies, but deciding which trials to
442 exclude may vary across studies. Losos et al. (2002) pointed out that 49% of the 65 studies
443 published between 1979 and 1999 on lizard sprinting abilities did not mention sub-maximal
444 trials, and that only a few studies clearly stated that they excluded these trials. Although we
445 excluded all sub-maximal trials, no individual was excluded from our study. Nevertheless,
446 some variation in motivation must remain among and within retained trials, and, because of
447 the potential covariance it can induce between performance and behaviour, a better
448 appreciation of variation in raw performance measures is warranted (Berberi and Careau
449 2019).

450

451 *Variation in running speed across levels*

452 To our knowledge, only two studies so far have followed a multilevel approach (Araya-Ajoy
453 et al. 2018) and used extra random effects to partition variance in running speed across
454 different temporal scales (Berberi and Careau 2019; Lailvaux et al. 2019). In these studies,
455 17-19% of the variance in running speed occurred at the among-individual level, whereas
456 35% of the variance occurred at that level in our dataset. These relatively low estimates of

457 long-term repeatability imply that many repeated tests per individual are required to
458 properly quantify individual differences in locomotor performance. In contrast to Berberi
459 and Careau (2019) and Lailvaux et al. (2019), we retained running speed measures taken at
460 each meter of the racetrack. Interestingly, the levels with the lowest amount of variance
461 were V_{test} and V_{trial} . Therefore, running speed did not vary much between tests conducted on
462 a given individual throughout the season and between trials conducted on a given day,
463 which is quite encouraging because it suggests that variation in motivation was low at these
464 levels.

465 About half of the variance in running speed resided in the V_e component, which
466 consists of variation in motivation and measurement error. To reduce measurement error in
467 our running speed measurements, we should have used a high speed camera that records at
468 a faster rate than 30 frames per sec. Still, variation in motivation from meter to meter within
469 trials was evident (PA, pers. obs.), which gave us the idea of exploring how behaviour
470 covaries with running speeds recorded at different positions of the race track. We found that
471 docility was correlated with running speed recorded over the first meter of the race track at
472 the within-individual level. Therefore, on a given test day, an individual who remained more
473 immobile during the bag test than its own average ran faster than usual on the first meter of
474 the racetrack. This suggests that individuals who were, for unknown reasons, more fearful of
475 humans on a given day, froze for a longer period during the bag test and displayed a higher
476 acceleration when running away from the chaser. Given that docility and speed were
477 measured in different locations and using different tools, correlated measurement error is
478 unlikely to have caused the r_e between the two traits. Therefore, the r_e must have been
479 caused by correlated phenotypic plasticity with respect to factors that were unaccounted for
480 in our experiment (Brommer and Klueen 2012; Careau and Wilson 2017a, b). Note that the

481 relationship between docility and speed was not apparent in the analyses of sprint speed
482 (Table 3) because the fastest running speed is usually reached in the second and third
483 meters of the race track. Hence, our results show the insights that can be gained from
484 analysing raw running performance measurements, especially when trying to relate
485 performance to behaviours that involve reactions to human presence.

486

487 *Repeatability and behavioural syndrome*

488 Repeatability of behavioural traits is generally higher in the field than in the laboratory,
489 presumably because individuals live in heterogenous environments that permanently
490 influence their behaviour, increasing among-individual differences and therefore
491 repeatability (Bell et al. 2009). In our case, however, adjusted repeatability was $R=0.319$ for
492 docility and $R=0.30$ for exploration, respectively, which is slightly under the reported average
493 repeatability of behaviours ($R=0.37$) (Bell et al. 2009). We also found that the more
494 explorative individuals were less docile. Similar behavioural syndromes have been previously
495 observed in a number of other populations of mammals between docility and exploration
496 (Montiglio et al. 2012; Careau et al. 2015) and between docility, exploration, and activity
497 (Petelle et al. 2015). A similar behavioural syndrome is also exhibited in birds, between
498 docility (assessed with a “back test”) and exploration (Hall et al. 2015) and between docility,
499 aggressivity, and breathing rate (Brommer and Klueen 2012). Thus, the behavioural syndrome
500 we found in bush Karoo rats is very similar to what has been reported for many other
501 species.

502 These behavioural syndromes appears to be reflective of the “flight or fight”
503 response, and have been associated with the proactive-reactive continuum of coping style

504 strategies (Koolhaas et al. 1999). According to the literature on coping styles, individuals
505 consistently differ in their physiological and behavioural response towards stressful
506 situations. Proactive individuals tend to interact with the stressor, while reactive individuals
507 tend to avoid it. Applying this idea to our species, proactive individuals were likely those who
508 moved more in the handling bag trying to escape (therefore being less docile), and who also
509 travelled longer distances in the open-field test (being more explorative). By contrast,
510 reactive individuals were likely those who froze during the bag test and did not travel long
511 distances in the open-field test. More stress-related measures are needed to confirm the
512 associations between docility and exploration behaviour with coping styles in our species.

513

514 *Lack of relationship with RMR*

515 RMR has been previously found to be a repeatable trait in many taxa, with an average
516 estimate of $R = 0.39$ in mammals (White et al. 2013). In this study, the repeatability of RMR
517 was $R=0.203$ after controlling for date, body mass, sex, and test sequence. In other words,
518 only $\approx 20\%$ of the total variance in RMR was attributed to differences among individuals and
519 $\approx 80\%$ of the variance was due to within-individual variation (plasticity) and measurement
520 error. Generally, the repeatability of metabolic rate declines with increasing time between
521 measurement (White et al. 2013), but we think this is an unlikely explanation for the
522 relatively low R observed in our study considering the number of repeated measures we
523 took over a relatively short field season (February 2nd to May 21st). The relatively low
524 repeatability of RMR might be explained by the fact that this study was conducted on wild-
525 caught animals where natural conditions (i.e., food availability and predation risk) varying
526 within individuals affect differently the expression of the metabolism, compared to more

527 stable laboratory conditions (Dingemanse et al. 2009; Kontiainen et al. 2009; Auer et al.
528 2016). The field conditions also forced us to use relatively short respirometry tests (i.e.,
529 animals were only kept 4h in the metabolic chambers), which might have amplified the
530 influence of stress in our RMR measures.

531 We did not find correlations between RMR and any of the other traits we measured
532 (docility, exploration, or sprint speed). Given the relatively low repeatability of RMR and
533 number of individuals sampled, it is possible that we had low power to detect any
534 relationship with RMR. Nevertheless, our results support neither the allocation nor the
535 performance model; instead, it appears the independent model applies in our population, in
536 which RMR and behaviours are not correlated but where non-resting measurements of
537 metabolism (such as the daily energy expenditure) are expected to be correlated to
538 behaviour (Careau and Garland 2012). A recent meta-analysis on the covariance between
539 RMR and behaviour pointed out that RMR was positively correlated with behaviours that
540 likely have consequences for energy gain (e.g., foraging), or expenditure (e.g., sustained
541 running speed), but was not correlated with behaviours that have uncertain energetic
542 outcomes such as the two behavioural traits used in this study (Mathot et al. 2019).
543 Although RMR and behaviours are not correlated in the independent model, behavioural
544 traits still have an influence on the non-resting part of the energy budget (e.g., (Careau et al.
545 2015). In such cases where the independent model applies, the energetic impacts of
546 personality would only be detectable through the measurement of daily energy expenditure,
547 which includes the energetic costs of activity in addition to basal costs of living (and other
548 costs, e.g., thermoregulation).

549

550 **Conclusions**

551 Although it is intuitive to think that bolder and more explorative individuals should be better
552 equipped to deal with the increased risks resulting from those behaviours (trait
553 compensation), empirical evidence in rodents show this is not the case. Instead, it appears
554 that sprint speed is co-specialised with vigilance and exploratory behaviour in rodents (this
555 study; Blumstein et al. 2004; Newar and Careau 2018; Piquet et al. 2018). Future research
556 should tackle the implications of trait co-specialisation for the pace of life, especially survival
557 in prey species. It will also be important to evaluate the contribution of motivation
558 underlying individual co-variation in personality and performance. Doing so might involve
559 using methods for measuring performance with different levels of stress, for exemple tests
560 that rely on individual's survival instincts (i.e., forced swimming), tests with human-induced
561 stress, and tests where individuals perform without being forced. Finally, it will be important
562 to continue partitioning variance in raw performance measurements to get a better sense of
563 where most of the variation occurs.

564

565 **Acknowledgments**

566 We are grateful for the support of Goegap Nature Reserve, Richard Askew, Florian Drouard,
567 and Pauline Vuarin for their help during data collection, and especially to Jennifer Thomson
568 for her deep involvement during data collection and trapping setup. We also thank two
569 anonymous reviewers for their constructive comments on a previous draft of this
570 manuscript. This study was made possible by the administrative and technical support of the
571 Succulent Karoo Research Station (registered South African NPO 122- 134).

572 **Declarations**

573 **Funding**

574 Funding was provided by the University of the Witwatersrand and the Natural Sciences and
575 Engineering Research Council of Canada.

576 **Conflict of interest**

577 We have no conflict of interest to declare.

578 **Ethics approval**

579 All procedures were approved by the University of Ottawa Animal Care Committee (protocol
580 #BL-2659), certified by the Canadian Council on Animal Care. All applicable international,
581 national, and/or institutional guidelines for the use of animals were followed

582 **Consent to participate**

583 Not applicable.

584 **Consent for publication**

585 Not applicable.

586 **Availability of data and material**

587 Databases used in this study are available as supplementary material.

588 **Code availability**

589 The code used to perform the statistical analyses is available as supplementary material.

590 **References**

- 591 Archer J (1973) Tests for emotionality in rats and mice: A review. *Anim Behav* 21:205–235
- 592 Auer SK, Bassar RD, Salin K, Metcalfe NB (2016) Repeatability of metabolic rate is lower for
593 animals living under field versus laboratory conditions. *J Exp Biol* 219:631–634
- 594 Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis.
595 *Anim Behav* 77:771–783
- 596 Bennett A (1989) Integrated Studies of Locomotor Performance. In: Wake DB, Roth G (eds)
597 Complex organismal functions: integration and evolution in vertebrates. John Wiley &
598 Sons Ltd, Chichester, pp 191–202
- 599 Berberi I, Careau V (2019) Performance trade-offs in wild mice. *Oecologia* 191:11–23
- 600 Blumstein DT, Runyan A, Seymour M, et al (2004) Locomotor ability and wariness in yellow-
601 bellied marmots. *Ethology* 110:615–634
- 602 Boon AK, Réale D, Boutin S (2008) Personality, habitat use, and their consequences for survival
603 in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* 117:1321–1328
- 604 Bouwhuis S, Quinn JL, Sheldon BC, Verhulst S (2014) Personality and basal metabolic rate in a
605 wild bird population. *Oikos* 123:56–62
- 606 Boyer N, Réale D, Marmet J, et al (2010) Personality, space use and tick load in an introduced
607 population of Siberian chipmunks *Tamias sibiricus*. *J Anim Ecol* 79:538–547
- 608 Bozinovic F (1992) Rate of basal metabolism of grazing rodents from different habitats. *Am*
609 *Soc Mammal* 73:379–384
- 610 Brommer JE, Klueck E (2012) Exploring the genetics of nestling personality traits in a wild

611 passerine bird: Testing the phenotypic gambit. *Ecol Evol* 2:3032–3044

612 Butler MW, Toomey MB, McGraw KJ, Rowe M (2012) Ontogenetic immune challenges shape
613 adult personality in mallard ducks. *Proc R Soc Lond B* 279:326–333

614 Careau V, Garland T (2012) Performance, personality, and energetics: correlation, causation,
615 and mechanism. *Physiol Biochem Zool* 85:543–571

616 Careau V, Montiglio PO, Garant D, et al (2015) Energy expenditure and personality in wild
617 chipmunks. *Behav Ecol Sociobiol* 69:653–661

618 Careau V, Thomas D, Humphries MM, Réale D (2008) Energy metabolism and animal. *Oikos*
619 117:641–653

620 Careau V, Thomas D, Pelletier F, et al (2011) Genetic correlation between resting metabolic
621 rate and exploratory behaviour in deer mice (*Peromyscus maniculatus*). *J Evol Biol*
622 24:2153–2163

623 Careau V, Wilson RS (2017a) Performance trade-offs and ageing in the ‘world’s greatest
624 athletes.’ *Proc R Soc B* 284:20171048

625 Careau V, Wilson RS (2017b) Of uberfleas and krakens: Detecting trade-offs using mixed
626 models. *Integr Comp Biol* 57:362–371

627 Carter AJ, Feeney WE, Marshall HH, et al (2013) Animal personality: What are behavioural
628 ecologists measuring? *Biol Rev* 88:465–475

629 Chang C, Li CY, Earley RL, Hsu Y (2012) Aggression and related behavioral traits: The impact of
630 winning and losing and the role of hormones. *Integr Comp Biol* 52:801–813

631 Chen J, Qi Y, Wu Y, Wang X, Tang Y (2019) Covariations between personality behaviors and

632 metabolic/performance traits in an Asian agamid lizard (*Phrynocephalus vlangalii*). PeerJ
633 e7205

634 Cornwell TO, McCarthy ID, Biro PA (2020) Integration of physiology, behaviour and life history
635 traits: personality and pace of life in a marine gastropod. Anim Behav 163:155–162

636 Daan S, Masman D, Groenewold A (1990) Avian basal metabolic rates: Their association with
637 body composition and energy expenditure in nature. Am J Physiol-Reg I 259:R333-R340

638 Dall SRX, Houston AI, McNamara JM (2004) The behavioural ecology of personality: Consistent
639 individual differences from an adaptive perspective. Ecol Lett 7:734–739

640 Dewitt TJ, Sih A, Hucko JA (1999) Trait compensation and cospecialization in a freshwater snail:
641 size , shape and antipredator behaviour. Anim Behav 58:397–407

642 Dingemanse NJ, Both C, van Noordwijk AJ, et al (2003) Natal dispersal and personalities in
643 great tits (*Parus major*). Proc R Soc Lond B 270:741–747

644 Dingemanse NJ, Kazem AJN, Réale D, Wright J (2010) Behavioural reaction norms: animal
645 personality meets individual plasticity. Trends Ecol Evol 25:81–89

646 Dingemanse NJ, Réale D (2005) Natural selection and animal personality. Behaviour 1159–
647 1184

648 Dingemanse NJ, Van Der Plas F, Wright J, et al (2009) Individual experience and evolutionary
649 history of predation affect expression of heritable variation in fish personality and
650 morphology. Proc R Soc Lond B 276:1285–1293

651 Djawdan M, Garland T (1988) Maximal running speeds of bipedal and quadrupedal rodents.
652 Am Soc Mammal 69:765–772

653 du Plessis A, Kerley GIH, Winter PED (1991) Dietary patterns of two herbivorous rodents:
654 *Otomys unisulcatus* and *Parotomys brantsii* in the Karoo. S Afr J Zool 26:51–54

655 Fraser DF, Gilliam JF, Daley MJ, et al (2001) Explaining leptokurtic movement distributions:
656 Intrapopulation variation in boldness and exploration. Am Nat 158:124–135

657 Garland T Jr, Losos JB (1994) Ecological morphology of locomotor performance in squamate
658 reptiles. In: Wainwright PC, Reilly S (eds) Ecological Morphology: Integrative Organismal
659 Biology. University of Chicago Press, Chicago, pp 240-302

660 Gifford ME, Clay TA, Careau V (2014) Individual (Co)variation in standard metabolic rate,
661 feeding rate, and exploratory behavior in wild-caught semiaquatic salamanders. Physiol
662 Biochem Zool 87:384–396

663 Gilmour AR, Gogel BJ, Cullis BR, Thompson R (2009) Asreml. Asreml 33:3–8

664 Hall ML, van Asten T, Katsis AC, et al (2015) Animal personality and pace-of-life syndromes:
665 Do fast-exploring fairy-wrens die young? Front Ecol Evol 3:28

666 Herrel A, Andrade DV, De Carvalho JE, et al (2009) Aggressive behavior and performance in
667 the tegu lizard *Tupinambis meriana*. Physiol Biochem Zool 82:680–685

668 Hossie T, Landolt K, Murray DL (2017) Determinants and co-expression of anti-predator
669 responses in amphibian tadpoles: a meta-analysis. Oikos 126:173-184

670 Kern EMA, Robinson D, Gass E, et al (2016) Correlated evolution of personality, morphology
671 and performance. Anim Behav 117:79–86

672 Killen SS, Marras S, Mckenzie DJ (2011) Fuel, fasting, fear: Routine metabolic rate and food
673 deprivation exert synergistic effects on risk-taking in individual juvenile European sea

674 bass. *J Anim Ecol* 80:1024–1033

675 Kontiainen P, Pietiäinen H, Huttunen K, et al (2009) Aggressive ural owl mothers recruit more
676 offspring. *Behav Ecol* 20:789–796

677 Koolhaas JM, Korte SM, de Boer SF, et al (1999) Coping styles in animals: Current status in
678 behavior and stress- physiology. *Neurosci Biobehav Rev* 23:925–935

679 Krams IA, Niemelä PT, Trakimas G, et al (2017) Metabolic rate associates with, but does not
680 generate covariation between, behaviours in western stutter-trilling crickets, *Gryllus*
681 *integer*. *Proc R Soc B* 284:20162481

682 Kuenzi AJ, Zumbrum MM, Hughes K (2005) Ear tags versus passive integrated transponder
683 (PIT) tags for effectively marking deer mice. *Intermt J Sci* 11:66-70

684 Lailvaux SP, Cespedes AM, Houslay TM (2019) Conflict, compensation, and plasticity: Sex-
685 specific, individual-level trade-offs in green anole (*Anolis carolinensis*) performance. *J Exp*
686 *Zool A* 331:280–289

687 Losos JB, Creer DA, Schulte JA (2002) Cautionary comments on the measurement of maximum
688 locomotor capabilities. *J Zool* 258:57– 61

689 Le Galliard JF, Paquet M, Cisel M, Montes-Poloni L (2013) Personality and the pace-of-life
690 syndrome: Variation and selection on exploration, metabolism and locomotor
691 performances. *Funct Ecol* 27:136–144

692 Martin JGA, Réale D (2008) Temperament, risk assessment and habituation to novelty in
693 eastern chipmunks, *Tamias striatus*. *Anim Behav* 75:309–318

694 Mathot KJ, Dingemanse NJ, Nakagawa S (2019) The covariance between metabolic rate and

695 behaviour varies across behaviours and thermal types: meta-analytic insights. *Biol Rev*
696 94:1056–1074

697 Michelangeli M, Goulet CT, Kang HS, et al (2018) Integrating thermal physiology within a
698 syndrome: Locomotion, personality and habitat selection in an ectotherm. *Funct Ecol*
699 32:970–981

700 Mikolajewski DJ, Johansson F (2004) Morphological and behavioral defenses in dragonfly
701 larvae: Trait compensation and cospecialization. *Behav Ecol* 15:614–620

702 Moiron M, Laskowski KL, Niemelä PT (2020) Individual differences in behaviour explain
703 variation in survival: a meta-analysis. *Ecol Lett* 23:399–408

704 Monceau K, Dechaume-Moncharmont FX, Moreau J, et al (2017) Personality, immune
705 response and reproductive success: an appraisal of the pace-of-life syndrome hypothesis.
706 *J Anim Ecol* 86:932–942

707 Montiglio PO, Garant D, Pelletier F, Réale D (2012) Personality differences are related to long-
708 term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Anim*
709 *Behav* 84:1071–1079

710 Newar SL, Careau V (2018) The fast and the curious: locomotor performance and exploratory
711 behaviour in eastern chipmunks. *Behav Ecol Sociobiol* 72:27

712 Noble DWA, Nakagawa S (2018) Planned missing data design: stronger inferences, increased
713 research efficiency and improved animal welfare in ecology and evolution. *bioRxiv*,
714 <https://doi.org/10.1101/247064>

715 Ostfeld RS, Miller MC, Schnurr J (2017) Ear tagging increases tick (*Ixodes dammini*) infestation
716 rates of white-footed mice (*Peromyscus leucopus*). *J Mammal* 74:651–655

- 717 Petelle MB, Martin JGA, Blumstein DT (2015) Heritability and genetic correlations of
718 personality traits in a wild population of yellow-bellied marmots (*Marmota flaviventris*).
719 J Evol Biol 28:1840–1848
- 720 Piquet JC, López-Darias M, van der Marel A, et al (2018) Unraveling behavioral and pace-of-
721 life syndromes in a reduced parasite and predation pressure context: personality and
722 survival of the Barbary ground squirrel. Behav Ecol Sociobiol 72:147
- 723 Pough FH (1989) Organismal performance and Darwinian fitness: approaches and
724 interpretations. Physiol Zool 62:199–236
- 725 Price T, Langen T (1992) Evolution of correlated characters. Trends Ecol Evol 7:307–310
- 726 Riechert SE, Hedrick AV (1993) A test for correlations among fitness-linked behavioural traits
727 in the spider *Agelenopsis aperta* (Araneae, Agenelidae). Anim Behav 46:669-675
- 728 Sih A, Bell AM, Johnson JC, Ziemba RE (2004) Behavioral syndromes: an integrative overview.
729 Q Rev Biol 79:241–77
- 730 Smith BR, Blumstein DT (2008) Fitness consequences of personality: A meta-analysis. Behav
731 Ecol 19:448–455
- 732 Speakman J (1997) Factors influencing the daily energy expenditure of small mammals. Proc
733 Nutr Soc 56:1119–1136
- 734 Speakman JR, Król E, Johnson MS (2004) The functional significance of individual variation in
735 basal metabolic rate. Physiol Biochem Zool 77:900–915
- 736 Stamps J, Groothuis TGG (2010) The development of animal personality: Relevance, concepts
737 and perspectives. Biol Rev 85:301–325

738 Stamps JA (1991) Why evolutionary issues are reviving interest in proximate behavioral
739 mechanisms. *Integr Comp Biol* 31:338–348

740 van Overveld T, Matthysen E (2010) Personality predicts spatial responses to food
741 manipulations in free-ranging great tits (*Parus major*). *Biol Lett* 6:187–190

742 Weber JM (2011) Metabolic fuels: Regulating fluxes to select mix. *J Exp Biol* 214:286–294

743 White CR, Schimpf NG, Cassey P (2013) The repeatability of metabolic rate declines with time.
744 *J Exp Biol* 216:1763–1765

745 Wolak ME (2012) Nadiv: An R package to create relatedness matrices for estimating non-
746 additive genetic variances in animal models. *Methods Ecol Evol* 3:792–796

747 Wood MD, Slade NA (1990) Comparison of ear-tagging and toe-clipping in prairie voles,
748 *Microtus ochrogaster*. *J Mammal* 71:252–255

749 Yuen CH, Pillay N, Heinrichs M, et al (2016) Personality traits are consistent when measured
750 in the field and in the laboratory in African striped mice (*Rhabdomys pumilio*). *Behav Ecol*
751 *Sociobiol* 70:1235–1246

752

753 **Table 1** Descriptive statistics for body mass (measured in the field), docility (time spent
 754 immobile during a 1-min bag test), exploration (distance moved in a 5 min open-field test),
 755 sprint speed (fastest speed reached over 1 meter on a given day), and resting metabolic rate
 756 (RMR; lowest O₂ consumption over 4.5 min) in Karoo bush rats in the Goegap Nature
 757 Reserve (South Africa, 2018), including the number of individuals sampled (N_{ID}), total
 758 number of observations (n_{obs}), units, mean, standard deviation (sd), and range (minimum to
 759 maximum)

	Body mass	Docility	Exploration	Sprint speed	RMR
N_{ID}	45	44	45	44	44
n_{obs}	285	244	119	177	123
Units	g	sec	cm	m·s ⁻¹	mlO ₂ ·min ⁻¹
Mean	90.60	53.67	1309.65	3.22	1.20
sd	15.15	11.89	8.89	0.53	0.30
Min	50.20	5.80	1.00	1.54	0.62
Max	127.60	60.00	4008.02	4.29	2.03

760

761

762 **Table 2** Effects of sex, test sequence, and Julian day on A) body mass, B) docility (time spent
763 immobile during bag test), C) exploration (distance moved in a 5min open-field test), D)
764 sprint speed (fastest speed reached over 1 meter on a given day), and E) resting metabolic
765 rate (RMR) in 45 Karoo bush rats, as estimated in separate univariate mixed models. Body
766 mass was also included as a covariate in B-E. Shown are the estimates (\pm SE), denominator
767 degrees of freedom (df_{den}), Wald F -statistic, and P values. Bold values are significant
768 estimates (see Table 1 for sample size, Fig. 2 for variance estimates, and Table 3 for
769 correlations obtained from the multivariate model)

Trait	Source	Estimate \pm SE	df_{den}	F	P
A) body mass					
	Intercept	0.199 \pm 0.190			
	Sex_[m]	0.958 \pm 0.395	42.5	5.9	0.0196
	Test sequence	0.000 \pm 0.011	255.8	0.0	0.9895
	Julian day	-0.002 \pm 0.002	259.2	1.5	0.2164
B) docility					
	Intercept	0.314 \pm 0.635			
	Sex _[m]	0.034 \pm 0.303	35.7	0.0	0.9118
	Body mass	-0.005 \pm 0.007	73.1	0.7	0.4214
	Test sequence	-0.005 \pm 0.033	100.3	0.0	0.8811
	Julian day	0.002 \pm 0.005	90.6	0.2	0.6752
C) exploration					
	Intercept	1.111 \pm 0.622			
	Sex _[m]	-0.033 \pm 0.313	40.5	0.0	0.9171
	Body mass	-0.003 \pm 0.006	101.3	0.3	0.6021
	Test sequence	-0.361 \pm 0.094	100.2	14.6	0.0002
	Julian day	-0.001 \pm 0.005	72.8	0.1	0.7951
D) sprint speed					
	Intercept	-0.185 \pm 0.346			
	Sex_[m]	-1.043 \pm 0.339	40.3	9.5	0.0037
	Body mass	0.003 \pm 0.002	147.1	1.6	0.2148
	Test sequence	0.041 \pm 0.016	170.8	6.4	0.0120
	Julian day	-0.003 \pm 0.005	167.4	0.3	0.5696
E) RMR					
	Intercept	-4.685 \pm 0.499			
	Sex _[m]	0.144 \pm 0.217	36.3	0.4	0.5129
	Body mass	0.036 \pm 0.005	44.4	48.2	<0.0001
	Test sequence	-0.053 \pm 0.078	114.3	0.5	0.4957
	Julian day	0.021 \pm 0.004	71.5	30.2	<0.0001

770

771

772 **Table 3** Among-individual correlations (r_{ind}) and within-individual correlations (r_e) between
773 docility (time spent immobile during bag test), exploration (distance moved in a 5min open-
774 field test), sprint speed (fastest speed reached over 1 meter on a given day), and resting
775 metabolic rate (RMR) in 45 Karoo bush rats. All estimates were extracted from a single
776 multivariate mixed model (see Table 1 for sample size and Fig. 2 for variance estimates).
777 Profile likelihoods were used to calculate the 95% confidence interval (CI) of r_{ind} and r_e

Trait 1	Trait 2	Among-individual correlations			Residual correlations		
		$r_{ind} \pm SE$	95% CI		$r_e \pm SE$	95% CI	
			lower	upper		lower	upper
Exploration	Docility	-0.740 \pm 0.216	-0.968	-0.382	0.078 \pm 0.104	-0.060	0.211
Sprint speed	Docility	0.280 \pm 0.198	-0.009	0.531	0.096 \pm 0.090	-0.028	0.217
Sprint speed	Exploration	-0.399 \pm 0.213	-0.659	-0.076	-0.151 \pm 0.111	-0.296	0.002
RMR	Docility	-0.050 \pm 0.309	-0.485	0.363	0.108 \pm 0.106	-0.035	0.246
RMR	Exploration	-0.247 \pm 0.337	-0.666	0.254	-0.085 \pm 0.126	-0.250	0.087
RMR	Sprint speed	0.088 \pm 0.263	-0.278	0.443	0.140 \pm 0.111	-0.016	0.288

778

779

780

781

782

783

784

785

786

787

788

789 **Figure captions**

790 **Fig. 1** A) Body mass (g) and B) sprint speed ($\text{cm} \cdot \text{sec}^{-1}$) as function of sex, C) resting metabolic
791 rate (RMR; $\text{mlO}_2 \cdot \text{min}^{-1}$) as function of body mass, and D) distance (m) moved during an
792 open-field test and E) sprint speed as function of test sequence in 7 males (blue dots) and 38
793 females (red triangles) Karoo bush rats. Shown are partial residuals (accounting for other
794 effects in the models, see Table 2)

795

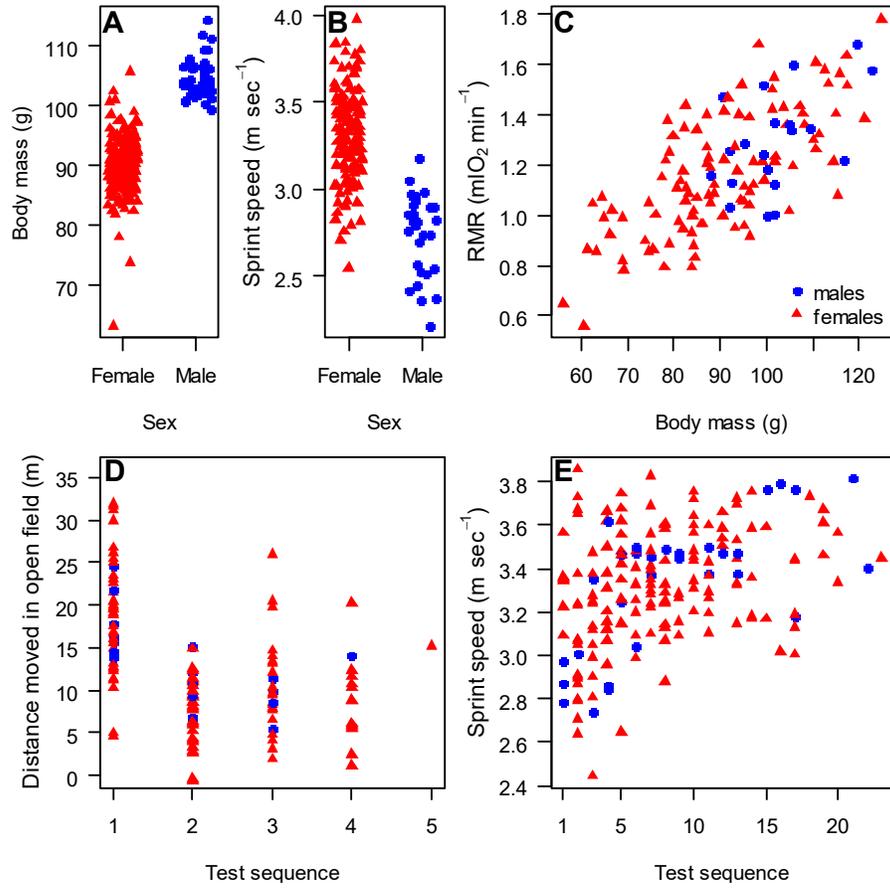
796 **Fig. 2** Among- and within-individual variation in A) body mass, B) time spent immobile during
797 bag test, C) distance moved in the open-field test, D) sprint speed, and E) resting metabolic
798 rate (RMR) in 7 males (blue dots) and 38 females (red triangles) Karoo bush rats. Shown are
799 residuals from a linear model on the raw scale that included body mass (except in A), sex,
800 test sequence, and Julian day. In each panel, individuals are ordered along the x-axis
801 according to their mean trait values. Among-individual variance (V_{ind}), residual variance (V_e),
802 and repeatability (R) estimates with standard errors (SE) were extracted from linear mixed
803 models on z-standardised traits (mean = 0, total variance = 1)

804

805 **Fig. 3** Representation of the among-individual correlations (r_{ind}) between (A) time spent
806 immobile in the bag test and distance moved in the open field and (B) sprint speed and
807 distance moved in the open field in 7 males (blue dots) and 38 females (red triangles) Karoo
808 bush rats. Displayed are the best linear unbiased predictors ($\text{BLUPs} \pm \text{SE}$) extracted from the
809 multivariate model (see Table 3 for correlation estimates) with z-standardised traits (mean =
810 0, variance = 1)

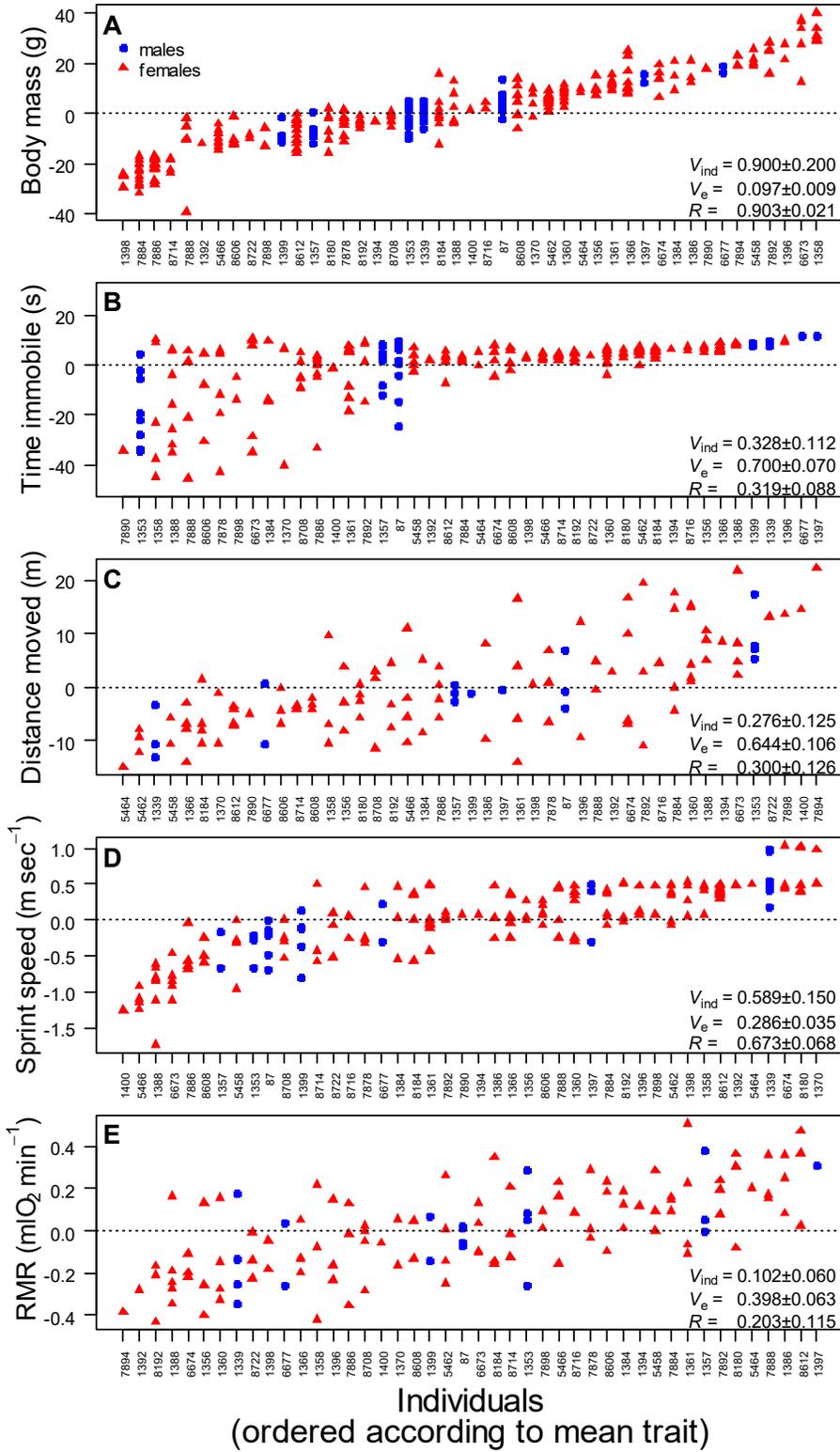
811

812 **Fig. 4** Representation of the among-individual correlations ($r_{ind} \pm SE$, blue dots) and within
813 individual correlations ($r_e \pm SE$, red triangles) between distance moved in the open field
814 (Exploration), time spent immobile in the bag test (Docility) and running speeds at each
815 meters during the performance test for 7 male and 38 female Karoo bush rats. Correlation
816 estimates were extracted from the second linear mixed models on z-standardised traits
817 (total variance = 1). Asterisks denote estimates that are significantly different from 0
818
819



820

821 Fig 1.



822

823 Fig.2

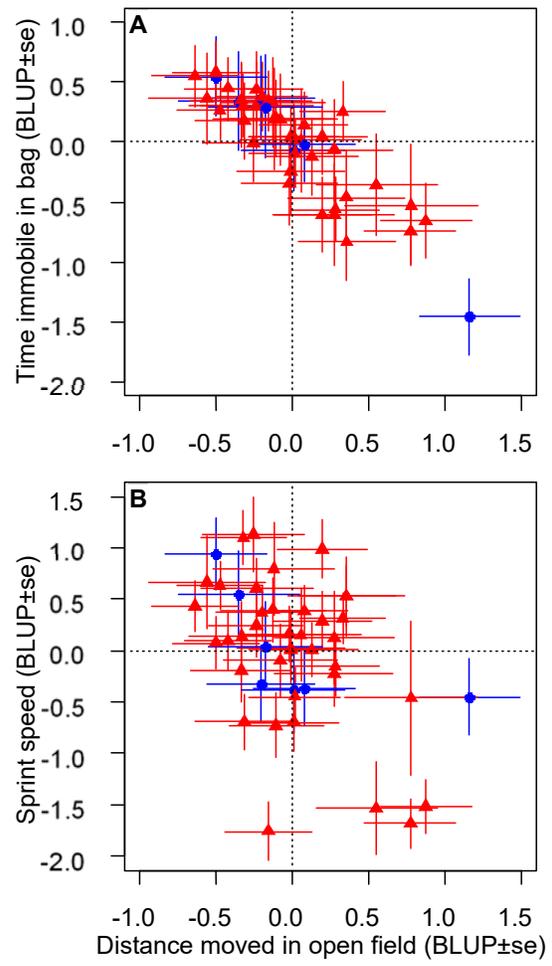


Fig. 3

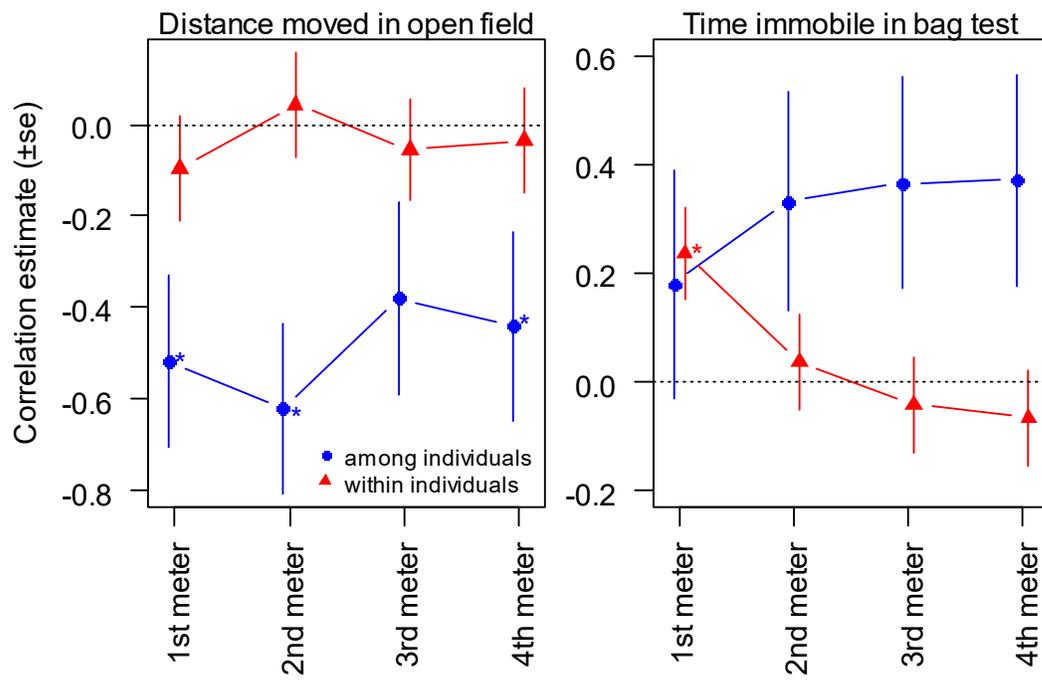


Fig. 4

Supplementary material (tables)

The fast and the curious II:
performance, personality and metabolism
in Karoo bush rats

Behavioral Ecology and Sociobiology

Paul Agnani*, Jennifer Thomson, Carsten Schradin, and Vincent Careau

*Author for correspondence:

pagnani@uottawa.ca

ORCID: 0000-0002-1137-0774

Department of Biology

University of Ottawa

30 Marie Curie, Ottawa, ON, CANADA, K1N 6N5

Tel: (613) 562-5800 x6349

Fax: (613) 562-5486

Table S1 Variance in running speed and metabolic rate across four distinct levels; V_{ind} : variance among individuals as estimated by individual identity fitted as random effect, V_{test} : variance among tests (on separate days) within individuals as estimated by the combination of individual identity and date as a random effect, V_{trial} : variance among trials within tests as estimated by the combination of individual identity, date, and trial as a random effect, and V_e : residual variance among successive measurements within in a given trial (for running speed) or test (for metabolic rate; there is no V_{trial} component for metabolic rate because only a single trial was conducted per respirometry test).

Variance component	Running speed			Metabolic rate		
	estimate	±	SE	estimate	±	SE
V_{ind}	0.351	±	0.098	0.325	±	0.112
V_{test}	0.115	±	0.026	0.371	±	0.073
V_{trial}	0.062	±	0.017			
V_e	0.523	±	0.021	0.327	±	0.024

Table S2 Among-individual correlations (r_{ind}) and within-individual correlations (r_e) between docility (time spent immobile during bag test), and exploration (distance moved in a 5 min open-field test) and running speed at each meter during the performance trial (speed-1 = first meter; speed-2 = second meter, speed-3 = third meter, and speed-4 = fourth meter) in 45 Karoo bush rats. All estimates were extracted from a single multivariate mixed model.

Trait 1	Trait 2	Among-individual correlations	Residual correlations
		$r_{ind} \pm SE$	$r_e \pm SE$
Speed-2	Speed-1	0.993 ± 0.033	0.368 ± 0.075
Speed-3	Speed-1	0.897 ± 0.063	0.230 ± 0.082
Speed-4	Speed-1	0.854 ± 0.080	0.087 ± 0.086
Speed-3	Speed-2	0.970 ± 0.031	0.502 ± 0.064
Speed-4	Speed-2	0.970 ± 0.038	0.375 ± 0.074
Speed-4	Speed-3	0.999 ± NA	0.563 ± 0.056
Docility	Speed-1	0.180 ± 0.210	0.236 ± 0.085
Docility	Speed-2	0.332 ± 0.202	0.036 ± 0.088
Docility	Speed-3	0.366 ± 0.195	-0.042 ± 0.088
Docility	Speed-4	0.372 ± 0.195	-0.066 ± 0.089
Exploration	Speed-1	-0.517 ± 0.190	-0.096 ± 0.116
Exploration	Speed-2	-0.622 ± 0.185	0.044 ± 0.115
Exploration	Speed-3	-0.380 ± 0.212	-0.055 ± 0.111
Exploration	Speed-4	-0.441 ± 0.208	-0.034 ± 0.113
Docility	Exploration	-0.822 ± 0.187	0.136 ± 0.102

