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

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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.

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

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

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

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

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

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

Methods

Study site

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

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

Behavioural test

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

Performance test

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

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

Respirometry

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

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 water vapor sensors (FoxBox, RH-300; Sable systems). After monitoring the baseline channel for 5 min, the system sequentially sampled the 3 chambers for 10 min each, after which another baseline measurement was taken. This process was repeated 3 more times, yielding a total of four 10 min samples for each individual on a given day. For each 10 min sample, we extracted the lowest mean O_2 consumption over a period of 4:30 min. The lowest of these four estimates was retained as the RMR of that individual on that day. While in the chambers, individuals were monitored using a webcam (Microsoft Livecam HD-3000) to ensure that they were resting (i.e., not moving). We did not discard any estimates as individuals were always immobile for the timestamps corresponding to the lowest O_2 consumptions.

Statistical analyses

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

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

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

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

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

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

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

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

Results

Descriptive statistics

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

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

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

Variance in running speed and metabolic rate

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

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

Effect of mass, sex and test sequence

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

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

Among- and within-individual correlations

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

Behaviour vs running speed

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

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

Discussion

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

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

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

Variation in running speed across levels

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

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

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

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

Repeatability and behavioural syndrome

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

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

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

Lack of relationship with RMR

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

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

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

Conclusions

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

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Declarations

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Conflict of interest

We have no conflict of interest to declare.

Ethics approval

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

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

Databases used in this study are available as supplementary material.

Code availability

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

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

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

Table 3 Among-individual correlations (r_{ind}) and within-individual correlations (r_e) between docility (time spent immobile during bag test), exploration (distance moved in a 5min open-field test), sprint speed (fastest speed reached over 1 meter on a given day), and resting metabolic rate (RMR) in 45 Karoo bush rats. All estimates were extracted from a single multivariate mixed model (see Table 1 for sample size and Fig. 2 for variance estimates). 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 ± 0.216	-0.968	-0.382	0.078 ± 0.104	-0.060	0.211
Sprint speed	Docility	0.280 ± 0.198	-0.009	0.531	0.096 ± 0.090	-0.028	0.217
Sprint speed	Exploration	-0.399 ± 0.213	-0.659	-0.076	-0.151 ± 0.111	-0.296	0.002
RMR	Docility	-0.050 ± 0.309	-0.485	0.363	0.108 ± 0.106	-0.035	0.246
RMR	Exploration	-0.247 ± 0.337	-0.666	0.254	-0.085 ± 0.126	-0.250	0.087
RMR	Sprint speed	0.088 ± 0.263	-0.278	0.443	0.140 ± 0.111	-0.016	0.288

Figure captions

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

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

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

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

Fig 1.

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

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