



Active and explorative individuals are often restless and excluded from studies measuring resting metabolic rate: Do alternative metabolic rate measures offer a solution?



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HIGHLIGHTS

- Active and bold individuals are often excluded from studies measuring RMR.
- No relationship between RMR and personality.
- Of 73 free-living striped mice tested, 21 did not rest in the metabolic chamber.
- In the moist season, personality predicted time being active in metabolic chambers.
- Positive relationship between personality and alternative metabolic rates in the moist season.

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ABSTRACT

It has often been proposed that bolder, more explorative or more active individuals also have a higher resting metabolic rate (RMR), indicating metabolic costs of these personality types. However, such individuals might often be restless and thus excluded from RMR datasets, leading to a significant sampling bias. We tested (1) whether such a bias occurs when animals are measured for a relatively common but short time period of 3 h, and if so, (2) whether alternative measures of metabolic rate, that allow the incorporation of non-resting individuals, would reveal associations between metabolism and personality. For this, we studied free-living individuals of the African striped mouse (*Rhabdomys pumilio*) both during the moist season (N = 25 individuals) with high food availability and the dry season (N = 48 individuals) with low food availability. We assessed variation in the latency to explore a novel object, and the time spent active and time spent in the centre of a neutral arena. We examined links between personality and (i) RMR and (ii) four alternative metabolic rate (MR) metrics: average MR, highest MR, lowest MR and span of MR. Twenty-nine percent of the measured individuals had to be excluded from our RMR study because they remained restless during respirometry trials. Striped mice showed a behavioural syndrome where fast explorers also spent more time in centre and more time active than slow explorers. Individuals that did not rest during respirometry trials were faster explorers and in the moist season, they were also more active and spent more time in the centre than individuals that rested. We found no relationship between RMR and the behavioural syndrome, which might be due to the exclusion of individuals with a certain behavioural type, leaving a subset of compliant individuals. In the moist season, we found positive relationships between the behavioural syndrome and span of MR and lowest MR. In the dry season, low food availability may mask links between the behavioural syndrome and alternative MR measures due to reduced overall activity in striped mice. Our study demonstrated the importance to consider personality when measuring RMR and suggests that some alternative MRs may be useful to examine relationships between metabolism and personality when it is impossible to measure individuals over extended time periods.

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1. Introduction

Between-individual variation and within-individual consistency in physiological and behavioural traits has been a recent focus in behavioural and ecological research [1–3]. Much attention has been

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paid to animal personality, defined as individual behavioural differences which are consistent over time and/or across contexts [4]. Individual variation in one type of behaviour is often linked with variation in other types of behaviour, resulting in behavioural syndromes [5], where each individual has a specific behavioural type within a syndrome [3]. Animal personality and behavioural syndromes have become a research focus because of their influence on life-history traits [6–8] and individual fitness [9–11].

There is evidence suggesting that between-individual variation in physiological parameters such as metabolic rate underlies variation in several life-history traits and individual fitness (reviewed in: [12–14]). Measures of basal metabolic rate (BMR; measured in post-absorptive, inactive, normothermic, non-reproductive, adult individuals during their inactive period and in their thermoneutral zone [15]) and resting metabolic rate (RMR; measured in non-fasting animals in their thermoneutral zone [16]) are very similar when measured within the thermoneutral zone [17]. Both terms are often used interchangeably, and therefore we will refer to both here as RMR. High intra-specific variation in RMR has been reported in many taxa [12,18]. However, to date, researchers still struggle to explain this variation [16,19], and personality has been suggested as one important factor contributing to some of this variation [19]. Many studies have investigated the functional link between personality and metabolism [reviewed in: 2,20], but the findings are ambiguous (reviewed in: [13,20]): some studies found no link between personality and RMR [21–24], while others reported either a positive [25,26] or negative [27–29] relationship.

In the past, physiological ecologists have considered several sampling biases with regard to measurements of metabolic rate. Such biases included measurement duration [30–33], sampling regime (continuous vs. interrupted) [34] and sampling frequency [34]. However, alongside biases introduced by a specific setup, timing and/or duration of respirometry trials, the selection of study individuals may also lead to a sampling bias. For example, a problem arises when an individual's personality influences whether it can be utilised in respirometry studies, similar to evidence demonstrating that personality influences individual trappability and thus inclusion in studies [35–38]. During metabolic measurements, highly explorative, more active or bolder individuals may be more restless (i.e. not sitting still), and consequently may be more likely to be excluded from respirometry studies than individuals which are less explorative, less active and less bold. Excluding certain personality types from a study could bias conclusions drawn when relating metabolic rate (MR) to personality and life-history traits. However, we lack information about how common such a bias is because few respirometry studies actually report the number of animals excluded due to restlessness [19]. For example, 7.7% of red squirrels (*Tamiasciurus hudsonicus*) [39], 16.8% of weasels (*Mustela nivalis*) [40] and 41.6% of deer mice (*Peromyscus maniculatus*) [41] had to be excluded because they remained active in respirometry chambers. However, these studies did not provide information on the personality traits of individuals or whether individuals that remained active differed in their personality from inactive individuals. Consequently, we cannot assess whether the conclusions drawn from such studies may be biased to a subset of compliant individuals. Moreover, only few respirometry studies aimed to incorporate personality in metabolic measurements, for example by assessing activity levels within metabolic chambers [24,27]. Therefore, it is possible that respirometry studies may be biased by the personality traits of their study subjects.

Careau et al. [19] proposed that researchers should “extract other features that measure the influence of activity on MR” (p. 647) in order to incorporate personality in respirometry studies. For example, measurements of peak metabolism [41,42], time needed to reach the lowest MR [27,43], MR during the first 5–10 min of a respirometry run [41,44] and average MR over extended periods of time [44–46] have recently been used as additional measures of metabolic rate. Such additional measures of MR could then be used to examine relationships between personality, metabolism, behaviour, and fitness.

For example, initial peak metabolism of fish was negatively correlated with courtship display intensity [42] and latency to escape was positively correlated with MR of the first 10 min, maximum MR and average MR [44]. As for RMR [47] and personality traits [4,48,49], it is essential to evaluate the repeatability of alternative metabolic rates before linking them to other traits of interest [19]. A study relating personality to RMR and alternative MR measurements should ideally be conducted on a species in which a large number of free-living individuals can be tested.

The diurnal African striped mouse (*Rhabdomys pumilio*) offers a good opportunity to compare RMR with alternative MRs of individuals which express different personalities. Personality traits of free-living striped mice are repeatable over time and personality traits measured in the laboratory reflect individual behaviour in nature [50]. Since October 2014, we routinely measured RMR of striped mice at the Succulent Karoo Research Station, South Africa. In these two years we have observed large variation in individual behaviour within respirometry chambers, and in two years 77 out of 296 individuals tested never rested during respirometry trials, suggesting a personality bias on RMR in this species. Due to logistical constraints, we could conduct respirometry trials only during the active phase of striped mice. Therefore, the likelihood of having restless individuals was presumably higher than if we had conducted respirometry trials during the inactive phase.

The aims of this study were to: (i) determine the sampling bias in the dataset resulting from excluded animals due to restlessness during respirometry trials, (ii) determine whether excluded individuals (non-resting) differ in personality traits from resting individuals, (iii) assess the occurrence of a behavioural syndrome, (iv) examine the relationship between the behavioural syndrome and RMR and (iv) re-analyse the dataset using alternative MRs suggested by Careau et al. [19] in order to examine relationships between these measures and the behavioural syndrome. We expected a sampling bias due to personality, especially that individuals excluded from RMR (but not alternative MR) measurements would be more active, more explorative and spent more time in the centre of an arena than individuals which rested in respirometry trials.

2. Material and methods

2.1. Study site and animals

We collected data from December 2014 to October 2015 in the Goegap Nature Reserve, situated in the Succulent Karoo semi-desert biome of South Africa. This biome is characterized by moist winters (June–August) with an average annual rainfall of 160 mm at our field site, followed by high food availability in spring (breeding season; August–November) and hot dry summers (December–May) with low food availability. Temperatures vary from below zero to 25 °C during winter and spring, and from 5 to 40 °C during summer [51, 52]. At our field site, striped mice are facultatively group-living, and groups typically consist of one breeding male, one to four breeding females and their philopatric offspring of both sexes [51]. The breeding season typically lasts 3–4 months, in which females can give birth to 2–3 litters [53].

We continuously monitor the study population and mark all individuals permanently with numbered ear-tags (National Band and Tag, Newport, KY), and temporarily with hair dye (Inecto, Pinetown, South Africa) for individual recognition during behavioural observations (for details of standard field procedures see [54]).

2.2. Metabolic rates

To determine RMR, highest MR, lowest MR, average MR and span of MR we took metabolic measurements of 23 adult males and 25 adult females during the dry season, and 14 adult males and 11 adult

females during the moist season. To evaluate the relationship between personality and MRs each individual was included once in the dataset (either in the moist or dry season). For each individual, the MR measurement was selected that was closest in time to when its personality test was conducted. We conducted respirometry trials and personality tests within 5 days of each other on average (\pm SD 34 days) in the dry season and within 8 days (\pm 26 days) in the moist season. We measured oxygen consumption ($\text{ml O}_2 \text{ h}^{-1}$) at the Succulent Karoo Research Station in a field laboratory of $6 \times 6 \text{ m}$, built especially for respirometry measurements. We trapped adult striped mice at their nest at sunrise using Sherman-style live-traps ($26 \times 9 \times 9 \text{ cm}$). Measuring MR during the active phase of the animals, instead of their inactive phase, may have resulted in elevated levels of activity in the metabolic chambers and thus, exclusion of individuals from the RMR study. However, we trapped individuals in the mornings because striped mice are solitary foragers [51], which makes locating and trapping of individuals at midday, when individuals are less active, difficult. We did not keep and fast individuals for extended periods because isolating individuals from their social groups may lead to problems in the social dynamics between group members. All individuals were trapped around sunrise at their nest before they left to forage, making it very likely that they had not yet fed when they were trapped. We brought them to the laboratory immediately after trapping, where we weighed and then placed them in one of the three respirometry chambers. Each chamber was equipped with a metal grid to separate mice from urine and faeces. We used an open circuit respirometry system (Foxbox, Sable Systems, New Jersey, USA). We initiated O_2 measurement and video recorded the mice in the metabolic chambers using a webcam (Microsoft HD webcam). The metabolic chambers were immersed in a propylene container and temperature was controlled using a temperature controller (Pelt5, Sable Systems).

We measured RMR at $30 \text{ }^\circ\text{C} \pm 1 \text{ }^\circ\text{C}$, which lies within the species' thermoneutral zone [52]. We alternated measurements between individuals and measured each of the three mice for a total of 40 min ($4 \times 10 \text{ min}$). To account for any drift in the analyser we measured oxygen concentration in an empty baseline chamber for 5 min before and for 10 min after we measured oxygen consumption of the three individuals. This cycle was repeated four times, resulting in a data collection period of 3 h (see Fig. S1 for an example of a 3 h measurement sequence). Longer measurements were not feasible because some small mammals (e.g. shrews, rodents) become very active when they are food deprived [55,56]. The air flow through the chambers ($\sim 700 \text{ ml min}^{-1}$) was controlled by a flow regulator (FB8, Sable Systems) and measurements of oxygen consumption were taken every 3 s using an oxygen analyser (Foxbox, Sable Systems). We calibrated the oxygen analyser to an upper and lower value in dry air weekly (for more detailed information concerning the respirometry setup see [57]). We analysed metabolic records using a macro program in ExpeData software (Sable Systems). After taking measurements, we weighed mice again, rewarded them with a small amount of food (as compensation for lost foraging opportunities) and subsequently released them at their nest. To establish RMR, we used the mean of the lowest 89 readings (equivalent to 4.45 min) of oxygen consumption per individual [57]. Additionally, we visually checked all videos for the determined period to confirm that individuals were resting (i.e. motionless and not showing piloerection). Using the video software Kinovea 0.8.15 (www.kinovea.org) we measured the time (in seconds) each mouse was active (i.e. running, autogrooming, gnawing on metal grid) in the metabolic chamber.

We assessed four measurements in addition to RMR: (i) average MR over the entire respirometry run (40 min per individual); (ii) lowest spontaneous MR during an entire respirometry run (i.e. 1-min average);

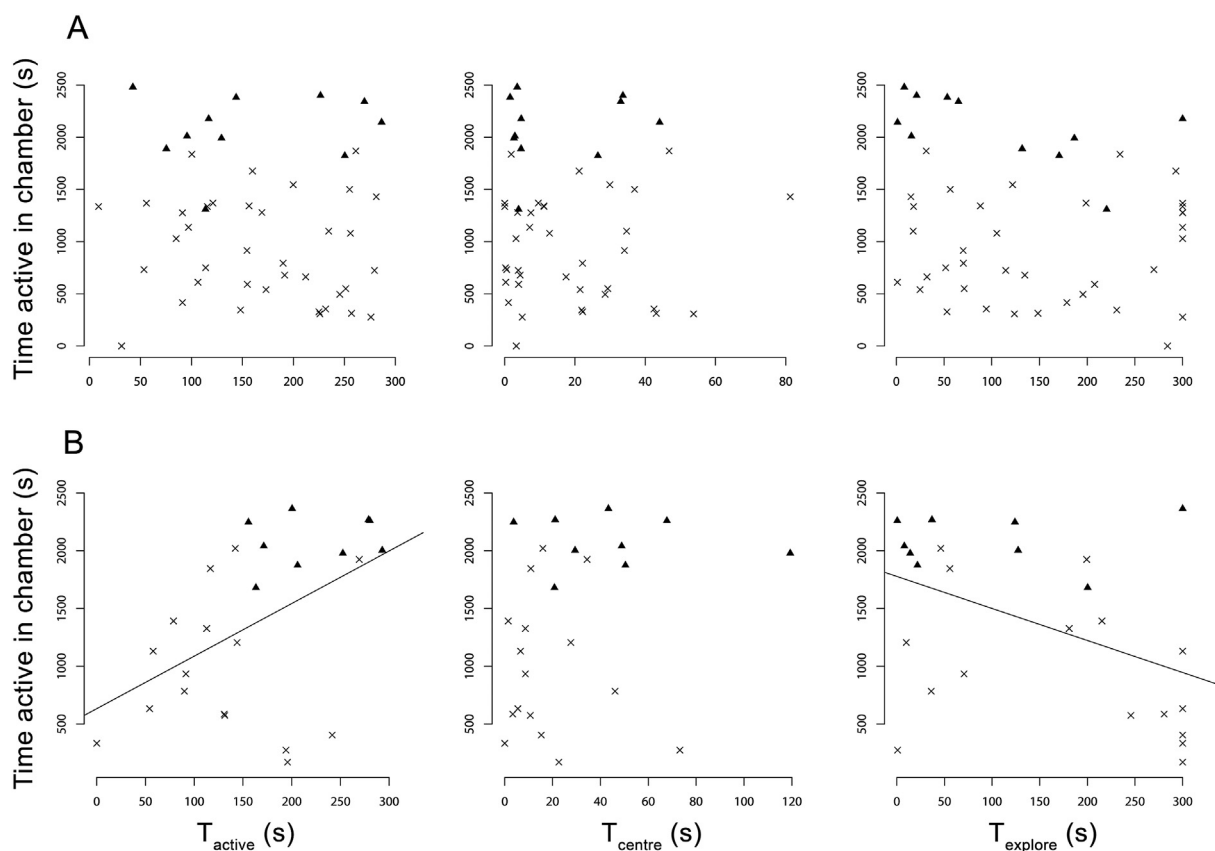


Fig. 1. Personality traits and time spent active in the metabolic chamber. Differences are shown for T_{active} , T_{centre} and T_{explore} during the (A) dry season (resting: $N = 36$, non-resting: $N = 12$) and (B) moist season (resting: $N = 16$, non-resting: $N = 9$; regression lines are given for all individuals together; individuals which did not rest in respirometry runs are indicated by a filled triangle, individuals which rested by \times).

Table 1
Repeatability estimates for personality traits and metabolic rates of striped mice *Rhabdomys pumilio*.

	Trait	R ± SE	95% CI	P value ^a
Personality	T _{explore}	0.70 ± 0.23	0.34–0.96	0.003
	T _{active}	0.11 ± 0.04	0.04–0.17	0.010
	T _{centre}	0.017 ± 0.025	0.0–0.07	0.15
Metabolic rate	RMR	0.49 ± 0.05	0.36–0.52	< 0.0001
	Average MR	0.31 ± 0.10	0.22–0.49	0.0001
	Lowest MR	0.44 ± 0.05	0.34–0.48	< 0.0001
	Highest MR	0.19 ± 0.05	0.05–0.21	0.004
	Span of MR	0.23 ± 0.09	0.04–0.33	0.004

^a Traits that showed significant repeatability appear in bold.

(iii) highest spontaneous MR during an entire respirometry run (i.e. 1-min average); and (iv) the span between highest MR and lowest MR.

2.3. Personality traits

We conducted personality tests from February to March 2015 (dry season) and July to August 2015 (moist season) on all 73 individuals for which we also collected metabolic measurements. We measured all traits in a laboratory at the research station, and tested all individuals in the mornings, when striped mice are highly active [58]. We trapped individuals at their nests around sunrise and transported them to the research station. We transferred individuals into a type III Perspex cage (38 × 22 × 15 cm) lined with sand. In the dry season, we tested 23 adult males and 25 adult females that were on average 5.5 ± 1.0 months old, and in the moist season we tested 14 adult males and 11 adult females that were on average 9.0 ± 1.8 months old. Seasonal differences in age are a direct result of the species' life-cycle, where individuals that are born in spring (August–November) must survive the dry season in order to breed in the following spring [59].

Using standard tests, we assessed three personality traits following the protocols previously used for striped mice [60]. First, we measured time spent active (T_{active}; often termed 'activity') and time spent in centre (T_{centre}; often termed 'boldness') using an open field test [61]. We placed each individual on the same side of the arena (80 × 65 × 94 cm) and video recorded its behaviour for 5 min. We measured T_{active} as the number of seconds individuals spent actively moving (e.g. running, jumping, and autogrooming) and not sitting motionless. We measured T_{centre} as the number of seconds an individual spent in the centre of the arena (at least one mouse length away from the wall). After 5 min elapsed, we measured T_{explore} (often termed 'exploration') using a novel object test [62,63]. For this, we placed a fixed and a mobile object (fixed: plastic toy attached to ground; mobile: ping pong ball) at the far end of the arena ca. 10 cm from the arena wall (while the test mouse was on the opposite side of the arena) and video recorded the mouse for 5 min. Striped mice show no preference for either of the two objects [60], and thus we measured T_{explore} as the latency (in seconds) between the start of a trial and an individual's first physical contact with either object. If animals 'froze' by not moving for 5 min, we set the latency to the maximum of 300 s, and T_{active} and T_{centre} to the minimum of 0 s. After each test we cleaned the arena with 70% alcohol. Each mouse received five sunflower seeds and was returned to its nest. We extracted data on the personality traits using the video software Kinovea 0.8.15 (www.kinovea.org).

2.4. Repeatability

To examine repeatability of RMR and all alternative MRs we used a second respirometry trial for 62 out of the 73 individuals used in this

study (MRs of 11 individuals could not be measured repeatedly due to disappearance or death). Respirometry trials were conducted within 89 days of each other on average (±63 days). To determine repeatability of T_{active}, T_{centre} and T_{explore} we included all individuals for which these traits were measured at least twice (two measurements: N = 32, three measurements: N = 5). Personality tests were conducted within 28 days of each other on average (±4 days).

2.5. Statistical analyses

We conducted all analyses in R3.3.2 [64]. We tested for normality of RMR and alternative MRs using Shapiro-Wilk test and log transformed span of MR to reach normality. We ran correlations using Kendall's rank correlation coefficient (tau) to examine whether different personality traits correlated and to test if alternative MRs correlated with RMR. We used a χ^2 test to evaluate whether the proportion of individuals that had to be excluded due to restlessness differed between seasons. We used logistic regressions to determine whether individuals that rested in metabolic chambers differed in personality traits (T_{active}, T_{centre}, T_{explore}) from individuals that did not rest. We tested for an interaction between season and personality traits, and used Mann-Whitney U tests to examine differences in traits between resting and non-resting individuals post hoc. We used linear regressions to assess whether the time an individual was active in the metabolic chamber could be predicted by its personality traits.

Before any MR measurements can be related to personality traits, the repeatability of both MR measurements and personality traits should be determined ([19], p. 647). Using the R package rptR [65] we calculated the coefficient of repeatability R, its standard error and estimated the 95% confidence intervals (CI) around the repeatability estimates for RMR, all alternative MRs and personality traits. We used body mass as a fixed factor when examining repeatability of all five MRs.

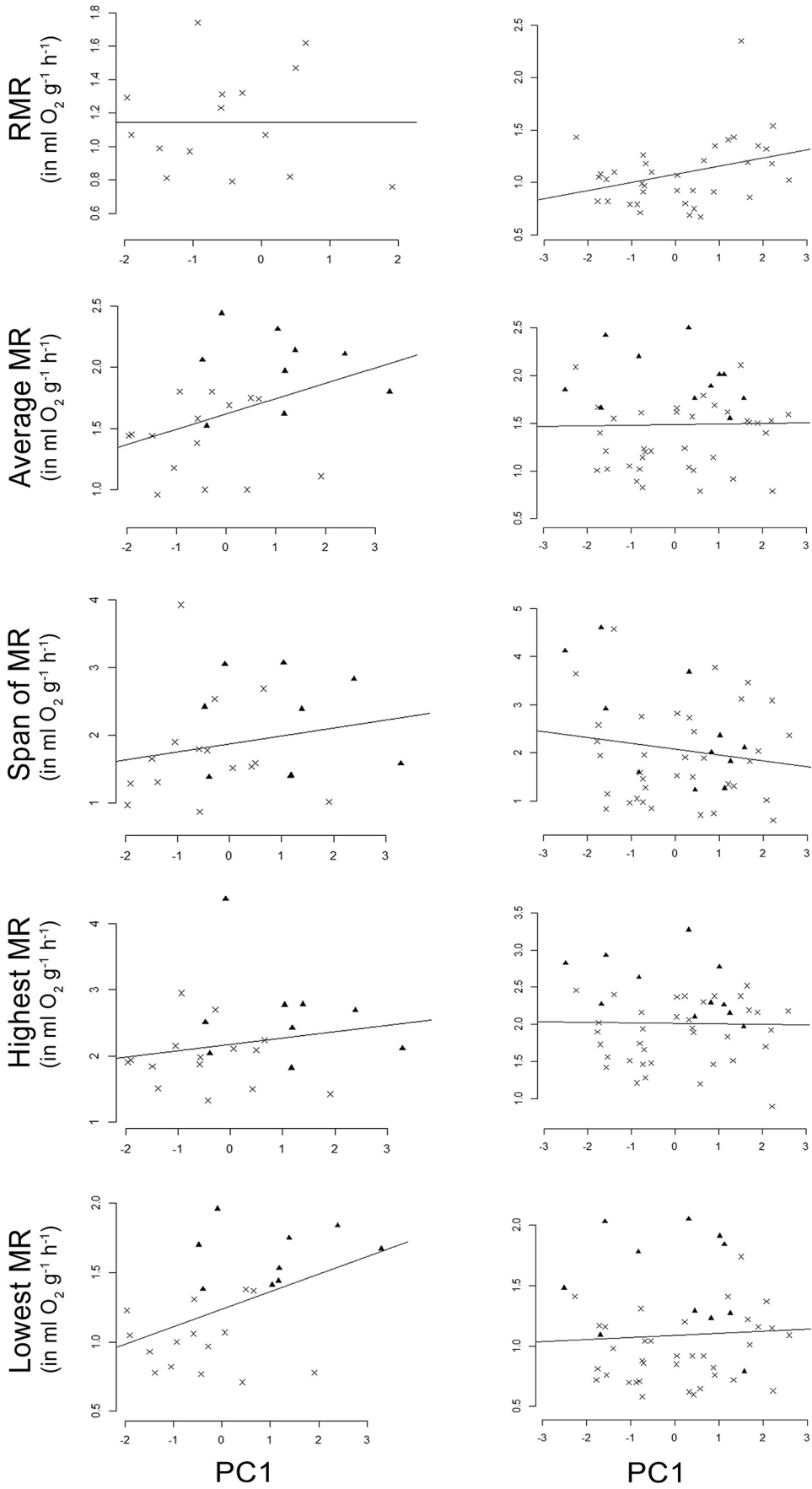
All personality traits correlated with each other (forming a behavioural syndrome [5]), and thus we ran one principal components analysis (PCA) for each season to illustrate relationships between the measured behavioural variables. Following the Kaiser–Guttman criterion [66] we retained the principal component with an eigenvalue > 1, which we visually validated using a scree plot. The retained principal component (PC1) was then used as a composite behaviour variable in further analysis.

To assess relationships between whole-animal MRs (RMR, highest, lowest, average and span) and PC1 we fit LMMs with the 'lmer' function from the lme4 package [67]. We ran separate models for each season because seasons at the study site vary greatly in ambient temperature and food availability [51,68], which can affect RMR [69]. For each season, we ran five models in which we used one MR (i.e. RMR or one of the four alternative MRs) as the response variable; PC1, body mass, sex, time spent active in the metabolic chamber (40 min for average MR and span of MR; 1 min for highest MR and lowest MR) and number of times previously in respirometer as fixed factors. We included number of times previously in respirometer as a factor because 62% of the study animals had experienced the respirometer prior to the measurement used for this study and thus, habituation to the respirometer may have occurred [19]. We used group ID as random factor because more than one individual was measured per group. In all models, we tested for an interaction between sex and personality trait because sex differences in personality traits are commonly observed [70]. To determine the significance of full models compared to corresponding null models we used likelihood ratio tests. When these tests showed no significant differences, we terminated the analyses at this point, and if the difference was significant, we used a stepwise backward method for model selection. For model validation, we visually inspected Q–Q plots

Fig. 2. Relationships between PC1 (behavioural syndrome) and mass-adjusted metabolic rates (RMR, average MR, span of MR, highest MR and lowest MR) of striped mice *Rhabdomys pumilio* in the moist (N = 25) and the dry season (N = 48) (regression lines are given for all individuals together; individuals which did not rest in respirometry runs are indicated by a filled triangle, individuals which rested by ×).

Moist season

Dry season



and scatterplots of residuals plotted against fitted values, and we checked for the assumptions of homogeneous and normally distributed residuals. We determined R^2 for the minimal adequate model with the function 'rsquaredGLMM' from the MuMIn package [71] and R^2 for each fixed factor. Because we conducted multiple comparisons, we adjusted P values using the Benjamini-Hochberg method [72]. All statistical tests were two-tailed and we assigned significance at $\alpha \leq 0.05$.

3. Results

3.1. Influence of personality traits on behaviour in the metabolic chamber

Five females and seven males (25%) in the dry season and four females and five males (36%) in the moist season did not rest during respirometry trials (see Table S1 for descriptive statistics for all MRs). The proportion of individuals that had to be excluded due to restlessness did not differ between seasons ($\chi^2 = 2.35$, $df = 1$, $P = 0.12$). Whether individuals rested in the metabolic chamber was influenced by the interaction between T_{active} and season ($z = -2.39$, $P = 0.01$) and by T_{explore} ($z = 2.05$, $P = 0.04$), but there was no seasonal difference concerning T_{explore} ($z = -1.23$, $P = 0.21$), and the interaction between

T_{centre} and season had no influence on whether individuals rested in the metabolic chamber ($z = -1.85$, $P = 0.06$). Post hoc tests showed that individuals that did not rest were faster explorers than individuals that rested ($U = 3.54$, $P = 0.02$). In the moist season, individuals which did not rest during respirometry trials were also more active ($U = 127$, $P = 0.001$) and spent more time in the centre ($U = 113$, $P = 0.019$; Fig. S2) during personality tests than individuals that rested. In the dry season, resting and non-resting individuals did not differ with regard to T_{active} ($U = 187$, $N = 48$, $P = 0.50$; Fig. S2) and T_{centre} ($U = 180$, $P = 0.39$ Fig. S2).

In the moist season, the time individuals spent active in the metabolic chamber was positively predicted by the personality trait T_{active} ($F = 7.21$, $R^2_{\text{adjust}} = 0.20$, $df = 23$, $P = 0.013$; Fig. 1B) and negatively predicted by T_{explore} ($F = 5.89$, $R^2_{\text{adjust}} = 0.17$, $df = 23$, $P = 0.023$; Fig. 1B). In contrast, T_{centre} did not predict the time individuals spent active in the metabolic chamber ($F = 2.04$, $R^2_{\text{adjust}} = 0.04$, $df = 23$, $P = 0.16$; Fig. 1B). In the dry season, time active in chamber was not predicted by any of the three measured personality traits (T_{active} : $F = 0.001$, $R^2_{\text{adjust}} = -0.02$, $df = 41$, $P = 0.97$; T_{centre} : $F = 0.029$, $R^2_{\text{adjust}} = -0.023$, $df = 41$, $P = 0.86$; T_{explore} : $F = 0.80$, $R^2_{\text{adjust}} = -0.005$, $df = 41$, $P = 0.38$; Fig. 1A).

Table 2
Results of LMMs examining links between PC1 (behavioural syndrome) and different measures of metabolic rate in striped mice *Rhabdomys pumilio* during the dry and moist season. Results of minimal models are reported.

	Factor	Estimate \pm SE	t value	P adjusted ^b	R ² model	R ² fixed factor		
Moist season^a								
Average MR	(Intercept)	2.676 \pm 12.66	0.21	0.83	0.83			
	Body mass	0.971 \pm 0.32	2.95	0.022		0.01		
	Time active chamber	0.018 \pm 0.002	8.47	<0.0001		0.74		
	PC1	0.764 \pm 1.18	0.64	0.631		0.01		
	Sex	-9.568 \pm 3.35	-2.85	0.022		0.07		
	No. in respirometer	1.514 \pm 1.711	0.884	0.582		0.01		
	Span of MR	(Intercept)	5.111 \pm 0.38	13.33		<0.0001	0.65	
		Body mass	-0.023 \pm 0.00	-2.33		0.03		0.02
		PC1	0.219 \pm 0.04	4.49		0.0002		0.06
		Sex	0.264 \pm 0.11	2.35		0.03		0.08
Highest MR	PC1 \times sex	-0.376 \pm 0.06	-5.33	<0.0001		0.49		
	(Intercept)	54.840 \pm 28.10	1.95	0.018	0.54			
	Body mass	-0.245 \pm 0.60	-0.40	0.821		0.04		
	Time active chamber	0.826 \pm 0.24	3.35	0.018		0.19		
	PC1	-0.510 \pm 2.21	-0.23	0.821		0.01		
	Sex	-12.02 \pm 7.25	-1.65	0.165		0.04		
No. in respirometer	7.21 \pm 3.43	2.10	0.098	0.11				
Lowest MR	(Intercept)	-17.426 \pm 17.57	-0.99	0.33	0.65			
	Body mass	1.691 \pm 0.43	3.87	<0.001		<0.01		
	Time active chamber	0.470 \pm 0.10	4.43	<0.001		0.27		
	PC1	3.58 \pm 1.35	2.64	0.019		0.09		
	Sex	-19.22 \pm 5.03	-3.82	0.002		0.26		
Dry season^a								
Average MR	(Intercept)	-15.527 \pm 7.92	-1.95	0.012	0.79			
	Body mass	1.381 \pm 0.235	5.87	<0.0001		0.01		
	Time active chamber	0.018 \pm 0.001	11.87	<0.0001		0.70		
	PC1	0.032 \pm 0.69	0.047	0.962		<0.01		
	Sex	-5.364 \pm 2.33	-2.29	0.040		0.07		
	No. in respirometer	-1.483 \pm 1.20	-1.23	0.271		<0.01		
	Span of MR	(Intercept)	3.145 \pm 4.63	6.79		<0.0001	0.44	
		Body mass	0.024 \pm 1.37	1.78		0.082		<0.01
		Time active chamber	0.001 \pm 9.06	4.08		<0.0001		0.25
		PC1	-0.074 \pm 3.98	-1.85		0.082		0.03
Sex		-0.294 \pm 1.35	-2.16	0.054	0.03			
No. in respirometer		-0.214 \pm 6.99	-3.05	0.008	0.12			
Lowest MR	(Intercept)	-0.226 \pm 8.34	-0.02	0.978	0.70			
	Body mass	0.897 \pm 0.27	3.31	0.006		0.11		
	Time active chamber	0.586 \pm 0.06	9.04	<0.001		0.59		
	PC1	-0.160 \pm 0.82	-0.193	0.978		<0.01		
	Sex	-1.537 \pm 2.71	-0.56	0.978		<0.01		
	No. in respirometer	0.342 \pm 1.45	0.235	0.978		<0.01		

^a When the full model was not significantly different from the null model ($P > 0.05$) no results are reported for this model.

^b Variables that significantly influenced MR appear in bold.

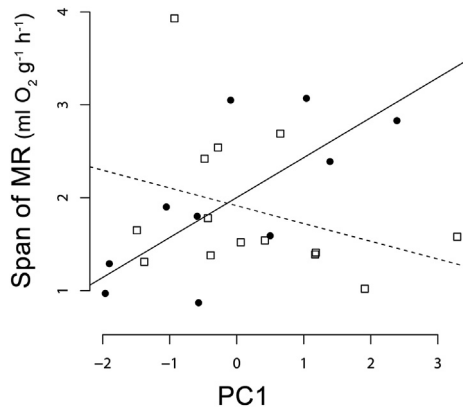


Fig. 3. Difference in the relationship between PC1 (behavioural syndrome) and mass-adjusted span of MR of female (full regression line: $R^2 = 0.58$, $P = 0.005$) and male (dashed regression line: $R^2 = 0.10$, $P = 0.25$) striped mice *Rhabdomys pumilio* during the moist season (females are indicated by filled circles and males by open squares).

3.2. Behavioural syndrome

All three personality traits correlated with each other (T_{centre} and T_{active} : Kendall's tau = 0.53, $P < 0.001$; T_{centre} and T_{explore} : tau = -0.34, $P < 0.0001$; T_{active} and T_{explore} : tau = -0.25, $P = 0.001$; Fig. S3). Kaiser-Guttman analysis of the PCA revealed one component (PC1) that explained 66% of the variance in the moist season and one component (PC1) that explained 69% of the variance in the dry season. Factor loadings after varimax rotation were T_{explore} : -0.71, T_{centre} : 0.88, T_{active} : 0.88 in the dry season and T_{explore} : -0.78, T_{centre} : 0.89, T_{active} : 0.77 in the moist season. In both seasons PC1 had positive loadings with T_{centre} and T_{active} , and negative loadings with T_{explore} .

3.3. Repeatability

Individuals displayed significant repeatability in T_{explore} and low repeatability concerning T_{active} , while they did not show repeatability in T_{centre} (Table 1). Individuals displayed significant repeatability in all MRs, although highest MR and span of MR showed only low coefficients of repeatability (Table 1).

3.4. Relationship between metabolic rates and the behavioural syndrome

In the moist season, there was no relationship between PC1 and RMR ($\chi^2 = 2.74$, $df = 5$, $P = 0.74$, $R^2 = 0.16$; Fig. 2). There was a

positive relationship between PC1 and span of MR and lowest MR (Table 2; Fig. 2). The interaction between sex and PC1 influenced span of MR (Table 2), where females, but not males, with higher values of PC1 also had a higher span of MR (Fig. 3). There was no relationship between PC1 and average MR and highest MR (Table 2; Fig. 2). Sex significantly influenced average MR and lowest MR (Table 2), where females had higher levels than males. Average MR and lowest MR increased significantly with body mass, whereas span of MR decreased significantly with body mass (Table 2).

In the dry season, there was no relationship between PC1 and RMR ($\chi^2 = 6.94$, $df = 5$, $P = 0.23$, $R^2 = 0.17$; Fig. 2). There was also no relationship between PC1 and any of the measured MRs (highest MR: $\chi^2 = 12.11$, $df = 6$, $P = 0.059$, $R^2 = 0.22$; Fig. 2; for results of other MRs see Table 2). Sex influenced average MR (Table 2), where males had higher levels than females. Average MR and lowest MR (Fig. 4) increased significantly with body mass, and average MR, span of MR and lowest MR increased significantly with the time spent active in the respirometer (Table 2). Span of MR decreased significantly with the number of times an individual had previously been in the respirometer (range 0–3 times; Table 2).

4. Discussion

Striped mice showed a behavioural syndrome where fast explorers also spent more time active and more time in the centre of an arena than slow explorers. We found no relationship between the behavioural syndrome and RMR, which several other previous studies also failed to find [21,22,24]. However, our result might have been a consequence of excluding 29% of the study individuals due to their restlessness during metabolic measurements. Individuals that spent a large proportion of time active in the metabolic chamber (i.e. animals excluded from our RMR study) were also fast explorers and (only in the moist season) individuals that spent more time active and in the centre during personality tests. A similar relationship between activity and both behavioural testing and metabolic measurements was found in meadow voles (*Microtus pennsylvanicus*) [24]. Our study demonstrates that excluding non-resting individuals from respirometry studies may bias the sample used towards individuals with less active, less explorative and shy behavioural types.

Studies that measure MR for much longer periods (>12 h) could potentially avoid the reported sampling bias by allowing many more individuals to calm down, enabling reliable measures of RMR. However, longer measurements are often not feasible because some small mammals (e.g. rodents, shrews) become hyperactive when food deprived [55,56]. Moreover, in sociable species, such as striped mice, isolating individuals for extended periods from their groups can create problems

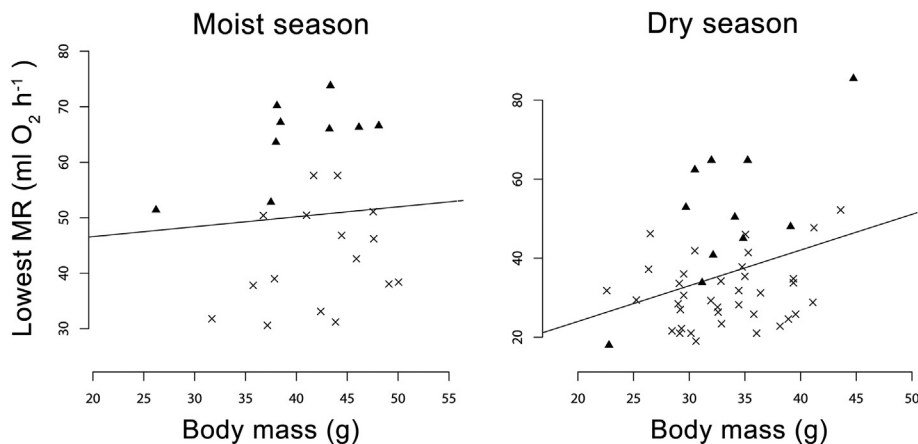


Fig. 4. Relationship between whole-animal lowest MR and body mass of striped mice *Rhabdomys pumilio* during the moist season ($R^2 = 0.005$, $P = 0.72$) and the dry season ($R^2 = 0.11$, $P = 0.02$) (regression lines are given for all individuals together; individuals which did not rest in respirometry runs are indicated by a filled triangle, individuals which rested by ×).

with the group's social dynamics, and can possibly be unethical. This might explain why most studies on free-living small mammals measure RMR for short periods, typically between 1 h and 6 h [25,39,40,73–75]. However, these studies may face a similar 'personality bias' as reported in our study.

In striped mice, measurements of all alternative MRs correlated with RMR in both seasons (Table S2). However, because RMR could only be measured for resting animals these correlations may be biased towards animals with a certain behavioural type. The time that individuals were active in the metabolic chamber explained 74% and 70% of the observed variance in average MR in the moist and dry season, respectively, emphasizing the importance of activity on MR. The strong effect of activity on MR has previously been documented [76], and our results highlight the need to include an index of activity during respirometry trials in the analysis of alternative MRs. When we used alternative measures of MR and included all individuals, we found positive relationships between PC1 and span of MR and lowest MR in the moist season. Thus, we can conclude that, in the moist season, for any given level of activity in the metabolic chamber, individuals with a higher PC1 value (i.e. fast explorers, spent more time active and more time in the centre) had a higher span of MR and lowest MR than those with a lower PC1 value. It may be of interest for future studies to examine whether such differences can also be linked to other life-history characteristics such as reproductive output and lifespan.

The relationship between MR and the behavioural syndrome in striped mice was influenced by sex, and we found different patterns in this relationship between the seasons. A study on root voles (*Microtus oeconomus*) also found an effect of both factors, where RMR was positively related to personality in the non-breeding season (low ambient temperatures and low food availability) and (marginally significant) negatively during the breeding season [25]. In the Succulent Karoo, ambient temperature is high and food availability is very low during the dry season, and striped mice remain inactive for large parts of the day [77], reducing their RMR [78] and daily energy expenditure (Rebecca Rimbach, unpublished data). Seasonal adjustments of RMR are well-documented in many vertebrates, where RMR typically decreases with increasing ambient temperatures [79–83]. A reduction in RMR and overall activity may mask links between MR and personality traits in the dry season. In support, evidence has accumulated suggesting that stressors (e.g. low food availability, high population density) can both mask or amplify (depending on their severity) relationships between metabolism and personality (reviewed in: [84]).

We did not find any link between RMR and striped mice's behavioural syndrome, but we found a strong positive relationship with span of MR in females, but not males, during the moist season. Differences between the sexes concerning personality traits are common [70,85,86] and similar sex-differences have been reported in other small mammals [25,87] and birds [27]. In striped mice, sex-differences only occurred in the moist season (which included the start of the mating season), where fast exploring and highly active females (but not males) that spent much time in the centre of an arena (high PC1 score) also had a higher span of MR. This sex-difference may result from a greater energetic investment into reproduction by females [88,89], because they need to prepare for gestation and lactation.

Apart from short measurement duration, one limitation of our study is that we measured metabolic rates during the active phase of striped mice [58]. This approach may have increased the probability that individuals remained restless and thus were excluded from the RMR study. One alternative would have been to measure RMR around mid-day, when striped mice are less active, but locating and trapping individuals at that time is difficult because striped mice forage solitarily [51]. Another alternative could have been to measure sleeping metabolic rate instead of RMR. However, thermoregulatory benefits gained from sleeping in huddling groups are the main reason for group-living in striped mice [90]. Thus, separating individuals during the night might increase stress and consequently influence metabolic rate. Whether

this would have lead individuals with a certain behavioural type to be more stressed and restless is unknown. However, our finding that personality traits of striped mice influence whether their RMR can be measured or not is valid and the question of whether this could be avoided by measuring MR in the inactive phase is an important consideration for future research.

This study is a first step towards a more comprehensive understanding of the relationship between metabolism and personality. Our study demonstrated the importance to consider the personality traits of study animals when measuring RMR, especially with regard to a sampling bias caused by the exclusion of animals with a certain behavioural type from RMR studies. We recommend that future respirometry studies report the number of excluded animals, and the reasons for their exclusion, which would broaden our knowledge concerning the extent of and patterns in this potential bias, for example whether it might be taxon, sex, age or season specific. We propose that future respirometry studies should either measure individuals for extensive periods (>12 h) to increase the likelihood that individuals with all personality types will rest. Or if this is not possible, as in our study, they should consider alternative MRs in addition to RMR, which would allow for the inclusion of a larger number of individuals in studies.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.physbeh.2017.02.037>.

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