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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.

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