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Is there a linkage between metabolism and personality in small mammals? The root vole (*Microtus oeconomus*) example

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ABSTRACT

Significant inter-individual variation in the rate of animal metabolism is a widespread phenomenon that has started to accumulate general interest. Here we follow recent calls to focus on linkage between the variation in energy metabolism and animal personality. By using wild caught root voles as a study species, we examined the relationship between the behavioral patterns (assessed in open field test) and resting metabolic rate (RMR), both of which are known to show large individual differences and intra-individual consistency in voles. Our results showed only a weak relationship between personality traits and metabolism, since the most parsimonious model (according to AICc) explaining RMR included only body mass and season as factors (explaining 84.8% of variation in RMR). However, the next two alternative models (within ΔAICc = 2) also included the personality trait reflecting proactive behaviors (PC1) in addition to body mass, sex and season (85.2 and 85.8% of RMR variance explained, respectively). In all, our study does not provide compelling support for recent ideas of close linkage between behavior and metabolism. Still, our study highlights that even in the case of wild caught individuals, when behavior and metabolism often carry effects of both intrinsic and extrinsic conditions, the potential metabolic effects of varying energetically costly behaviors cannot be neglected.

1. Introduction

The rate of energy metabolism is a fundamental vertebrate characteristic because it determines the pace at which animals require fuel. It can be expressed using the resting metabolic rate (RMR), which is a widely used measure of energy expenditure in small rodents. The studies demonstrating that RMR (or a very closely related trait–basal metabolic rate, BMR) is significantly correlated with many physiological and ecological variables, for instance, species richness and distribution, lifespan, litter size and other life-history parameters, have just recently started to accumulate [1–6].

The main factor affecting RMR is body mass, which explains up to 95% of the variation in this trait on an interspecific level [7]. The remaining variance has been attributed to phylogenetic relationships, to environmental conditions such as temperature, altitude and food availability, and to food habits, age, sex or social and reproductive status [1–10]. Conversely, on an intraspecific level, the explanatory power of body mass is much lower (usually less than 40% of explained variance), often even non-significant [11–16]. As Careau et al. [15] highlight, variance among species, populations or experimental groups in (resting) metabolic rate is often less than 10%; nevertheless, these variances have been extensively studied. In contrast, differences among conspecific individuals can be higher than 200%, but these have been largely ignored ([15] and references therein).

RMR is typically measured by respirometry when an animal is placed into a metabolic chamber for several hours. The chamber presents an unknown environment in the form of an empty box that is usually free of scents; however, placing animals into such an environment, together with handling, represents for most of them a stressful situation. Responses to stress and metabolism are both mainly controlled by the hypothalamic–pituitary–adrenal (HPA) axis and are, thus, tightly linked (e.g., [17,18]). How an individual copes with a novel situation varies within the type of its behavioral responses, which are then likely to affect metabolic rate. The type of behavioral response is characteristic for each individual, genetically determined and consistent over time and across situations (e.g., [19]). It is referred to as "coping style" [20], "temperament" [21] or "personality" [22] (the last term will be used in this paper). The most common method to assess animal personality is to measure behavior in a new environment, which is often regarded as the fundamental index of individual general behavior [23,24]. A novel

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situation usually presents appropriate stimuli that elicit the expression of particular personality components; for example, activity, exploration, emotionality and/or fear, making it possible to score different personality types. Moreover, novelty-induced stress can elucidate individual differences in HPA regulation; therefore, we can expect to find linkages between metabolism and personality traits. Measures of both RMR and personality have been shown to be consistent and repeatable in small mammals [25–29].

Two types of reactions to stress are usually recognized. First, individuals can actively handle the situation and manifest aggression or escape. This type of the reaction is called *proactive* and is accompanied by a combination of neurophysiological mechanisms that increase heart rate, muscle tonus and O_2 and glucose consumption—i.e., high sympathetic reactivity. The other type of response is referred to as *reactive* and involves immobility and passiveness. This response is characterized by high parasympathetic reactivity [30,31]. It has been shown that proactive individuals are usually more active, explorative, bold and aggressive than reactive individuals [31,32], which suggests that it is an energetically demanding strategy. Proactive individuals should, thus, expend energy at higher rates.

Inspired by Speakman [33], Careau et al. [15] proposed two hypotheses describing potential relationships between metabolism and proactive behaviors (activity and other energy-demanding behaviors). The ‘performance model’ suggests that RMR reflects the total energy available to an individual, and animals with higher RMR are able to gain, process, and invest more energy in activity. Thus, it can be expected that there will be a positive relationship between the rate of metabolism and proactive behavior. In contrast, the ‘allocation model’ presumes that an animal must allocate a fixed amount of energy between competing processes, such as RMR or activity, and the relationship between them is negative. The available literature on this topic tends to support the performance model ([34–39], but see [40]), however, the evidence so far is insufficient to reach a conclusion, and combined data on both behavior and metabolism in populations–particularly in wild populations–are still badly needed.

Our study follows the recent calls of Careau et al. [15] and Biro and Stamps [41] and attempts to develop our understanding on the relationship between metabolism and personality characteristics. By using wild caught individuals of a common rodent, the root vole (*Microtus oeconomus*), we aimed to provide a rare test for this question. Root vole represents a species in which population densities, competition, food quality and predation pressure vary from year to year, factors which have been shown to cause balancing selection on different phenotypes and to maintain variability of life-history strategies in wild populations (e.g., [42–45]).

2. Material and methods

2.1. Study area and subjects

The study was conducted in Northeast Poland at Biebrza National Park (53° 21′ 0″N, 22° 35′ 29″E). The voles were captured using wooden traps in May, September and November of 2008; traps were checked at 9:00 a.m. and 6:00 p.m. After capture, all animals were transported to the laboratory where they were weighed to the nearest tenth of a gram using an electronic scale (Scout Pro 400 g, OHAUS) and sexed. In total, 109 voles were captured and measured (29 in May, 31 in September, and 49 in November; all of these individuals were captured and measured only once). During experiments, animals were individually housed in plastic cages with water and food (commercial food pellets, hay, carrot, and apples) provided ad libitum. The voles were released at the place of their capture when the experiments were completed. The rodents were collected and subjected to all procedures with permission from nature conservancy authorities (Local Ethical Committee, Bialystok, Poland, permit no. 6/2006, 9 February 2006; and Biebrza National Park permit number: PNE-510-4-456/07, 30 January 2007).

2.2. Behavioral experiments

The first day after trapping, voles were subjected to a behavioral experiment, the open field test (OFT), which helped us to estimate basic personality characteristics for each individual. OFT is widely used in behavioral research of mammals, especially rodents. Behavior in an unknown environment is commonly regarded as the fundamental index of individual general behavior [23]; this test, above all, reveals traits such as activity, exploration, fearfulness and emotionality (see, e.g., [46–48] and references therein). Each animal was carefully removed from its cage and placed into a corner of the experimental apparatus in a transport jar. Latency to (voluntarily) enter an unknown open environment reflects individual's anxiety (see e.g., [49]). The jar was removed when the animal had left it. The apparatus was an arena of 1 × 1 m made from Plexiglas with opaque walls that were 80 cm high. The arena was illuminated during testing by a lamp with a 75 W bulb placed at a height of 1.5 m and by the lights in the experimental room (60 lx in the arena). After each trial, the arena was cleaned using 90% ethanol. All trials were recorded for five minutes (starting when the animal entered the arena) with a digital camera placed next to the lamp. The records were analyzed using the Observer Video-Pro 3.0 (Noldus Information Technology, Wageningen, Netherlands). We measured latency (LA), frequency (FR) and total duration (TD) of the following behaviors: ambulation, immobility (being still), self-grooming, rearing (standing on hind legs), scanning (attentively observing surroundings), jumping, gnawing and scratching the arena; furthermore, we counted the feces produced. Ten most important, commonly used and interpretable variables were chosen for further analyses (Table 1). Jumping, ambulation, rearing, scratching and gnawing are commonly understood to represent proactive behavior while the other variables represent reactive behaviors (e.g., [31]). The tests were performed between 9:00 a.m. and 4:00 p.m. (light phase).

2.3. Metabolic measurement

On the subsequent day, we examined voles' RMR. This parameter is not as precise as basal metabolic rate (BMR), but it avoids hyperactivity and thermoregulation abnormality due to starvation, a practice that is necessary prior to the measurement of BMR [11]. We measured oxygen consumption (ml O_2 h^{-1}) in a positive-pressure, open-circuit respirometry system in the thermoneutral zone of this species at 30 °C [50]. Outside atmospheric air was pushed through a column of Drierite (W.A. Hammond Drierite Co.) to remove water vapor and then forced through a copper coil submerged with the metabolic chamber in a water bath to control temperature. The air stream was divided into reference and measurement streams; each stream was fed into a

Table 1
PCA loadings for behaviors measured in the open field test. Behaviors for which loadings were ≥0.6 (in absolute value; in bold in the table) were used for the interpretation of the components.

	PC1	PC2	PC3	PC4
Ambulation (TD)	−0.218	0.164	**−0.808**	−0.291
Immobility (TD)	0.029	0.114	0.059	**0.903**
Gnawing/scratching (LA)	0.144	**0.857**	−0.025	0.077
Gnawing/scratching (TD)	−0.037	**−0.898**	0.033	−0.041
Jumping (FR)	**−0.885**	−0.044	−0.090	−0.007
Jumping (LA)	**0.850**	0.119	−0.052	0.071
Grooming (FR)	0.022	0.067	**0.646**	−0.391
Rearing (TD)	**−0.719**	0.018	−0.097	0.101
Scanning (TD)	**0.621**	0.423	0.358	0.200
Defecation	−0.145	0.155	**0.596**	−0.147
Proportion of total variance explained	0.250	0.180	0.158	0.114