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Metabolic–behavioural performance for overwinter survival in a wild rodent

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Modern evolutionary theory predicts that integrated phenotypes, including interacting fitness-related complex traits such as behaviour, physiology and morphology, jointly influence animal performance. However, studies have examined these aspects of biology independently in relation to fitness. We investigated how phenotypic characteristics collectively affect overwinter survival in a wild population of yellow-necked mice. We measured behavioural activity, basal metabolic rate and body mass in late autumn, released marked mice and recaptured survivors in spring to reassess their phenotypes. Mice grew, increased metabolic rate and decreased distance moved over the winter, but when those changes were accounted for, the phenotypes were intra-individually consistent. The simultaneous selective advantages of elevated metabolism and behavioural activity during autumn suggest that the interplay between physiology and behaviour is subject to selection. Despite the lack of significant phenotypic covariation between metabolic rate and behaviour, their additive survival benefits suggest that elevated activity facilitates the development of costly metabolism in free-ranging animals. As metabolism and body mass share 84% of the common variance, we hypothesized that selectively advantageous high metabolism supports overwinter growth. The results support postulates that the behaviour–physiological phenotype is the first line of selective responses and that plasticity is an important source of variation in individuals' performance.

1. Introduction

Fitness-related traits, such as behaviour, metabolism and size, often co-express, yet they are frequently studied in isolation [1]. This is adverse to the integrated phenotype concept of modern evolutionary theory [1,2], hindering our understanding of adaptive mechanisms and the contribution of traits to fitness [1]. For example, metabolic allometries [3] are optimized and constrained through the coevolution of growth rate and energy processing, which interactively influence individual fitness components, such as survival and reproduction [1,4].

The relationship between energetics and fitness can be understood through two opposing yet not mutually exclusive hypotheses: allocation and performance [5–7]. For instance, certain activity-related behaviours can be viewed as costly functions shaped by energy allocation principles or as components of energy performance mechanisms that enhance resource acquisition [5,8]. Consistent individual differences in behaviours and animal personalities are thought to arise from evolutionary trade-offs among various life-history strategies [9]. For example, proactivity, in contrast to reactivity, is predicted to enhance current reproduction but may compromise survival, longevity and future reproduction [9]. However, there has yet to be evidence supporting the idea that proactivity, or any other behavioural trait, consistently impacts

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fitness, such as survival [10,11]. This lack of consistency may be attributed to interdependence among phenotypic traits, as predicted by the pace-of-life syndrome hypothesis [12]. The hypothesis suggests that fitness consequences associated with animal personalities interplay with, or are mediated by, other functions [12], like energy metabolism ([13]; example in [14]).

Some of the previous inconsistent results of the metabolism–fitness [1] and behaviour–physiology associations [15] might have emerged from the common practice of statistical correction of metabolism for variation in size (i.e. allometry). Such manipulation might result in the removal of a significant part of the mechanistically important variation in metabolic rate [3,16]. Effectively, those studies assumed the size, e.g. body mass, as an independent variable and metabolism as unidirectionally dependent on size when considering fitness effects [17]. It is somewhat in opposition to theoretical predictions and empirical knowledge: body mass and metabolic rate coevolve [1,4,18], and body mass is a product of growth rate that depends on the rate of energy acquisition, transformation and allocation [3]. Therefore, studies on size-corrected metabolism might miss the essential components of fitness-related variance linked to coevolution among the correlated organismal (e.g. growth) functions. It may lead to incorrect conclusions where fitness is attributed to variation in size, while it might be (at least partially) a product of variance in bioenergetics.

Only two studies, so far, have considered the fitness of behaviour–physiology co-expression, and only in a single cold-blooded species [19,20]. Here, we fill this gap by testing whether the integrated phenotype affects individual fitness in wild warm-blooded species. We focus on basal metabolic rate (BMR) as a measure of maintenance metabolism in endotherms because this trait links to many aspects of animal performance (exercise metabolism [21], growth [22], behaviour [23] and spatial ecology [24]) and as such can lead to many energetic and life-history trade-offs [25]. The ‘compensatory’ hypothesis predicts that individuals with a low maintenance metabolism can survive better on fewer resources and can allocate more to growth and reproduction [26,27]. By contrast, the ‘increased intake’ hypothesis predicts that animals with a high maintenance metabolism, reflecting more efficient metabolic machinery, can assimilate more energy to invest in fitness [28,29]. We examined whether the survival component of fitness in wild yellow-necked mice (*Apodemus flavicollis* (Melchior, 1834)) is related to maintenance metabolism and/or size. By doing so, we advocate for phenotypic tests of individual fitness that rely less on assumptions and are, therefore, less restrictive. To distinguish between morphological and physiological sources of fitness relatedness and to avoid assumptions about the directionality of the size–metabolism relationship, we tested whether selection operates on residual metabolic rate, independent of the animals’ size or on size-predicted whole-body metabolism. Finally, we tested whether the selection mechanism occurs independently or along with selection on consistent activity behaviour, testing between allocation and performance mechanisms.

2. Methods

(a) Study system

We studied a wild population of the yellow-necked field mouse from the old-growth Białowieża Natural Forest (52.45′ N 23.46′ E). In autumn (16 November–8 December 2022), 25 females and 23 males, all subadults (born in the preceding summer; determined by body mass and degree of abrasion of scales on tail [30]), were captured in 1 ha (10 × 10 m) grid of 121 points (two traps per point). To ensure a high recapture rate during the following spring, we run 12 day-long trapping sessions (26–31 March and 25–30 April 2023) on an extended grid with two added lines on each side (resulting in approx. 2 ha grid of 225 points with 450 traps). Trapped mice (with wooden traps baited with carrot, oat and sunflower seed) were transported to a laboratory at the Mammal Research Institute of the Polish Academy of Sciences (Białowieża, Poland), approximately 10 km apart. Mice were individually marked with transponders (IPTT-300; Biomedic Data Systems Inc.) and weighed to the nearest 0.1 g (ScoutPro 200; Ohaus) under a 2% mixture of isoflurane (Iso-Vet) anaesthesia. Animals were kept in the walk-in climatic chamber (16 ± 2°C, natural photoperiod) in individual cages (Techniplast 1264), supplemented with shelter (plastic tube) and wood chip bedding. We provided water and food (apples and rodent food; Versele-Laga, Deinze, Belgium) ad libitum. After the experimental procedures, the animals were released at capture locations. Experimental procedures were approved by the Local Committee for Ethics in Animal Research in Olsztyn, Poland (decision no. 67/2020).

(b) Activity behaviour

The intensity of mice activity was quantified using an open-field test (OFT) in an arena (1 × 1 × 1 m, made of white PVC, illuminated with four 4.8 W, 470 lm lightbulbs) during a day following capture. The arena was cleaned with 70% ethanol between trials. Animals were tested individually by relocating to a corner of the arena inside their home cage shelter (plastic tube). Once the animal entered the arena, the tube was removed. If the animal did not enter the arena voluntarily, it was placed in the arena corner. Individuals were allowed to explore the arena for 5 min, remotely observed and recorded from outside of the behavioural room (with a Hero 5 GoPro Inc. camera). We assessed the total distance moved during OFT automatically (in the Animal Tracker plugin, ImageJ [31]) and defined activity behaviour as the distance covered, divided by the time of movements, subtracting time when animals were immobile (i.e. freezing behaviour; see the electronic supplementary material). This standard marker of activity behaviour [32] was found to be repeatable in our mice population [33].

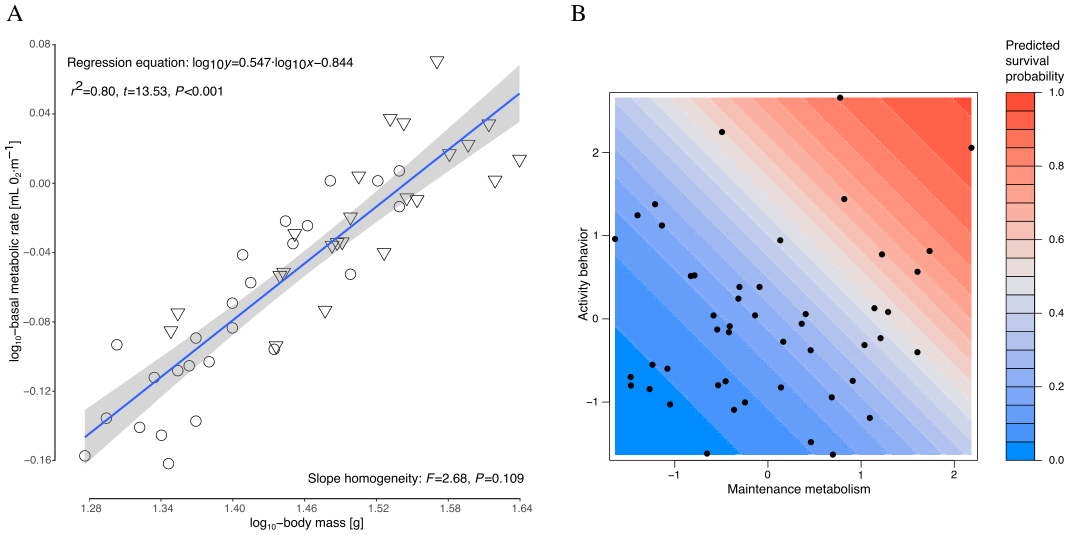

Figure 1. (A) Relationship between basal metabolic rate and body mass in female (circle) and male (triangle) mice measured in autumn. The homogeneity of slopes in males and females was compared using analysis of covariance. (B) Relationship between probability of survival (1, survive; 0, no survival) in winter and maintenance metabolism (standardized basal metabolic rate) and activity behaviour (standardized distance moved during activity) measured in autumn.

(c) Maintenance metabolism

Metabolic rate was measured a day after OFT using indirect calorimetry in an open-flow respirometry system designed to measure six animals simultaneously. Metabolic rate was measured on post-absorptive animals (during daytime, ≥6 h after last possible consumption of food) resting in thermoneutral temperature (30°C [34]) in individual glass chambers (300 ml) during 4 h long trials. Incurrent flow rates (approx. 200 ml min^{-1} dried with silica gel) were measured continuously (FlowBar-8; Sable Systems International; henceforth SSI). Excurrent air from animal chambers was sampled (with flow 80 ml min^{-1}) sequentially (multiplexer, Sable System) between six animals and two control lines to measure oxygen concentration in two analysers (FC10, SSI). Air from each flow line was sampled 24 times for 140 s every 10 min. Metabolic rate was calculated as the average of the last 20 s readings of each sample of VO_2 (eqn (10.2) [35]), assuming a 0.8 respiratory exchange ratio. BMR was defined as the average of the three lowest 20 s means obtained for individual mice.

(d) Statistical analyses

To test the intraindividual consistency of phenotypes, we estimated intraclass correlation coefficients for sex-standardized (subtracted from the male or female population mean and divided by the male or female population standard deviation) values of body mass (m_b), BMR, residual metabolism (adjusted for mass, rBMR) and activity behaviour (AB) using the 'irr' R package. To account for the allometric nature of metabolic scaling, rBMR was calculated as residuals from ordinary least square regression between $\log_{10}$-transformed BMR and $\log_{10}$-transformed m_b [36]. Phenotypic correlations between sex-standardized values of m_b and BMR, rBMR and AB measured in autumn were obtained as Pearson product–moment correlations using the 'stats' R package.

Overwinter survival was measured as a binary predictor, presence–absence, in the spring grid of autumn phenotyped mice. Thus, the analysis assumed that unrecaptured mice in the following spring did not survive the winter. To test the strength and direction of survival selection on studied phenotypes, we used logistic regression with logit-link function in generalized linear models (GLM) of the 'stats' R-package. We applied a stepwise algorithm for trait selection for the final model interpretation using the 'MASS' R package. Overwinter survival was included as a binary response (1 or 0) variable, and sex-standardized autumn m_b, BMR, rBMR and AB obtained in autumn were included as explanatory covariates. The variables for the final model were forward selected using the Akaike Information Criterion (AIC) in a stepwise algorithm with the function 'stepAIC'. The ΔAIC of ≥ 2 for a candidate variable was assumed as a significant improvement for further model steps when compared with a previous one (as well as to other candidate variables within a given step). Selection gradients were calculated using the linear model on standardized variables and relative survival, following Lande & Arnold [37]. All statistics were calculated in R (v. 4.3.1).

3. Results

(a) Population, variation and covariation

In total, we captured 48 and 31 individuals in autumn and spring, respectively. Thirteen individuals marked in autumn were recaptured in spring (27% survived). During the spring session, no autumn-marked individuals were recaptured in the additional lines, suggesting that animals remained in their autumn home ranges (but long-distance dispersion cannot be excluded). All of the mice phenotyped in autumn were recaptured during the first four nights of the March session (six males and seven females). Body mass, BMR (but not rBMR) and AB consistently differed among individuals when adjusted for the population-level temporal variation (table 1). Body mass and BMR were highly correlated ($r = 0.84$ (95%CI: 0.74,0.91), $p < 0.001$), and m_b considered as a predictor explained 80% of the variation in BMR ($r^2 = 0.80$, $t = 13.53$, $p < 0.001$; figure 1A). Neither m_b nor BMR or rBMR correlated significantly with AB (table 2).

(b) Survival selection

Mortality during winter did not differ between males (74%) and females (72%; $\chi^2 = 0.01$, $p = 0.91$). Two-step analysis resulted in a model that included BMR and AB. Still, it did not indicate m_b or rBMR as significant predictors explaining variation in the overwinter survival of mice (table 3). According to this model, the overwinter survival was positively correlated with both BMR (β [s.e.] = 0.59 [0.22], $\alpha = 0.97$ [0.41], $z = 2.35$, $p = 0.019$) and AB ($\beta = 0.52$ [0.22], $\alpha = 0.86$ [0.42], $z = 2.06$, $p = 0.039$; figure 1B).

4. Discussion

In our study, variation in the level of activity and metabolism of individuals were the primary predictors of animal overwinter survival, assuming plausible emigration as insignificantly impacting our main conclusions. Mice that were more active and had higher whole-body metabolism survived better than those that were less active and had lower metabolism (table 3 and figure 1B). In contrast, neither body size nor size-corrected residual metabolism was the main predictor of the mice's overwinter survival in this population (table 3).

The high autumn body mass in wild animals is usually associated with their chances of surviving winter, sometimes saliently assuming some unmeasured physiological properties (e.g. rates of growth and fat accumulation) [38–42]. Despite, as predicted in the metabolic theory of ecology, the BMR scales as an exponent of body mass (in mammals: 0.46–0.78 [43,44]; in our study: 0.55), studies on body size effects on survival rarely directly refer to the associated variation in metabolism, and if they do, they consider its residual variance only [40,45–47]. The previous studies indicate a strong positive genetic covariation between body mass and whole-body metabolism, suggesting that individuals' energy expenditures can quickly change through coevolution between mass and metabolism [48,49] (see also [18]). Thus, statistical separation of phenotypic variance solely attributed to metabolism from that solely attributed to body mass might not be possible [3,16]. Instead, attempting that separation might yield bias, e.g. when natural selection acts simultaneously on both size and metabolism or on metabolism and associated growth rate. Some studies showed that residual variation in metabolism could undergo stabilizing selection [45,50–53], suggesting that the selection acts on body mass-predicted metabolism or size-metabolism co-expression. The use of residual variation of metabolism, accounting for body mass, is motivated by an argument that the body composition of metabolically active organs explains the residual variance in metabolism [54]. However, organ size explains rather a minor portion of individuals' variance in residual basal metabolism, and those estimates were rather inconsistent among experiments and study systems [54–60] (but see [22,61]). Consequently, statistically correcting for variation in size may not be the most optimal, as it might remove important sources of mechanistic variation [3], resulting in residuals referring only to partial variance in metabolic rate.

Most of the studies in the field of fitness–phenotype relation refer to the BMR of adult, non-growing, non-reproducing and non-performing animals. At the same time, natural selection operates on animal metabolism, associated with growth [40,51], reproduction [46,53] and ageing [62]. Survivor mice here increased body mass by approximately 20% (table 1), confirming overwinter growth [63], suggesting that the minimum metabolic rate we measured was likely associated with additional costs related to growth [40,51]. In our previous study, the maintenance metabolism of subadult yellow-necked mice measured in autumn predicted their growth until the middle of the winter [63]. Thus, survival selection on metabolism detected here might actually promote development under challenging winter conditions, where metabolic machinery supports energy transformation and assimilation, concordant with the 'increase-intake' hypothesis [64]. Metabolic traits are strongly genetically linked with growth-related characteristics [65]. For example, an experiment on laboratory mice showed that selection for high basal metabolism resulted in a correlated response in increased growth rate and likely associated intestinal length [22]. Thus, growth rate and adult body size can depend on metabolism (essential for energy assimilation) onset as the maintenance cost of early postembryonic development [66].

As growth depends on a continuous energy supply, selection promoting expensive metabolic machinery and supporting fast growth is possible only when energy acquisition is facilitated by behaviour. Likely, due to this limitation, fast-growing chipmunks were the least likely to survive [51], and growing squirrels with high metabolism but little food hoards were eliminated from the population [40]. Yet, simultaneous effects of maintenance metabolism and consistent individual differences in behaviour on survival [19,20] have been studied only in the ectothermic model so far, which fundamentally differ in energetic requirements from endotherms (e.g. endotherms have several times lower maintenance metabolism [67]). In the study on lizards, metabolism and behaviour were independent and suggested alternative mechanisms to improve growth rate and survival by either low energy expenditure and high exploration or high energy expenditure and low exploration [19]. However, the lizards with a high metabolism and low exploration grew faster and tended to survive better than those with a low metabolism and high exploration [19]. In our experiment, overwinter mice survivors were not only characterized by high metabolism (and associated size) but they were also the most active individuals. Activity behaviour can improve individuals' exploration of space, aiding food detection and acquisition capabilities [5,8] (see for our mice species [68]). From this perspective, our study suggests the operation of the performance mechanisms, where fast-growing mice with high metabolism and

Table 1. Variation and repeatability (ICC, intraclass correlation coefficients) for body size (m_b, body mass), whole-body (BMR) and adjusted for m_b residual (rBMR) maintenance metabolism (basal metabolic rate) and activity behaviour (AB, distance moved per time of activity). Agreement refers to the degree of absolute agreement among individual measurements, while consistency refers to systematic differences between individual measurements. CV, coefficient of variation; CI, confidence intervals; a, in autumn; s, in spring. Tests of differences between seasons: ns, not significant, *<0.05, **M < 0.01, ***<0.001.

trait	mean	range	CV	agreement		consistency	
				ICC [95% CI]	*p*	ICC [95% CI]	*p*
m_b (g)	35.0 (a: 31.5, s: 38.5)***	a: 25.1–38.1 s: 31.9–50.2	16.96	0.22 [−0.09,0.63]	0.167	0.58 [0.07,0.85]	0.015
BMR (ml min^{-1})	1.05 (a: 0.96, s: 1.14)***	a: 0.85–1.18 s: 0.93–1.29	12.47	0.18 [−0.07,0.57]	0.187	0.56 [0.04,0.84]	0.018
rBMR (ml min^{-1})	0.00 (a: −0.02 s: 0.02)^{ns}	a: −0.05–0.03 s: −0.03–0.05	6.49	−0.07 [−0.48,0.45]	0.603	−0.08 [−0.59,0.48]	0.602
AB (m min^{-1})	12.35 (a: 13.90, s: 10.80)**	a: 9.32–18.63 s: 5.66–16.30	25.12	0.27 [−0.13,0.67]	0.124	0.47 [−0.08,0.80]	0.045

Table 2. Phenotypic correlations (*r*) between body size (m_b, body mass), whole animal (BMR) and adjusted for m_b residual (rBMR) maintenance metabolism (basal metabolic rate) and activity behaviour (AB, distance moved per time of activity) in mice captured in autumn, separately for mice that survived or not the winter. The homogeneity of slopes (S-H) between survivors and non-survivors was compared using analysis of covariance, assuming metabolism or m_b as predictors and behaviour as the dependent variable. CI, confidence intervals.

traits	all animals, *n* = 48		survivors, *n* = 13		non-survivors, *n* = 35		S-H
	r [95% CI]	*p*	*r* [95% CI]	*p*	*r* [95% CI]	*p*	*p*
AB~m_b	0.03 [−0.26,0.31]	0.863	0.12 [−0.46,0.63]	0.694	−0.19 [−0.50,0.15]	0.265	0.370
AB~BMR	0.11 [−0.18,0.39]	0.442	0.35 [−0.25,0.76]	0.236	−0.18 [−0.49,0.16]	0.298	0.095
AB~rBMR	0.11 [−0.18,0.38]	0.466	0.28 [−0.32,0.72]	0.357	−0.05 [−0.38,0.29]	0.783	0.293

Table 3. Results of stepwise model components selection for logistic regression with logit-link function explaining variation in overwinter survival. Body size (m_b, body mass), whole-body (BMR) and adjusted for m_b residual (rBMR) maintenance metabolism (basal metabolic rate) and activity behaviour (AB, distance moved per time of activity) were included as candidate explanatory variables. Stepwise best components and the final model are represented in bold.

step/explanatory variable	AIC
survival~1 (step 0)	58.1
+BMR	**52.4**
+AB	54.0
+m_b	54.4
+rBMR	58.3
survival~BMR (step 1)	52.4
+AB	**49.4**
+m_b	54.4
+rBMR	54.4
survival~BMR+ AB (step 2)	**49.4**
+m_b	51.0
+rBMR	51.3

high activity levels survive better to the following breeding season. While the breeding success of surviving individuals was not assessed directly, the observed high metabolism may correlate with increased reproductive success, as demonstrated in laboratory mice [69,70]. This possibility remains to be tested for our study animal (but see [71]). This, together with our survival results, indicates that the 'increase-intake' model for the evolution of a high level of basal energy metabolism in wild animals is a realistic scenario, but only when accompanied by high behavioural performance [5].

5. Conclusion

Our study indicates that the survival component of individual fitness links to whole metabolism rather than to mass-specific metabolism, suggesting that strongly correlated body mass evolves in response to selection on metabolism and growth rate. Our study also showed parallel survival selection between behavioural activity and metabolism, where the benefits of high activity should aid resource collection needed for physiological growth and maintenance. Despite parallel selective advantages of behaviour and metabolism, we found no evidence of a consistent phenotypic correlation between activity level and metabolic rate at the individual level. However, the metabolic rate and behaviour can also be correlated at the within-individual level, highlighting the significance of poorly studied plasticity mechanisms for phenotype maintenance in the wild [6,72]. Thus, our results support the operation of the behavioural–metabolic performance model only on the selective and not on the phenotypic level, suggesting that a high level of plasticity is involved in this phenomenon.

Ethics. Experimental procedures were approved by the Local Committee for Ethics in Animal Research in Olsztyn, Poland (decision no. 67/2020).

Data accessibility. All data are available as electronic supplementary material.

Supplementary material is available online [73].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. J.S.B.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, validation, visualization, writing—original draft, writing—review and editing; K.Z.: funding acquisition, supervision, validation, writing—review and editing; K.I.: investigation, writing—review and editing; Z.B.: conceptualization, validation, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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