RESEARCH PAPER

Spontaneous activity rates and resting metabolism: Support for the allocation model of energy management at the amongindividual level

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Funding information

This research was supported by an ARC Future Fellowship and an ARC Discovery Grant to P.A.B. BA was employed to collect these data using funds from an Australian Research Council Discovery grant awarded to PAB (DP 110104750).

Editor: Leonida Fusani

Abstract

Despite continuing interest in the proximate energetic constraints on individual variation in behavior, there is presently equivocal evidence for correlations between metabolism and behavior at the among-individual level. Possible reasons for this include imprecise estimates of individual mean behavior and metabolism due to no repeated measures on one or more of the traits, analyses that do not take into account the labile nature of these traits and the uncertainty in individual estimates, and changing environmental conditions not accounted for. In this empirical study, we repeatedly measured activity rates and resting metabolic rates (RMR) of individual male mosquitofish over an extended period, lasting several months under constant laboratory conditions. Repeatability of each trait was significant (RMR: R = .41; activity: R = .72), indicating consistent variation among individuals, making covariance between them possible. Contrary to expectations, bivariate mixed model analysis revealed that more active individuals had lower RMR (r = -.58) after accounting for mass effects and other covariates. This result suggests that high activity rates require individuals to allocate less energy toward maintenance, and thus provides evidence for the "allocation" model of energy management. We suggest that it would be valuable to study whether and how behavior-RMR correlations change over individual lifetime, a topic that has yet to be addressed.

KEYWORDS

activity, energetics, pace of life, personality

1 | INTRODUCTION

Consistent individual differences in both metabolic and behavioral traits are now well described in the literature and evidenced by significant trait repeatability (*ca.* R = .4) for each of these trait classes (Bell, Hankison, & Laskowski, 2009; Nespolo & Franco, 2007; White, Schimpf, & Cassey, 2013; Wolak, Fairbairn, & Paulsen, 2012). Previous studies thus indicate that individuals differ from one another, but exhibit rather low within-individual consistency over time (Biro & Stamps, 2015). Presently, considerable research attention is focussed on understanding this among- and within-individual trait variance, by both physiologists and behaviorists (Burton, Killen, Armstrong, & Metcalfe, 2011).

In contrast to this large literature on labile trait repeatability, the extent to which these traits can and should covary, and under what circumstances they do so, are still not yet clear (Burton et al., 2011; Killen, Marras, Metcalfe, McKenzie, & Domenici, 2013; Royauté, Berdal, Garrison, & Dochtermann, 2018). Conceptual and theoretical

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work has suggested that metabolism and behavior should be correlated due to functional links—given that energy fuels all life processes, then if individuals vary in their ability to acquire food and convert it to energy, or differ in their allocation of energy to behavioral activity versus resting metabolism, then individuals will also vary in the expression of levels of behavior (Metcalfe, Taylor, & Thorpe, 1995, Careau, Thomas, Humphries, & Reale, 2008, see review in Biro & Stamps, 2010).

How and why metabolic rate and behavior should be correlated at the among- and within-individual level depends on our assumptions about how energy acquisition and allocation are managed, referred to as energy management models. There is evidence to support the "increased intake" or "performance" model of energy management, whereby resting metabolic rate (RMR) reflects the costs of running energetically expensive organs that in turn support energy expenditure on a sustained basis (Daan, Masman, & Groenewold, 1990, Ricklefs, Konarzewski, & Daan, 1996, Nilsson, 2002, see also reviews in Careau et al., 2008, and in Biro & Stamps, 2010, Auer, Killen, & Rezende, 2017). In this scenario, those individuals with high RMR should be able to sustain energetically costly activities to a greater extent than those with low RMR, and evidence seems to support positive correlations between RMR and measures of sustained energy output (Auer et al., 2017). In other words, if RMR reflects energetic capacity (sustained energy output), individuals with consistently higher RMR should also express consistently higher levels of energetically costly behaviors, and/or behavior that increases intake rates (Biro & Stamps, 2010). Under an alternative view, the "allocation" or "compensation" model predicts that individuals have a fixed energy budget, meaning that those individuals that spend relatively more energy on behavioral activities must therefore allocate less to resting (=maintenance) metabolism (Careau et al., 2008; Nilsson, 2002).

Presently, empirical evidence for among-individual correlations between behavior and metabolism, if present, is equivocal. Several studies have reported positive correlations between metabolic rate and behavior (e.g., (Careau et al., 2011; Huntingford et al., 2010; Martins, Castanheira, Engrola, Costas, & Conceição, 2011; Metcalfe et al., 1995; Myles-Gonzalez, Fox, Burness, Rooke, & Yavno, 2015), while others have not (e.g., Farwell & McLaughlin, 2009, Timonin et al., 2011, Le Galliard, Paquet, Cisel, & Montes-Poloni, 2013, Mathot, Martin, Kempenaers, & Forstmeier, 2013, Merritt, Matthews, & White, 2013, Gifford, Clay, & Careau, 2014; see also reviews in Biro & Stamps, 2010, and Baktoft et al., 2016, Biro, Fanson, & Santostefano, 2016). Amongst studies that do report on significant correlations, these are weak or differ amongst contexts or groups (Lantová, Zub, Koskela, Šíchová, & Borowski, 2011, Reid, Armstrong, & Metcalfe, 2011, Killen, Marras, Ryan, Domenici, & McKenzie, 2012, Reid, Armstrong, & Metcalfe, 2012, Bouwhuis et al., 2014, Pang, Fu, & Zhang, 2015). Indeed, a recent meta-analysis which focused on "pace of life syndromes" studies revealed little to no average correlation between levels of various behaviors and metabolism (Royauté et al., 2018).

One reason why trends between behavior and metabolism appear equivocal, and correlations hover around zero, may be that many studies have not addressed the labile nature of these traits (numerous studies do not contain repeated measures of both metabolic rate and behavior (Biro & Stamps, 2010; Royauté et al., 2018). Without repeated measures on both traits, correlations between them are necessarily biased toward zero when repeatability values are relatively low (discussed by Adolph & Hardin, 2007). Related to this, is the need to use statistical methods, specifically bivariate mixed models, that take into account the labile nature and uncertainties in estimates of individual mean values when estimating amongindividual correlations. Another reason is that we should not simply expect all behaviors to be similarly correlated with metabolism, as not all behaviors necessarily have substantial energy costs nor clear effects on energy intake (Biro & Stamps, 2010; Mathot, Nicolaus, Araya-Ajoy, Dingemanse, & Kempenaers, 2014). Variable environmental conditions if not accounted for can confound relationships between behavior and metabolism (Biro & Stamps, 2010; Killen et al., 2013), and if trials are short in duration shy individuals may not achieve a non-stressed resting metabolism (Biro et al., 2016; Careau et al., 2008; Krams et al., 2017).

Here, we investigated the among-individual covariance between RMR and spontaneous activity rates in 30 male mosquitofish (Gambusia holbrooki), measured repeatedly over time in the laboratory under ad lib food conditions, and analyzed using a bivariate mixed model. We studied males following suggestions by Biro and Stamps (2010) that it would be best to study this topic in males that have largely stopped growing (the case in Gambusia) because opportunities for variation in energy allocation are fewer than for females, making it easier to study. We specifically tested the prediction that RMR should be positively correlated with the amount of time spent moving during daylight hours (spontaneous activity), under the assumption that it reflects the capacity to acquire energy under natural and laboratory conditions (e.g., Anholt, Werner, & Skelly, 2000; Biro, Post, & Parkinson, 2003), and at the same time has significant energy costs (Biro & Stamps, 2010; Boisclair & Tang, 1993; Careau et al., 2008). That is, we assume individuals are intrinsically energy limited under the ad libitum food conditions in the laboratory, limited by individual variation in their ability to consume and process food into energy, and that activity and daily energy expenditure are positively correlated (Meek, Lonquich, Hannon, & Garland, 2009; Rezende, Gomes, Chappell, & Garland, 2009; Sadowska, Gębczyński, & Konarzewski, 2013). Therefore, any correlations between spontaneous activity and measures of metabolism should exist due to functional and genetic links between metabolism and behavior, as demonstrated by artificial selection studies under ad lib food conditions (Eisenmann, Wickel, Kelly, Middleton, & Garland, 2009; Meek et al., 2009; Rezende et al., 2009; Sadowska et al., 2013; Waters et al., 2008).

2 | METHODS

2.1 | Study animals and housing

The fish used in this study were also part of another, extended, longitudinal study of among- and within-individual variation in behavior (Biro & Adriaenssens, 2013). Here, we used a portion of the previously published activity dataset to relate to measures of metabolic rate that were obtained in the present study. The portion of that data we used was two clusters, or "bursts", of activity sampling that corresponded to the bursts 3 and 4 described in Biro and Adriaenssens (2013). Specifically, we used 6 days of activity trials (=12 observations per individual) obtained 12 days prior to the first measure of metabolism, which required a total of 5 days to complete all 30 fish. This was followed by an interval of 20 days without measures of activity. Then, the second burst of activity sampling contained 3 days of consecutive activity measures (=6 observations per individual), and this burst of sampling was followed by a second measure of metabolism starting 4 days after the last behavioral assay.

Details of sampling fish from the wild, acclimation to the laboratory, and selection of individuals for the experiment are given in (Biro & Adriaenssens, 2013). Briefly, a total of 30 size-matched males were chosen to minimize size effects ($\bar{x} \pm SE = 0.225 \pm 0.004$ g; $\bar{x} \pm SE = 28.66 \pm 0.21$ mm). Fish were allocated to individual home tanks (20 × 13 × 13 cm, 2.8 L water volume) where they resided from April 26 until September 10 (when the experiment was terminated). The individual tanks were kept in a temperature-controlled room with a 12 hr/12 hr D/N photoperiod (fluorescent tubes). The bottom of each tank was covered with 2 cm of sand and transparent mosquito mesh was placed above the tanks preventing fish from jumping out. Tanks were subdivided into a sheltered and an open area. All lateral sides of the tank were covered with dark (shelter area) or white (open area) plastic except for the short side of the open area through which observations occurred. All experimental tanks were continuously supplied with clean water from the same flow through filtration system (ca. 1.8 L/h). Water temperature was held at 25°C (range = 24.4 to 26.3°C) over the entire experiment. On three separate occasions, tanks were randomly moved to avoid any systematic position effects on behavior.

2.1.1 | Assays of individual activity

The proportion of time each individual spent active was scored during one-hour trials. Trials involved repeated scans of each individual, made every 2 min, for a total of 30 scan samples per fish over 1 hr. At each scan, we noted whether the fish was active or inactive (i.e., motionless, that is if there was no change in position during the first 3 s after being spotted). Thus, activity represented an estimate of the proportion of time spent moving over one hour. Fish were observed twice daily, in the room, during the morning (10:30–12:00 hr) and again in the afternoon (15:00–17:00 hr) with the observer seated motionless in front of the tanks.

Fish received *ca*. 0.05 g high protein fish feed pellets (representing >10% of fish body wet weight which is above the amount of food required to feed to satiation), 1–3 times per day. This created variation in the time since last feeding (14–500 min, $\bar{x} = 219$ min) before activity observations were made. However, this was previously been shown to have no effect on activity at the mean level (Biro & Adriaenssens, 2013), nor has it any effect at the within-individual

level when assessed as a random slope effect in the present study

2.2 | Measurement of metabolism

(p > .1); hence, this factor was removed from the model.

Each respirometry trial measured oxygen consumption, 7 fish at a time in an 8-channel respirometry system (Loligo Systems) immersed in a 10 L temperature-controlled tank. Prior to transfer to respirometry chambers (diam. = 1.5 cm, length = 4 cm; volume = 6 ml), we fasted the fish for 36 hr. Then, fish were weighed (±0.001 g) and added to chambers in the late afternoon (14:00-16:00 hr) where they remained undisturbed overnight until the following morning at 09:00 hr. We used intermittent-closed respirometry, whereby water circulation alternated between a closed circuit (for measurement) and an open circuit (for flushing). One control chamber was always left empty to monitor background microbial respiration. An automated, computer-controlled system driven by AutoResp[™] software (Loligo Systems) simultaneously measured oxygen consumption in each of the chambers and controlled flushing and re-circulating pumps. Measurement cycles consisted of a 10 min flush, a 2 min waiting period, and an 8 min measurement period. The R^2 for the oxygen consumption slope over time using this cycle always exceeded .9, and oxygen content in chambers never fell below 85% air saturation. Constant temperature (25.0°C, range = ±0.1°C) was maintained using a computer-controlled pump that cycled the water into a heat exchanger immersed in a warm water bath. Fish were exposed to ambient light conditions (~10 hr light, 14 hr dark).

OXY-4 oxygen meters (Presens) were used to measure oxygen partial pressure, using fiber optic probes. Measurements occurred every second during the 8-min measurement phase. The slope of oxygen decline in chambers (determined by linear regression) was used to calculate whole-animal metabolic rate using the equation $MO_2 = k \times V$; MO_2 is the oxygen consumption rate (mg O_2/h), *k* is the slope of the oxygen consumption over time (mg $O_2/L/h$), and V is the respirometric volume. We then extracted the lowest value observed as our estimate of RMR. Following best practice, we used wholeanimal metabolic rate and accounted for mass in the data analyses (Hayes, 2001; Lighton, 2008). The overall average mass-corrected RMR was 184 mg $O_2/g/h$ (range = 138–240 among individuals).

2.3 | Data analysis

Data were analyzed using a bivariate mixed model (Proc Mixed, SAS 9.2); (Littell, Milliken, Stroup, Wolfinger, & Schabenberger, 2006). Activity data were logit transformed, and metabolic rate was intransformed to normalize the residuals. Then, both were standardized (to $\bar{x} = 0$, SD = 1) to facilitate both the bivariate analysis and the interpretation of model variances; time of day, and day of trial were centered. By centering these predictors, the intercept represents the predicted mean activity mid-way through the series of assays over time and at midday; this was particularly important given that we observed that individuals differed in temporal patterns of



FIGURE 1 Predicted mean values for individual activity rate and resting metabolic rate (RMR), and associated SE's for each, as extracted from the bivariate mixed-effects model. Values are expressed as deviations from the mean level model and are in units of standard deviations due to data standardization to mean zero and *SD* = 1. The overall average mass-corrected RMR was 184 mg $O_2/g/h$ (range = 138–240 among individuals)

activity across days (temporal reaction norms differed, evidenced by substantial random slope effect of day). In order to estimate the among-individual variance for each trait and covariance between them, we fitted a random intercept with respect to individual identity for each trait. In the case of activity only, we additionally fitted a random slope effect to account for the substantial (and significant) individual differences in temporal trend-lines of activity across days that were present in the data (Est = 1.72, SE = 0.57, p = .001); this was done primarily to satisfy the assumptions of the model, which require constant variance and independent observations, which are clearly violated when individuals differ in their temporal patterns of activity across days. It is not possible to fit a random slope effect for day of study for metabolism given only two repeat observations per individual. Since the variable "day" was mean-centered, the random intercept effect (i.e., random effect of ID) generates predictions which represent the average predicted activity for that individual, and it is the covariance between these predicted values and the predicted mean values for metabolic rate that we assessed and report on below.

For both activity and metabolism, we included mass as a fixed effect to account for the expected mass-dependency of metabolic rate and also to assess any mass-dependency of behavior (but there was none); we used the mass estimate at each metabolism assay as an estimate of the mass of fish in the preceding burst of activity assays. Day was also included as a fixed effect to capture any temporal trends in our longitudinal data for both traits; time of day was included as a fixed effect for activity only (because RMR is estimated overnight only). We used the Kenward-Roger method to determine *df* for tests of fixed effect parameter estimates, which produce *df* estimates that can be non-integer values. Finally, a separate residual variance was fit for each trait. All fixed and random terms were retained in this model; thus no model culling was performed. Because trait measurements were not matched in time and were separated by significant intervals, we did not fit within-individual residual covariance structure in the model.

3 | RESULTS

3.1 | Mean-level effects

As expected, fish that were larger and heavier had substantially higher metabolic rates than smaller ones (Est = 4.44, *SE* = 1.0, $t_{32.2} = 4.3$, p = .0002) but mass had no effect on activity (Est = -0.11, *SE* = 2.3, $t_{25.3} = -0.05$, p = .96). Activity was lower in morning assays than in afternoon assays (Est = -0.37, *SE* = 0.047, $t_{430} = -7.9$, p < .0001). Neither activity rates nor metabolism varied across days on average (Activity: Est = -0.21, *SE* = 0.27, $t_{26.2} = -0.78$, p = .44; Metabolism: Est = 0.032, *SE* = 0.69, $t_{21} = 0.05$, p = .96).

3.2 | Individual-level effects

After accounting for the mean-level effects described above, individual differences were evident for both traits. Trait variance was significant for metabolism (Est = 0.28, SE = 0.16, p = .04) generating a significant but moderately low repeatability of R = .41; by contrast, activity variance was relatively larger (Est = 0.68, SE = 0.20, p = .0003) generating a rather high repeatability, R = .72. Residual variances used to calculate the repeatability of each trait are 0.41 (SE = 0.13) and 0.26 (SE = 0.018) for RMR and activity respectively (e.g., Ract = 0.69/[0.69 + 0.26]). Given that among-individual variance was substantial for both traits, covariance between them was possible-indeed, there was a significant negative covariance (Est = -0.257, SE = 0.13), and thus correlation, between individual mean activity rates and their mean resting metabolic rates (r = -0.58; Likelihood ratio test, χ_1^2 = 4.4, p < .05). This correlation was estimated using the standard equation: $r = \text{COV}_{\text{RMR, activity}} / \sqrt{\text{VAR}_{\text{RMR}} \times \text{VAR}_{\text{activity}}}$. This indicated that individuals with higher mean activity rates had lower mean metabolic rates when at rest (Figure 1).

4 | DISCUSSION

We predicted that if RMR is a proximate mechanism underlying behavioral variation, then we expect that individuals that are generally more active would also have higher RMR, to the extent that RMR reflects energetic capacity (Auer et al., 2017; Biro & Stamps, 2010; Careau et al., 2008), increases intake rates of food (Anholt et al., 2000; Biro et al., 2003) and has significant energy costs (Biro & Stamps, 2010; Boisclair & Tang, 1993; Careau et al., 2008). Contrary to these predictions, we observed that RMR was negatively correlated with activity, which suggests that the "performance" model is not supported for this species in the laboratory (Daan et al., 1990, Ricklefs et al., 1996, Nilsson, 2002, see also reviews in Careau et al., 2008, and in Biro & Stamps, 2010, Auer et al., 2017).

A negative correlation between RMR and activity implies that individuals that are more active must allocate less energy to maintenance metabolism (RMR), indicating that individuals differ in their energy allocation to competing demands. This provides evidence for the "allocation" model of energy management (Daan et al., 1990, Ricklefs et al., 1996, Nilsson, 2002, see also reviews in Careau et al., 2008, Auer et al., 2017). This is a seemingly rare observation in the literature given that most correlations are very low but in the positive direction, whereas very few studies show evidence of a negative correlation (Careau, Beauchamp, Bouchard, & Morand-Ferron, 2019; Krams et al., 2017, 2018; Royauté et al., 2018). Given that the observed negative covariance between RMR and activity did not match our expectations under the performance model, this suggests that activity and underlying metabolic variation are not always linked together in ways as predicted by the majority of recent theoretical advances in this area (Biro et al., 2018; Biro & Stamps, 2008, 2010; Burton et al., 2011; Réale et al., 2010; Sih & Bell, 2008).

A negative correlation between RMR and an energy consuming behavior such as activity is surprising in light of experiments involving artificial selection. For example, differences among selected lines of fish show positive correlations between activity, RMR and growth (Allen, Rosenfeld, & Richards, 2016; Biro, Abrahams, Post, & Parkinson, 2006; Scott, Dhillon, Schulte, & Richards, 2014) consistent with the "performance" model (see above). Similarly, studies on selected lines of rodents also show positive correlations between activity and RMR (Eisenmann et al., 2009; Meek et al., 2009; Rezende et al., 2009; Sadowska et al., 2013; Waters et al., 2008). These experiments, together with several similar studies comparing across selected lines in domestic animals that differ in metabolic rate and behavior (reviewed by Biro & Stamps, 2010), suggest that among-individual (and genetic) correlations are generally positive. To help resolve situations where allocation versus performance models is operating, we need more longitudinal studies designed to estimate among- and within-individual correlations between resting/ basal metabolism and different behaviors, which we discuss further below. There is also a need to consider that correlations are not expected to remain the same in all situations and so context-dependency could be a priority research area for future studies (Burton et al., 2011; Killen et al., 2013).

While evidence indicates that the "allocation" model is operating in this species under laboratory conditions, whereby active individuals allocate less energy to maintenance requirements, it is possible this result is not one that is constant across the lifespan of these fish. We captured mature male fish with unknown age from the field and held them for a total of 6 months by the time all sampling was complete. It is possible then that the timing of sampling in the field was such that we had relatively old males (Pyke, 2005), and that these males were experiencing intrinsic energetic limitation leading to tradeoffs. That is, as individuals age their total daily energetic capacity necessarily decreases which could increase the likelihood of tradeoffs for individuals with a propensity to be active. Reductions ethology

in RMR and maximum metabolic rate due to age is a common observation in animals (Koch et al., 2011; Moe, Ronning, Verhulst, & Bech, 2009) and in humans as well (Lazzer et al., 2010; St-Onge & Gallagher, 2010). Of course, these suggestions are entirely speculative, but they do point to an interesting avenue for future research: Energy management models, as discussed above, do not make predictions for whether or not any one model should be consistent across individual lifetime.

Future studies could begin to resolve questions surrounding energy management models and whether they are consistent overtime or not, through simple longitudinal studies, or by controlling for age experimentally. Related to these points, it would also be informative to evaluate the among- and within-individual correlations between behavioral activities and metabolism early in life, mid-life and late in life during senescence. The latter requires paired measurements of behaviors and metabolism for several or more measures per individual to begin to partition among-individual trends from within-individual trends which may or may not operate in the same direction (for an example of this approach see Careau & Wilson, 2017).

Consistent with general patterns observed in the literature, our measure of swimming activity was repeatable, but greater in magnitude than observed in the majority of studies (Bell et al., 2009), whereas RMR had similar repeatability to other studies (ca. 0.4 on average (Nespolo & Franco, 2007, White et al., 2013). A limitation of our study, apart from a fairly small sample of males and a low number of repeated measures of RMR (only two repeated measures versus 18 for behavior), is the fact that we did not concurrently measure all traits over time to partition variation into among- versus within-individual (residual) variation. Concurrent sampling of RMR and behavior in close temporal proximity would have allowed us to test for within- and as well as among-individual correlations between behavior and metabolism, and this would provide us the potential to reveal within-individual tradeoffs between energy allocated amongst competing demands. Another factor potentially introducing unwanted variance into our data involves circadian disruption between lighting conditions during activity assays and the slightly different day/night light timing used in respirometer trials. Finally, it is possible that our measure of activity does not reflect well the energetic costs of activity in comparison to distance moved, which is more commonly used to estimate activity. However, the frequency of position changes from stationary to moving could even better reflect overall costs of movement, as it is likely more energetically costly to get the body moving from a stationary position than it is to keep it moving at a slow speed.

In conclusion, the most parsimonious explanation for our results is that there is indeed evidence for an among-individual correlation between activity rates and metabolism, but that it is negative. This seemingly rare observation provides an interesting counter-example to the results commonly found in the literature. It also highlights that while our strategy to control for size when sampling was a seemingly logical one, an even better strategy to employ in future studies would be to raise young in captivity to ensure that aging effects, or individual variation in aging, should not affect correlations.

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ACKNOWLEDGEMENTS

Thanks to Bart Adriaenssens for his careful attention to detail when collecting these data; BA was employed to collect these data using funds from an Australian Research Council Discovery grant awarded to PAB (DP 110104750).

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ETHICAL APPROVAL

All procedures and animal husbandry were approved by the Animal Ethics Committee, at the University of New South Wales, Australia. Permit number 4094975/2.

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REFERENCES

- Adolph, S., & Hardin, J. (2007). Estimating phenotypic correlations: Correcting for bias due to intraindividual variability. *Functional Ecology*, 21, 178–184. https://doi.org/10.1111/j.1365-2435.2006.01209.x
- Allen, D., Rosenfeld, J., & Richards, J. (2016). Physiological basis of metabolic trade-offs between growth and performance among different strains of rainbow trout. *Canadian Journal of Fisheries and Aquatic Sciences*, 73, 1493–1506. https://doi.org/10.1139/cjfas-2015-0429
- Anholt, B. R., Werner, E. E., & Skelly, D. K. (2000). Effect of food and predators on the activity of four larval ranid frogs. *Ecology*, 81, 3509– 3521. https://doi.org/10.1890/0012-9658(2000)081[3509:EOFAP O]2.0.CO;2
- Auer, S. K., Killen, S. S., & Rezende, E. L. (2017). Resting vs. active: A meta-analysis of the intra- and inter-specific associations between minimum, sustained, and maximum metabolic rates in vertebrates. *Functional Ecology*, 31(9), 1728–1738. https://doi. org/10.1111/1365-2435.12879
- Baktoft, H., Koed, A., Skov, C., Aarestrup, K., Jacobsen, L., Boel, M., ... Svendsen, J. C. (2016). Phenotypic variation in metabolism and morphology correlating with animal swimming activity in the wild: Relevance for the OCLTT (oxygen- and capacity-limitation of thermal tolerance), allocation and performance models. *Conservation Physiology*, 4, cov055. https://doi.org/10.1093/conphys/cov055
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. Animal Behaviour, 77, 771–783. https:// doi.org/10.1016/j.anbehav.2008.12.022
- Biro, P. A., Abrahams, M. V., Post, J. R., & Parkinson, E. A. (2006). Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *Journal of Animal Ecology*, 75, 1165– 1171. https://doi.org/10.1111/j.1365-2656.2006.01137.x
- Biro, P. A., & Adriaenssens, B. (2013). Predictability as a personality trait: Consistent differences in intraindividual behavioral variation. *The American Naturalist*, 182, 621–629. https://doi.org/10.1086/673213
- Biro, P. A., Fanson, K. V., & Santostefano, F. (2016). Stress-induced peak (but not resting) metabolism correlates with mating display intensity in male guppies. *Ecology and Evolution*, *6*, 6537–6545. https://doi. org/10.1002/ece3.2373

- Biro, P. A., Garland, T., Beckmann, C., Ujvari, B., Thomas, F., & Post, J. R. (2018). Metabolic scope as a proximate constraint on individual behavioral variation: Effects on personality, plasticity, and predictability. *The American Naturalist*, 192, 142–154. https://doi. org/10.1086/697963
- Biro, P. A., Post, J. R., & Parkinson, E. A. (2003). From individuals to populations: Risk-taking by prey fish mediates mortality in whole-system experiments. *Ecology*, 84, 2419–2431.
- Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, 23, 361– 368. https://doi.org/10.1016/j.tree.2008.04.003
- Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in Ecology and Evolution*, 25, 653–659. https://doi. org/10.1016/j.tree.2010.08.003
- Biro, P. A., & Stamps, J. A. (2015). Using repeatability to study physiological and behavioural traits: Ignore time-related change at your peril. *Animal Behaviour*, 105, 223–230. https://doi.org/10.1016/j.anbeh av.2015.04.008
- Boisclair, D., & Tang, M. (1993). Empirical analysis of the influence of swimming pattern on the net energetic cost of swimming in fishes. *Journal of Fish Biology*, 42, 169–183. https://doi.org/10.1111/j.1095-8649.1993. tb00319.x
- Bouwhuis, S., Quinn, J. L., Sheldon, B. C., Verhulst, S. (2014). Personality and basal metabolic rate in a wild bird population. *Oikos*, 123(1), 56–62.
- Burton, T., Killen, S., Armstrong, J., & Metcalfe, N. (2011). What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B: Biological Sciences*, 278, 3465–3473. https://doi.org/10.1098/ rspb.2011.1778
- Careau, V., Beauchamp, P. P., Bouchard, S., & Morand-Ferron, J. (2019). Energy metabolism and personality in wild-caught fall field crickets. *Physiology and Behavior*, 199, 173–181. https://doi.org/10.1016/j. physbeh.2018.11.023
- Careau, V., Thomas, D., Humphries, M. M., & Reale, D. (2008). Energy metabolism and animal personality. *Oikos*, 117, 641–653. https://doi. org/10.1111/j.0030-1299.2008.16513.x
- Careau, V., Thomas, D., Pelletier, F., Turki, L., Landry, F., Garant, D., & Réale, D. (2011). Genetic correlation between resting metabolic rate and exploratory behaviour in deer mice (Peromyscus maniculatus). *Journal of Evolutionary Biology*, 24, 2153–2163. https://doi. org/10.1111/j.1420-9101.2011.02344.x
- Careau, V., & Wilson, R. S. (2017). Performance trade-offs and ageing in the 'world's greatest athletes'. Proceedings of the Royal Society B: Biological Sciences, 284, 20171048.
- Daan, S., Masman, D., & Groenewold, A. (1990). Avian basal metabolic rates: Their association with body composition and energy expenditure in nature. American Journal of Physiology: Regulatory, Integrative and Comparative Physiology, 259, R333–340. https://doi.org/10.1152/ ajpregu.1990.259.2.R333
- Eisenmann, J. C., Wickel, E. E., Kelly, S. A., Middleton, K. M., & Garland, T. (2009). Day-to-day variability in voluntary wheel running among genetically differentiated lines of mice that vary in activity level. *European Journal of Applied Physiology*, 106, 613–619. https://doi. org/10.1007/s00421-009-1056-z
- Farwell, M., & McLaughlin, R. L. (2009). Alternative foraging tactics and risk taking in brook charr (Salvelinus fontinalis). Behavioural Ecology, 20, 913–921. https://doi.org/10.1093/beheco/arp059
- Gifford, M. E., Clay, T. A., & Careau, V. (2014). Individual (Co)variation in standard metabolic rate, feeding rate, and exploratory behavior in wild-caught semiaquatic salamanders. *Physiological and Biochemical Zoology*, 87, 384–396. https://doi.org/10.1086/675974
- Hayes, J. P. (2001). Mass-specific and whole-animal metabolism are not the same concept. *Physiological and Biochemical Zoology*, 74, 147–150. https://doi.org/10.1086/319310

ethology

- Huntingford, F. A., Andrew, G., Mackenzie, S., Morera, D., Coyle, S. M., Pilarczyk, M., & Kadri, S. (2010). Coping strategies in a strongly schooling fish, the common carp Cyprinus carpio. *Journal of Fish Biology*, 76, 1576–1591. https://doi. org/10.1111/j.1095-8649.2010.02582.x
- Killen, S. S., Marras, S., Metcalfe, N. B., McKenzie, D. J., & Domenici, P. (2013). Environmental stressors alter relationships between physiology and behaviour. *Trends in Ecology and Evolution*, 28, 651–658. https://doi.org/10.1016/j.tree.2013.05.005
- Killen, S. S., Marras, S., Ryan, M. R., Domenici, P., & McKenzie, D. J. (2012). A relationship between metabolic rate and risk-taking behaviour is revealed during hypoxia in juvenile European sea bass. *Functional Ecology*, 26, 134–143. https://doi.org/10.1111/j.1365-2435.2011.01920.x
- Koch, L. G., Kemi, O. J., Qi, N., Leng, S. X., Bijma, P., Gilligan, L. J., ... Wisløff, U. (2011). Intrinsic aerobic capacity sets a divide for aging and longevity. *Circulation Research*. https://doi.org/10.1161/CIRCR ESAHA.111.253807
- Krams, I. A., Niemelä, P. T., Trakimas, G., Krams, R., Burghardt, G. M., Krama, T., ... Kortet, R. (2017). Metabolic rate associates with, but does not generate covariation between, behaviours in western stutter-trilling crickets, Gryllus integer. Proceedings of the Royal Society B: Biological Sciences, 284, 20162481.
- Krams, I., Trakimas, G., Kecko, S., Elferts, D., Krams, R., Luoto, S., ... Krama, T. (2018). Linking organismal growth, coping styles, stress reactivity, and metabolism via responses against a selective serotonin reuptake inhibitor in an insect. *Scientific Reports*, *8*, 8599.
- Lantová, P., Zub, K., Koskela, E., Šíchová, K., & Borowski, Z. (2011). Is there a linkage between metabolism and personality in small mammals? The root vole (Microtus oeconomus) example. *Physiology and Behavior*, 104, 378–383. https://doi.org/10.1016/j.physbeh.2011.04.017
- Lazzer, S., Bedogni, G., Lafortuna, C. L., Marazzi, N., Busti, C., Galli, R., ... Sartorio, A. (2010). Relationship between basal metabolic rate, gender, age, and body composition in 8,780 white obese subjects. *Obesity*, 18, 71-78. https://doi.org/10.1038/oby.2009.162
- Le Galliard, J.-F., Paquet, M., Cisel, M., & Montes-Poloni, L. (2013). Personality and the pace-of-life syndrome: Variation and selection on exploration, metabolism and locomotor performances. *Functional Ecology*, 27, 136–144. https://doi.org/10.1111/1365-2435.12017
- Lighton, J. R. (2008). Measuring Metabolic Rates: A Manual for Scientists: A Manual for Scientists. Oxford, UK: Oxford University Press.
- Littell, R. C., Milliken, G., Stroup, W., Wolfinger, R., & Schabenberger, O. (2006). SAS for Mixed Models, (2nd ed.). Cary, NC: SAS Press.
- Martins, C. I., Castanheira, M. F., Engrola, S., Costas, B., & Conceição, L. E. (2011). Individual differences in metabolism predict coping styles in fish. *Applied Animal Behaviour Science*, 130, 135–143. https://doi. org/10.1016/j.applanim.2010.12.007
- Mathot, K., Martin, K., Kempenaers, B., & Forstmeier, W. (2013). Basal metabolic rate can evolve independently of morphological and behavioural traits. *Heredity*, 111(3), 175–181. https://doi.org/10.1038/ hdy.2013.35
- Mathot, K. J., Nicolaus, M., Araya-Ajoy, Y. G., Dingemanse, N. J., & Kempenaers, B. (2014). Does metabolic rate predict risk-taking behaviour? A field experiment in a wild passerine bird. *Functional Ecology*, 29, 239–249. https://doi.org/10.1111/1365-2435.12318
- Meek, T. H., Lonquich, B. P., Hannon, R. M., & Garland, T. Jr (2009). Endurance capacity of mice selectively bred for high voluntary wheel running. *Journal of Experimental Biology*, 212, 2908–2917. https://doi. org/10.1242/jeb.028886
- Merritt, L., Matthews, P. D., & White, C. (2013). Performance correlates of resting metabolic rate in garden skinks Lampropholis delicata. *Journal of Comparative Physiology B*, 183, 663–673. https://doi. org/10.1007/s00360-012-0736-x
- Metcalfe, N. B., Taylor, A. C., & Thorpe, J. E. (1995). Metabolic-rate, social-status and life-history strategies in Atlantic Salmon. Animal Behaviour, 49, 431–436. https://doi.org/10.1006/anbe.1995.0056

- Moe, B., Ronning, B., Verhulst, S., & Bech, C. (2009). Metabolic ageing in individual zebra finches. *Biology Letters*, 5, 86–89. https://doi. org/10.1098/rsbl.2008.0481
- Myles-Gonzalez, E., Fox, M. G., Burness, G., Rooke, A., & Yavno, S. (2015). To boldly go where no goby has gone before: Boldness, dispersal tendency, and metabolism at the invasion front. *Behavioral Ecology*, *26*, 1083–1090. https://doi.org/10.1093/beheco/arv050
- Nespolo, R. F., & Franco, M. (2007). Whole-animal metabolic rate is a repeatable trait: A meta-analysis. *Journal of Experimental Biology*, 210, 2000–2005. https://doi.org/10.1242/jeb.02780
- Nilsson, J. A (2002). Metabolic consequences of hard work. Proceedings of the Royal Society of London. Series B: Biological Sciences, 269, 1735– 1739. https://doi.org/10.1098/rspb.2002.2071
- Pang, X., Fu, S. J., & Zhang, Y. G. (2015). Individual variation in metabolism and swimming performance in juvenile black carp (Mylopharyngodon piceus) and the effects of hypoxia. *Marine and Freshwater Behaviour* and Physiology, 48, 431–443.
- Pyke, G. H. (2005). A review of the biology of Gambusia affinis and G. holbrooki. Reviews in Fish Biology and Fisheries, 15, 339–365. https://doi. org/10.1007/s11160-006-6394-x
- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 4051– 4063. https://doi.org/10.1098/rstb.2010.0208
- Reid, D., Armstrong, J. D., & Metcalfe, N. B. (2011). Estimated standard metabolic rate interacts with territory quality and density to determine the growth rates of juvenile Atlantic salmon. *Functional Ecology*, 25, 1360–1367. https://doi.org/10.1111/j.1365-2435.2011.01894.x
- Reid, D., Armstrong, J. D., & Metcalfe, N. B. (2012). The performance advantage of a high resting metabolic rate in juvenile salmon is habitat dependent. *Journal of Animal Ecology*, 81, 868–875. https://doi. org/10.1111/j.1365-2656.2012.01969.x
- Rezende, E. L., Gomes, F. R., Chappell, M. A., & Garland, T. (2009). Running behavior and its energy cost in mice selectively bred for high voluntary locomotor activity. *Physiological and Biochemical Zoology*, 82, 662–679. https://doi.org/10.1086/605917
- Ricklefs, R. E., Konarzewski, M., & Daan, S. (1996). The relationship between basal metabolic rate and daily energy expenditure in birds and mammals. *The American Naturalist*, 147, 1047–1071. https://doi. org/10.1086/285892
- Royauté, R., Berdal, M. A., Garrison, C. R., & Dochtermann, N. A. (2018). Paceless life? A meta-analysis of the pace-of-life syndrome hypothesis. *Behavioral Ecology and Sociobiology*, 72, 64. https://doi. org/10.1007/s00265-018-2472-z
- Sadowska, J., Gębczyński, A. K., & Konarzewski, M. (2013). Basal metabolic rate is positively correlated with parental investment in laboratory mice. Proceedings of the Royal Society B: Biological Sciences, 280, 20122576. https://doi.org/10.1098/rspb.2012.2576
- Scott, M. A., Dhillon, R. S., Schulte, P. M., & Richards, J. G. (2014). Physiology and performance of wild and domestic strains of diploid and triploid rainbow trout (*Oncorhynchus mykiss*) in response to environmental challenges. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 125–134.
- Sih, A., & Bell, A. M. (2008). Insights for behavioral ecology from behavioral syndromes. Advances in the Study of Behavior, 38, 227–281.
- St-Onge, M. P., & Gallagher, D. (2010). Body composition changes with aging: The cause or the result of alterations in metabolic rate and macronutrient oxidation? *Nutrition (Burbank, Los Angeles County, Calif.)*, 26, 152-155.
- Timonin, M. E., Carrière, C. J., Dudych, A. D., Latimer, J. G. W., Unruh, S. T., & Willis, C. K. R. (2011). Individual differences in the behavioural responses of meadow voles to an unfamiliar environment are not correlated with variation in resting metabolic rate. *Journal of Zoology*, 284, 198–205. https://doi.org/10.1111/j.1469-7998.2011.00792.x

* WILEY ethology

- Waters, R. P., Renner, K. J., Pringle, R. B., Summers, C. H., Britton, S. L., Koch, L. G., & Swallow, J. G. (2008). Selection for aerobic capacity affects corticosterone, monoamines and wheel-running activity. *Physiology and Behavior*, 93, 1044–1054. https://doi.org/10.1016/j. physbeh.2008.01.013
- White, C. R., Schimpf, N. G., & Cassey, P. (2013). The repeatability of metabolic rate declines with time. *Journal of Experimental Biology*, 216, 1763–1765. https://doi.org/10.1242/jeb.076562
- Wolak, M. E., Fairbairn, D. J., & Paulsen, Y. R. (2012). Guidelines for estimating repeatability. *Methods in Ecology and Evolution*, 3, 129–137. https://doi.org/10.1111/j.2041-210X.2011.00125.x

How to cite this article: Biro PA, Thomas F, Ujvari B, Adriaenssens B, Beckmann C. Spontaneous activity rates and resting metabolism: Support for the allocation model of energy management at the among-individual level. *Ethology*. 2019;00:1–8. <u>https://doi.org/10.1111/eth.12957</u>