RESEARCH PAPER

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

Peter A. Biro1 | **Frédéric Thomas²** | **Beata Ujvari¹** | **Bart Adriaenssens1** | **Christa Beckmann1,3**

¹Centre for Integrative Ecology, School of Life and Environmental Science, Deakin University, Geelong, VIC, Australia 2 CREEC/MIVEGEC, UMR IRD/CNRS/UM 5290, Montpellier Cedex, France

³School of Science and Health, Western Sydney University, Parramatta, NSW, Australia

Correspondence

Peter A. Biro, Centre for Integrative Ecology, School of Life and Environmental Science, Deakin University, Geelong, VIC 3216, Australia. Email: pete.biro@deakin.edu.au

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Abstract

Despite continuing interest in the proximate energetic constraints on individual vari‐ ation in behavior, there is presently equivocal evidence for correlations between me‐ tabolism 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 mos‐ quitofish 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 ($r = -0.58$) 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 "allo‐ cation" 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 behav‐ ioral 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 an‐ other, 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 pro‐ cesses, then if individuals vary in their ability to acquire food and convert it to energy, or differ in their allocation of energy to be‐ havioral 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 cor‐ relations 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) me‐ tabolism (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 re‐ cent meta‐analysis which focused on "pace of life syndromes" studies revealed little to no average correlation between levels of various be‐ haviors and metabolism (Royauté et al., 2018).

One reason why trends between behavior and metabolism ap‐ pear 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 meta‐ bolic 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 uncertain‐ ties in estimates of individual mean values when estimating among‐ individual 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 environ‐ mental 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 re‐ flects 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 metab‐ olism should exist due to functional and genetic links between me‐ tabolism 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 por‐ tion 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 fol‐ lowed 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 \times 13 \times 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 mos‐ quito mesh was placed above the tanks preventing fish from jump‐ ing 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 sepa‐ rate 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 dur‐ ing 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 (represent‐ ing >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 vari‐ ation in the time since last feeding $(14-500 \text{ min}, \bar{x} = 219 \text{ min})$ before activity observations were made. However, this was previously been shown to have no effect on activity at the mean level (Biro &

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Adriaenssens, 2013), nor has it any effect at the within‐individual level when assessed as a random slope effect in the present study (*p* > .1); hence, this factor was removed from the model.

2.2 | **Measurement of metabolism**

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 R² for the oxygen consumption slope over time using this cycle always exceeded .9, and oxygen content in chambers never fell below 85% air satura‐ tion. 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 $MO_2 = k \times V$; MO₂ is the oxygen consumption rate (mg O₂/h), *k* is the slope of the oxygen consumption over time (mg O₂/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 whole‐ animal metabolic rate and accounted for mass in the data analyses (Hayes, 2001; Lighton, 2008). The overall average mass-corrected RMR was 184 mg $O₂/g/h$ (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 in‐ transformed to normalize the residuals. Then, both were standard‐ ized (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 repre‐ sents 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

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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 O₂/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 iden‐ tity 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 ran‐ dom 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 pre‐ dicted 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 in‐ cluded 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, indi‐ vidual 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, $\chi_1^2 = 4.4$, $p < .05$). This correlation was estimated using the standard equation: *r*=COV_{RMR, activity/√VAR_{RMR}×VAR_{activity}. This indicated that indi-} viduals 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 gen‐ erally 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 nega‐ tively correlated with activity, which suggests that the "perfor‐ mance" 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 main‐ tenance 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 al‐ ways 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) con‐ sistent with the "performance" model (see above). Similarly, studies on selected lines of rodents also show positive correlations be‐ tween 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 es‐ timate 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‐depen‐ dency 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 individ‐ uals 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 ca‐ pacity necessarily decreases which could increase the likelihood of tradeoffs for individuals with a propensity to be active. Reductions in RMR and maximum metabolic rate due to age is a common ob‐ servation 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 specula‐ tive, but they do point to an interesting avenue for future research: Energy management models, as discussed above, do not make pre‐ dictions for whether or not any one model should be consistent across individual lifetime.

Future studies could begin to resolve questions surrounding en‐ ergy 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 indi‐ vidual to begin to partition among‐individual trends from within‐in‐ dividual 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‐ ver‐ sus 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 al‐ located amongst competing demands. Another factor potentially introducing unwanted variance into our data involves circadian dis‐ ruption 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 seem‐ ingly 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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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.

ORCID

Peter A. Bir[o](https://orcid.org/0000-0002-3565-240X) <https://orcid.org/0000-0002-3565-240X>

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8 \blacksquare **WILEY—ethology expectively binding**

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