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Source: Journal of Vertebrate Biology, 69(4)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: https://doi.org/10.25225/jvb.20057

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Journal of Vertebrate Biology
Open Access
J. Vertebr. Biol. 2020, 69(4): 20057
DOI: 10.25225/jvb.20057

Thermal independence of energy management in a tailed amphibian

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▸ **Received 9 June 2020; Accepted 31 July 2020; Published online 1 September 2020**

Abstract. The relationship between the minimum metabolic requirements (standard metabolic rate, SMR) and energy costs of non-mandatory physiological functions and behaviour is fundamental for understanding species responses to changing environmental conditions. Theory predicts that ectotherms manage their energy budget depending on whether the relationship between SMR and energy available for other tasks is negative (allocation model), neutral (independent model), or positive (performance model). Energy management has received more attention in endotherms than in ectotherms, where metabolic-behavioural relations may be affected by body temperature variation. We examined the predictions of energy management models at four body temperatures in alpine newts, *Ichthyosaura alpestris*, under laboratory conditions. High SMR reduced the amount of energy dedicated to food digestion and locomotor activity. The maximum metabolic rate for food digestion was positively related to SMR, while its relationship with locomotor activity was inconclusive. Body temperature affected the intercept but not the slope of these relationships. We conclude that (i) newts manage their energy budget according to the allocation model, (ii) energy management is insensitive to body temperature variation, and (iii) determining energy management models using indirect estimates may be misleading. These findings improve our understanding of the eco-evolutionary significance of SMR variation in tailed amphibians and other ectotherms.

Key words: daily energy expenditure, energy allocation, locomotor activity, newt, standard metabolic rate

Introduction

All functions and processes within an organism require energy. Accordingly, lifetime fitness is determined by the optimal allocation of acquired energy into maintenance, somatic growth, reproduction, and survival in a given habitat (Sibly & Calow 1986, Roff 1992, Stearns 1992). The mandatory energy cost of maintaining basic life functions, i.e. basal metabolic rate in endotherms, or standard metabolic rate (SMR) in ectotherms, varies up to two- or three fold among individuals within a population, even after controlling for confounding factors such as body mass, activity, or reproductive status (Careau et al. 2008, Burton et al. 2011). Maintenance costs constitute a substantial proportion (20-86%) of the total energy budget in ectotherms (Spotila & Standora 1985, van Marken Lichtenbelt et al. 1993, Peterson et al. 1998, Brown et al. 2002), so individual variation has a profound influence on the amount of energy available for fitness-related tasks.

In ectotherms, three basic energy management models predict the relationship between SMR and

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daily energy expenditure (DEE; Careau & Garland 2012, Mathot & Dingemanse 2015, Halsey et al. 2019; Fig. 1). The allocation model assumes that the DEE is fixed, so increased SMR should be compensated for by reducing energy available for physiological (food digestion) and/or behavioural (locomotor activity) tasks, i.e. daily metabolic scope (DMS). Hence, there should be a negative relationship between SMR and DMS. The slope of the relationship between DEE and SMR should be close to 0 (full allocation) or between 0 and 1 (partial allocation). The independence model assumes that SMR and DMS are unrelated and vary independently of one another. In this case DEE in relation to SMR should increase with a slope ≈1. The performance model (Nilsson 2002) assumes that SMR is positively associated with maximum metabolic rate (MMR) with a slope ≈1. If this assumption holds, DMS should increase as a function of SMR, resulting in higher DEE and the slope of the DEE-SMR relationship should be > 1. While the empirical verification of energy management models has received some attention in endotherms (Mathot & Dingemanse 2015, Halsey et al. 2019), the validity of model predictions is largely unknown in ectotherms.

Energy relationships are further complicated by the thermal dependency of metabolic traits (Gillooly et al. 2001, Clarke & Pörtner 2010). The exponential dependence of SMR on body temperature implies that an ectotherm will expend much more energy on maintenance at higher body temperatures than lower ones with a concomitant effect on the energy budget. In addition, body temperature may have disparate influence on activities contributing to DMS, such as spontaneous locomotor activity (Dell et al. 2011, Baškiera & Gvoždík 2019) than on SMR. Thermal stress, i.e. body temperatures outside an ectotherm's preferred range, may reveal, mask, or modulate the relationship between behavioural and physiological traits (Biro & Stamps 2010, Killen et al. 2014). However, if and to what extent body temperature variation affects these metabolic relations, remains virtually unknown.

Recent theory proposes that energy management models are key to understanding individual variation in behavioural traits (Careau et al. 2008, Biro & Stamps 2010, Careau & Garland 2012, Mathot & Dingemanse 2015). Accordingly, these models predict that energy-consuming behaviours, such as locomotor activity, should vary with SMR as DMS. Specifically, there should be a negative relationship between locomotor activity with SMR under the allocation model, no relationship under the independence model, and a positive relationship under the performance model

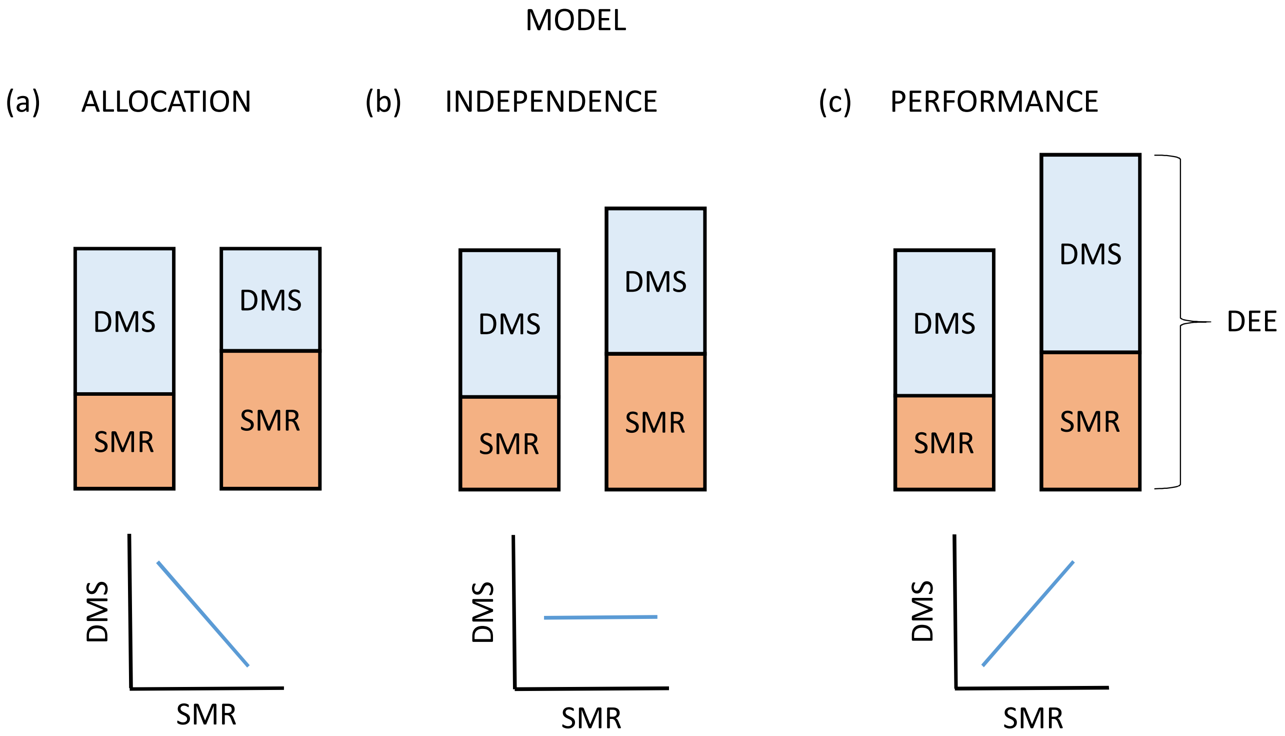

Fig. 1. Energy management models in ectotherms. (a) Allocation model predicts the same energy expenditure (DEE) in individuals (columns) with low and high standard metabolic rate (SMR). Accordingly, individuals with low SMR should invest more energy to non-mandatory physiological functions and behaviour (daily metabolic scope, DMS) and vice versa. (b) Independence model predicts unrelated SMR and DMS, but DEE increases with SMR. (c) Performance model predicts positive association between SMR and maximum metabolic rate. Both DMS and DEE should increase with SMR. Modified after Careau & Garland (2012), Mathot & Dingemanse (2015).

(Fig. 1). Although a recent meta-analysis showed the strongest support for the performance model (Mathot et al. 2019), the number of taxa examined is still too low to allow definite conclusions.

Here, we examined the predictions of energy management models in the alpine newt, *Ichthyosaura alpestris*. As amphibians, newts are representatives of the most globally threatened group of vertebrates (Stuart et al. 2004, Hof et al. 2011, Ficetola et al. 2015). Climatic change is a major factor in worldwide amphibian decline. Within-population variation in SMR is considered an important means of coping with the increasing stochasticity of environmental conditions induced by climate change (Burton et al. 2011). Accordingly, recent efforts have focused on the sources of SMR variation in newts, including food processing and digestion (Gvoždík & Kristín 2017), individual variation (Kristín & Gvoždík 2014a), seasonal acclimatization (Kristín & Gvoždík 2014b, Podhajský & Gvoždík 2016), interspecific interactions (Janča & Gvoždík 2017), heterospecific hybridization (Gvoždík 2012), or methodological issues (Kristín & Gvoždík 2012, 2016). However, without considering other metabolic traits, the interpretation of SMR variation is necessarily limited. The aims of this study are threefold. (i) To identify the energy management model in newts by examining the relationship between SMR and DMS. (ii) To compare the relationship between SMR and MMR, and SMR and locomotor activity with the assumptions and predictions of a given energy model. And finally, (iii) to discover whether body temperature affects the intercept and (or) slope of these relationships.

Material and Methods

Study species

The alpine newt is a 120 mm long tailed amphibian, which is widely distributed across Central and Western Europe. It usually has a biphasic lifestyle with an aquatic phase between April and June and a terrestrial phase during the rest of year (Griffiths 1996). Under laboratory conditions newts maintain their body temperatures between 16 and 20 °C, although they are mostly exposed to colder water temperatures in their native habitat (Hadamová & Gvoždík 2011, Balogová & Gvoždík 2015). Their food consists of various invertebrates, mostly earthworms and insect larvae (Griffiths 1996).

Metabolic and locomotor activity traits

For calculating the components of the daily energy budget, we used data from a previous study (Gvoždík & Kristín 2017). In short, wild-caught adult newts (n = 48) were kept under laboratory conditions (12-22 °C, natural photoperiod) for five months before the beginning of metabolic measurements. Newt SMR and metabolic rate during digestion were measured in individual newts at one of four ambient temperatures (10, 15, 20, and 25 °C). Previous measurements confirmed that newt body temperatures match ambient temperatures within respirometry chambers. The time duration of each trial (see below) precluded the use of a repeated-measures design in this case. Standard metabolic rate was measured as the minimum oxygen consumption in postabsorptive, non-reproductive, and non-moving individuals in the inactive phase of their daily cycle using a nine-channel intermittent respirometry system (Sable Systems, Las Vegas, USA) in a five-hour trial. Oxygen consumption during digestion was measured during a subsequent trial, which lasted from two to four days depending on body temperature. The respirometry chamber was flushed twice per hour, which provided data on minimum and maximum metabolic rates as well as total energy consumption throughout the trial. The size of the respirometry chamber (100 mL) allowed newts some motor activity, so their daily metabolic scope included energy costs of both food digestion and locomotion. Before calculating the daily energy budget components (kJ day^{-1}), we multiplied oxygen consumption values (mL) by the oxyjoule equivalent [16 + 5.164 (RQ)] (Lighton 2008) where RQ is mean respirometry quotient for this species during seasonal activity (RQ = 0.85, Kristín & Gvoždík 2014b). Accordingly, we calculated DEE as mean daily energy expenditure during postprandial respirometry measurements, SMR and MMR (kJ h^{-1}) as the minimum and maximum metabolic rate, respectively, and DMS as DMS = DEE – (24 × SMR) for each body temperature. Maximum metabolic rate was calculated only from inactive periods, so it represents the maximum energy consumption for food digestion. Newt behaviour was continuously monitored (5 s resolution) during respirometry trials, and we used these data to determine daily locomotor activity, calculated as the mean number of locomotor records per day.

Statistical analyses

Metabolic traits, i.e. SMR, MMR, DEE, and DMS, are body-mass dependent, so we used the body mass residuals for further analyses. We examined the relationships using a general linear model

Table 1. Descriptive statistics (mean ± standard deviation) of body mass (BM), standard metabolic rate (SMR), maximum metabolic rate for food digestion (MMR), daily energy expenditure (DEE), and daily metabolic scope (DMS) at four body temperatures in adult newts, *Ichthyosaura alpestris*. Recalculated data from Gvoždík & Kristín (2017).

T_b (°C)	*n*	BM (g)	SMR (kJ h^{-1})	MMR (kJ h^{-1})	DEE (kJ d^{-1})	DMS (kJ d^{-1})
10	12	2.45 ± 0.59	2.14 ± 0.54	3.79 ± 0.78	81.5 ± 21.4	30.0 ± 15.8
15	12	2.38 ± 0.62	2.89 ± 0.79	5.77 ± 1.21	116.0 ± 30.1	46.6 ± 15.3
20	12	2.40 ± 0.71	3.83 ± 1.24	8.65 ± 2.48	149.0 ± 36.7	57.6 ± 18.3
25	9	2.08 ± 0.44	6.06 ± 1.32	11.50 ± 1.90	212.0 ± 30.2	66.9 ± 20.1

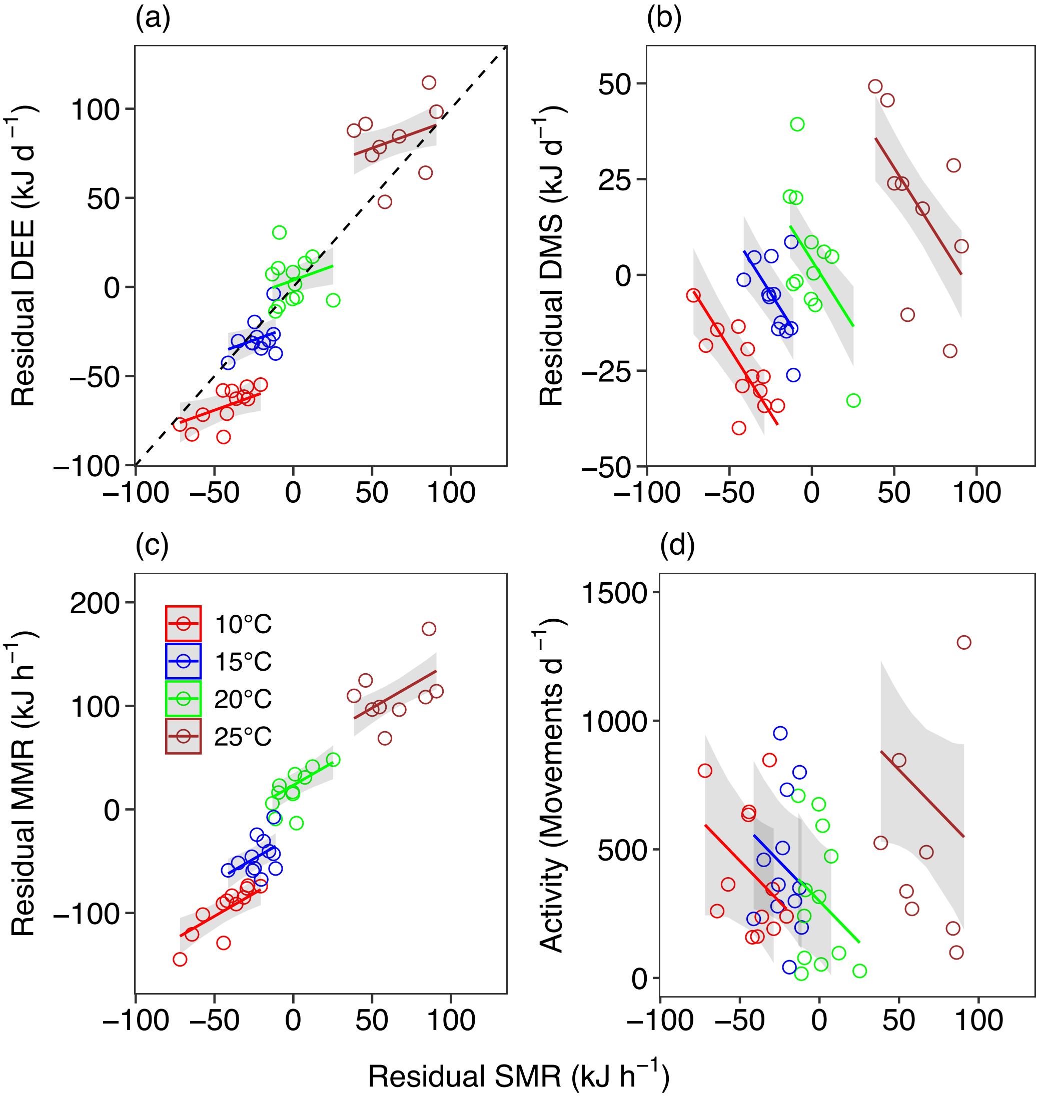

Fig. 2. The relationship between standard metabolic rate (SMR) and (a) daily energy expenditure (DEE), (b) daily metabolic scope (DMS), (c) maximum metabolic rate for food digestion (MMR), and (d) locomotor activity in adult newts, *Ichtyosaura alpestris*, at four body temperatures. Each data point is from one individual. Metabolic traits are their body mass residuals, locomotor activity is square-root transformed. Legend in (c) refers to all graphs. Dashed line in (a) denotes slope = 1 for comparison with data fits. Fits with 95% CIs are from the general linear model (see Table 3 for details).

(GLM). The full model included residual SMR as the covariate, and sex and body temperature and their interactions as categorical factors. We applied an information-theoretic approach (Burnham & Anderson 2002) to find the model with the best explanatory value for the fewest parameters. The number of candidate models was chosen with respect to sample size and inferred measures, i.e. the difference between the best model and all others (ΔAIC_c) and the probability of a given model being the best (AIC_c weight, w_i). The cut-off value for the model selection was based on Akaike's

Table 2. Model selection results according to Akaike's information criterion for small samples (AIC_c) and inferred measures, i.e. difference between the best model and all others (ΔAIC_c) and the probability of a given model to be the best one (AIC_c weight, w_i). In case of model similarity ($\Delta AIC_c < 2$), the final model was selected according to the lowest number of parameters (k). The best fit models are in bold. Model 1: ~Sex+SMR+Temperature+SMR*Temperature+Sex*SMR*Temperature; Model 2: ~Sex+SMR+Temperature+SMR*Temperature; Model 3: ~Sex+SMR+Temperature; Model 4: ~SMR+Temperature. SMR: standard metabolic rate, DEE: daily energy expenditure, DMS: daily metabolic scope, MMR: maximum metabolic rate, Activity: locomotor activity.

Trait	Model	k	AIC_c	ΔAIC_c	w_i
DEE					
	4	**6**	**362.6**	**0.0**	**0.65**
	3	7	364.0	1.4	0.32
	2	10	368.3	5.7	0.04
	1	14	374.3	11.7	0.00
DMS					
	4	**6**	**362.6**	**0.0**	**0.65**
	3	7	364.0	1.4	0.32
	2	10	368.3	5.7	0.04
	1	14	374.3	11.7	0.00
MMR					
	4	**6**	**402.7**	**0.0**	**0.53**
	3	7	403.7	1.0	0.32
	2	10	405.7	3.0	0.12
	1	14	408.0	5.4	0.04
Activity					
	4	**6**	**672.7**	**0.0**	**0.70**
	3	7	674.5	1.8	0.28
	2	10	679.3	6.6	0.03
	1	14	686.6	13.9	0.00

information criterion for small sample size (AIC_c), i.e. $\Delta AIC_c = 2$. In the event of two or more models having similar AIC_c, we chose the model with the fewest parameters. "Residual SMR" and "temperature" were always retained in the model, because their statistical results are essential to the aims of this study. Locomotor activity metric was square-root transformed prior to analysis. This approach produced a better model fit than using generalized linear modelling. Model residuals were visually checked for the presence of trend or outliers. Three values produced apparent outliers (< 25th percentile – 1.5*interquartile range [IQR] or > 75th percentile + 1.5*IQR), so they were dropped from the final analyses. Outlier removal made no qualitative difference to the results of the study. Given the relatively low sample size, we calculated factor exact P-values using permutation tests in addition to parametric statistics. However, the permutation approach produced results similar to parametric statistics in all models, so we present the latter results only. We applied Tukey's test with P-value adjustment for post-hoc comparisons among body temperatures. All analyses were performed in RStudio (version 1.2.5033) using "lmerTest" (Kuznetsova et al. 2017), "lmperm" (Wheeler & Torchiano 2016), "AICcmodavg" (Mazerolle 2020), and "emmeans" (Lenth 2019) packages.

Results

We calculated components of daily energy budget in adult alpine newts at four body temperatures (Table 1). Daily metabolic scope ranged from 32% at 25 °C to 40% at 10 °C of DEE. All minimum adequate models lacked statistically significant interactions (Table 2), so the explanatory variables affected residual DMS, MMR and locomotor activity in additive fashion. Sex has negligible explanatory value (Model 3 *vs.* Model 4 in Table 2), and was thus removed from the final model.

Residual DEE increased weakly with residual SMR (Table 3, Fig. 2a) and the intercept increased with body temperature ($F_{3,40} = 18.96$, $P < 0.001$;

Table 3. Results of minimum adequate models for the effect of body temperature and standard metabolic rate (SMR) on daily energy expenditure (DEE), daily metabolic scope (DMS), maximum metabolic rate (MMR), and locomotor activity in adult newts. Intercept: mean trait value at zero SMR in 10 °C group; Temperature 15-25 °C: differences between intercepts for 15-25 °C groups and intercept for 10 °C group; SMR: slope of relationship between trait and SMR. Note that all metabolic traits are body mass residuals. Statistically significant results are in bold.

Trait	Factor	Estimate (SE)	t_{40}	P
DEE				
	Intercept	–53.26 (7.07)	7.53	**< 0.001**
	Temperature 15 °C	31.39 (5.91)	5.32	**< 0.001**
	Temperature 20 °C	57.04 (7.91)	7.21	**< 0.001**
	Temperature 25 °C	115.26 (16.16)	7.13	**< 0.001**
	SMR	0.32 (0.14)	2.23	**0.03**
				Adjusted $R^2 = 0.94$
DMS				
	Intercept	–53.26 (7.07)	7.53	**< 0.001**
	Temperature 15 °C	31.39 (5.91)	5.32	**< 0.001**
	Temperature 20 °C	57.04 (7.91)	7.21	**< 0.001**
	Temperature 25 °C	115.26 (16.16)	7.13	**< 0.001**
	SMR	–0.68 (0.14)	4.78	**< 0.001**
				Adjusted $R^2 = 0.66$
MMR				
	Intercept	–59.25 (11.04)	5.37	**< 0.001**
	Temperature 15 °C	33.54 (9.22)	9.22	**< 0.001**
	Temperature 20 °C	82.55 (12.34)	12.34	**< 0.001**
	Temperature 25 °C	113.22 (25.23)	25.23	**< 0.001**
	SMR	0.88 (0.22)	3.95	**< 0.001**
				Adjusted $R^2 = 0.94$
Activity				
	Intercept	135.81 (221.75)	0.61	0.54
	Temperature 15 °C	155.80 (185.22)	0.84	0.41
	Temperature 20 °C	162.99 (248.00)	0.66	0.51
	Temperature 25 °C	992.50 (506.95)	1.96	0.06
	SMR	–6.39 (4.47)	1.43	0.16
				Adjusted $R^2 = 0.08$

Tukey test, $P < 0.001$ for all pairwise comparisons). Residual DMS decreased with residual SMR (Table 3, Fig. 2b). The intercept increased with body temperature ($F_{3,40} = 18.96$, $P < 0.001$) and the intercept at each body temperature differed from the others (Tukey test, $P < 0.001$ for all pairwise comparisons). Residual MMR was positively associated with residual SMR (Table 3, Fig. 2c). The intercepts varied with body temperature ($F_{3,40} = 16.03$, $P < 0.001$) and all pairwise comparisons differed with the exception of 20 °C and 25 °C ($P = 0.27$, $P < 0.01$ for remaining pairwise comparisons). There was no significant effect of residual SMR and body temperature on locomotor activity (SMR: $F_{1,40} = 0.51$, $P = 0.48$; temperature: $F_{3,40} = 2.66$, $P = 0.06$; Fig. 2d).

Discussion

Although energy metabolism has intrigued physiologists and ecologists for decades, the relationship among metabolic traits within the energy budget of ectotherms have received relatively little attention. The results of this study demonstrated that DMS decreased, while DEE and MMR increased with SMR in newts. The relationship between SMR and locomotor activity was inconclusive. Body temperature affected the intercepts, but not the slopes of these relationships.

The negative association between DMS and SMR indicates that individuals with higher metabolisms allocated less energy to food digestion and locomotion than individuals with lower SMR. This finding supports the allocation model of energy management (Fig. 1a) in newts. A similar conclusion was reached in plethodontid salamanders based on indirect evidence, i.e. a negative correlation between SMR and locomotor activity using advanced among- and within-individual analysis (Gifford et al. 2014). In our study, the relationship between locomotor activity and SMR was inconclusive among individuals. Further study is required to determine whether the weak relationship reflects the absence of an effect as opposed to high variance in the activity measure and insufficient sample size. A recent meta-analysis confirmed a similarly weak association between these traits across taxa (Mathot et al. 2019). Clearly, locomotor activity is an energy consuming behaviour, and so it should be negatively associated with SMR under the energy allocation model. However, the number of movements is only a rough measure of locomotor activity because the movements can vary in duration, speed, etc. In addition, spontaneous locomotor activity metrics, such as distance covered, average speed, or the frequency of movements, shows considerable variation among individuals (Baškiera & Gvoždík 2019). Hence, a relatively large sample size is required to obtain conclusive results concerning the association between SMR and locomotor activity (Videlier et al. 2019).

Some previous studies on SMR variation in newts can be interpreted in terms of the allocation model of energy management. For example, the reduction in SMR after transition from the aquatic to the terrestrial phase allows energy to be stored or allocated to other activities (Kristín & Gvoždík 2014b). In contrast, interspecific competition increases SMR without any reduction in locomotor activity or growth rate in juvenile newts (Janča & Gvoždík 2017), which is more in line with the independent energy management model. This suggests that energy management changes during ontogeny (Biro et al. 2005, Hou et al. 2008) or depends on context (Halsey et al. 2019), i.e. presence or absence of interspecific competition (see below).

Daily energy expenditure increased with SMR in newts. This positive relationship characterises the independent or performance models rather than the allocation energy management model (Careau & Garland 2012, Mathot et al. 2019), which seems contradictory to the negative association between DMS and SMR in our study. However, the slope of this relationship was between 0 and 1, which suggests partial energy allocation (Halsey et al. 2019). In addition, SMR constituted a major proportion of DEE (60-68%), which may contribute to the positive relationship. It may be that the positive relationship between SMR and DEE reflects individual variation in SMR (Mathot & Dingemanse 2015) rather than the energy management model.

Maximum metabolic rate increased with SMR. This result is surprising, because a positive association between these traits suggests the performance model rather than the allocation model (Careau & Garland 2012, Mathot & Dingemanse 2015). Given that the other results suggest the allocation model, it appears that metabolically-fast individuals performed below their maximum level under the laboratory conditions used. These conditions, however, provided no food resources, and thus we cannot rule out that newts may switch from the allocation to the performance model, if resources and competitors are available (see also Halsey et al. 2019). The increased growth rate in competitively dominant juvenile newts compared to submissive individuals with similar SMR (Janča & Gvoždík 2017) implies this possibility, but further experimental evidence is required before a definite conclusion can be drawn.

Body temperature affected the elevation (intercept), not the slope, of the relationship between SMR and other metabolic traits. Although thermal dependency varies between metabolic traits and locomotor activity traits in newts (Gvoždík & Kristín 2017, Baškiera & Gvoždík 2019), body temperature only produced additive effects in the model. This finding suggests that newt energy management is insensitive to body temperature variation in their native habitat (Šámajová & Gvoždík 2010, Hadamová & Gvoždík 2011). However, we have no data on the possible effect of thermally-induced plasticity on relationships among metabolic traits. Thermal acclimation or seasonal acclimatization of metabolic traits is common in tailed amphibians (Gatten et al. 1992, Kristín & Gvoždík 2014, Markle & Kozak 2018). Seasonal plasticity may induce disparate responses between physiological and behavioural traits (Winterová & Gvoždík, unpublished), which may affect the energy budget and further research is needed to fully understand the complex effects of thermal environment on energy management in newts.

Although our study provides an attempt to discriminate among energy management models in amphibians, it has limitations. The laboratory settings used are an oversimplification of the natural habitat of newts, thus our estimate of DEE likely underestimates average values in the field. Unlike squamate reptiles, birds, and mammals, rapid exchange of water between body and environment precludes the use of doubly labelled water to measure field metabolic rate in amphibians (Pough et al. 1992). Hence, the available estimates of amphibian energy budget were obtained by extrapolating SMR and the energy costs of various activities measured under laboratory conditions, which suffer from the same problems as our measurements. In addition, the accuracy of the extrapolation approach depends on the quality of the data on time spent on various activities and body temperature variation. This information is unavailable for many amphibian taxa because of their cryptic lifestyle. Hence, despite their limitations, our results are highly informative for this group.

In conclusion, our results show that newts manage their energy budget via partial allocation. That is, newts compensate for increased SMR by reducing energy expenditure on other physiological functions and behavioural activities. Not only do newts have the lowest maintenance costs among ectotherm vertebrates (Gatten et al. 1992, Kristín & Gvoždík 2012), their energy management further contributes to their economic lifestyle. In other vertebrate groups, the energy budget is mostly managed according to the independence or performance model (Auer et al. 2017, Mathot et al. 2019, but see Halsey et al. 2019). More data are necessary from under-studied groups, such as amphibians, to obtain a fuller picture of energy management and the relationship between metabolic and behavioural traits. Further studies should also consider individual (co)variation in thermal reaction norms for metabolic traits (Gifford et al. 2014) and regression dilution issues in testing the predictions of energy management models (Halsey & Perna 2019). On a general point, our results demonstrate that the DMS-SMR relationship is more useful in determining energy management models than the problematic or indirect evidence based on SMR covariation with other metabolic and behavioural traits, i.e. DEE reflects individual variation in SMR and locomotor activity metrics require a large sample size to attain an acceptable power. Finally, metabolic relationships are insensitive to body temperature variation. Although climate change may increase ectotherm body temperatures, and accordingly accelerate their metabolic rates in the near future (Dillon et al. 2010), this may happen without changing their energy management.

Acknowledgements

We thank two anonymous reviewers for their detailed and constructive comments on the previous version of this paper. This research was supported by the Czech Science Foundation (grant number 17-15480S to LG), the Institute of Vertebrate Biology of the Czech Academy of Sciences (RVO: 68081766 to LG) and the Department of Botany and Zoology, Faculty of Science, Masaryk University in Brno, Czech Republic (MUNI/A/1436/2018 to SB). L. Gvoždík conceived the ideas and analysed the data; S. Baškiera and L. Gvoždík wrote the manuscript. Both authors contributed critically to earlier drafts and gave final approval for publication.

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