

Research



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Evolutionary biology

A tropical arthropod unravels local and global environmental dependence of seasonal temperature–size response

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In most ectotherms, adult body size decreases with warming, the so-called ‘temperature–size rule’ (TSR). However, the extent to which the strength of the TSR varies naturally within species is little known, and the significance of this phenomenon for tropical biota has been largely neglected. Here, we show that the adult body mass of the soil mite *Rostrozetes ovulum* declined as maximum temperature increased over seasons in a central Amazonian rainforest. Further, per cent decline per °C was fourfold higher in riparian than in upland forests, possibly reflecting differences in oxygen and/or resource supply. Adding our results to a global dataset revealed that, across terrestrial arthropods, the seasonal TSR is generally stronger in hotter environments. Our study suggests that size thermal dependence varies predictably with the environment both locally and globally.

1. Background

Ectotherms generally grow smaller with warming in laboratories, across latitudes and over seasons, the so-called ‘temperature–size rule’ (TSR). While this pattern may be a by-product of the different thermal sensitivities of development and growth [1], several studies suggest that the TSR is an adaptive response to (and thus modulated by) oxygen and/or resource limitation [2–7]. Therefore, the strength of the TSR should vary naturally within species, but the extent of this variation is little known [8]. Further, theory predicts that the TSR optimizes resource allocation throughout ontogeny, the fitness gains of which would be highest in hotter environments [1]. However, data on the TSR are largely biased towards temperate species [7]. Thus, the significance of the TSR for tropical biota remains unclear, which complicates inferences about global patterns in its strength [7].

In this study, we addressed these issues by investigating the seasonal TSR in a tropical rainforest using a widespread parthenogenetic detritivore, the soil mite *Rostrozetes ovulum* (Berlese, 1908) (Acari: Oribatida) [9]. In central Amazonia, *R. ovulum* takes around six weeks to develop from egg to adult [10], and adult abundance peaks yearly for two to three months [9,10], suggesting a life cycle of four to five months. As adults occur year-long, development is subject to seasonal temperature fluctuations. Moreover, *R. ovulum*’s abundance is lower in bottomland, riparian forest relative to upland forest, possibly due to flood mortality and/or resource shortage [9]. Therefore, we tested (1) whether adult body size decreased with seasonal warming and (2) whether the strength of this decrease diverged between habitats.

Table 1. Top five generalized linear mixed models (gamma-distributed errors, log link, sampling transect as random factor) of seasonal variation in *R. ovulum*'s body mass ($n = 116$), ranked according to AICc. Number in bold indicates well-supported models ($\Delta\text{AICc} < 2$). $T_{\text{max},60}$: maximum daily temperature 0–60 days before sampling; $T_{\text{mean},60}$, $T_{\text{mean},90}$: mean daily temperature 0–60 and 30–90 days before sampling, respectively; habitat: riparian (0) or non-riparian forest (1).

model equation	R^2	ΔAICc
$\exp(13.61 - 0.25T_{\text{max},60} - 8.44\text{habitat} + 0.23T_{\text{max},60}\text{habitat})$	0.20	0.00
$\exp(7.37 - 0.15T_{\text{max},60} - 0.13\text{habitat})$	0.14	6.39
$\exp(7.75 - 0.16T_{\text{max},60})$	0.12	6.61
$\exp(16.99 - 0.54T_{\text{mean},90} - 11.49\text{habitat} + 0.41T_{\text{mean},90}\text{habitat})$	0.16	7.28
$\exp(22.09 - 0.72T_{\text{mean},60} - 13.26\text{habitat} + 0.47T_{\text{mean},60}\text{habitat})$	0.14	9.95

2. Material and methods

Field work was carried out in a primary forest remnant (800 ha) in Manaus, Brazilian Amazonia (03°04'34" S; 59°57'30" W). Annual rainfall is about 2200 mm, and mean monthly air temperature typically varies between 24 and 27°C [9]. The landscape comprises a mosaic of dry, clayish uplands and sandy bottomlands prone to periodic flooding [9].

We sampled 20, 20 m long transects distributed all over the study area and distant at least 150 m away from each other (electronic supplementary material, appendix S1, table S1). Ten transects were located along drainage catchments (riparian forest), and another ten on uplands at least 150 m away from any stream (non-riparian forest). Transects were sampled on eight occasions over a year (June, July, August and November 2014; and January, March, April and June 2015). In each transect, one soil sample was extracted each metre with an aluminium soil corer (3.5 × 3.5 × 5 cm). Soil samples were taken to the laboratory, where soil animals were extracted into 95% alcohol using a Berlese–Tullgren apparatus [9]. *Rostrozetes ovulum* adults were identified using a specialized key [11], and photographed under a microscope to measure their body length (L) and width (W) (μm). Body mass (M) was estimated using a well-established allometric equation: $\log M = -17.17 + 3.00 \log(L + W)$ [12].

Daily temperature readings were obtained from the nearest station of the Brazilian Institute for Meteorology, 1 km away from the study site (electronic supplementary material, appendix S1, table S2). In central Amazonia, monthly means of air and soil temperature (5 cm deep) correlate well ($r = 0.82$, $n = 18$) [13], and spatial variance in soil temperature is negligible, with no significant difference between riparian and non-riparian forests [14]. This justifies the use of data on nearby air temperature as a proxy for local soil temperature seasonality. We considered mean and maximum daily temperature readings for each day of 2014 and 2015. The maximum was used because it is more variable than the mean [13], and could be more relevant for developmental and growth rates.

We used generalized linear mixed modelling to model body mass (μg) as a gamma-distributed dependent variable with log link, which accounts for nonlinear, heteroscedastic responses. Transect was used as a random factor, to control for potential non-independence among individuals from the same transect. We considered five combinations of predictors representing alternative hypotheses on the drivers of body mass: (1) intercept-only model; (2) habitat as single predictor; (3) temperature as single predictor; (4) temperature and habitat as independent effects; and (5) an interaction between temperature and habitat. Models including temperature were expanded in two ways. First, we built separate models for mean and maximum temperature. Second, we considered different time windows for the effect of temperature on adult body mass. Because *R. ovulum* takes about two months to develop from egg to adult, current adult

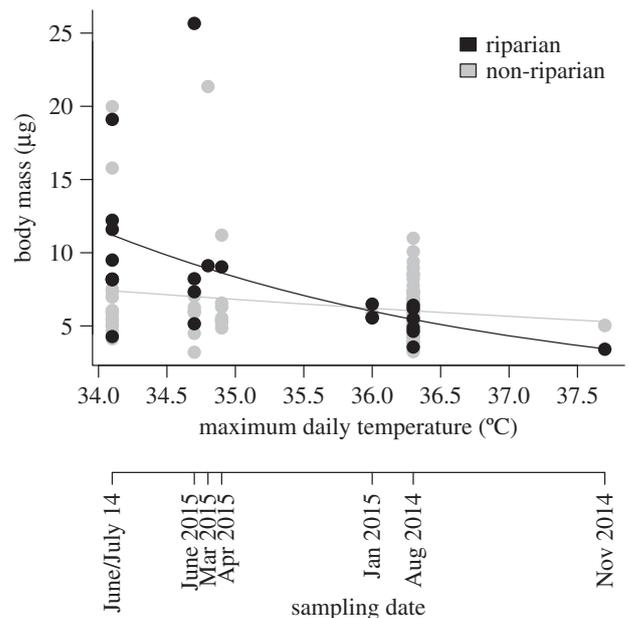


Figure 1. Relationship between *R. ovulum*'s body mass and maximum daily temperature 0–60 days before sampling in central Amazonia. Points represent individuals ($n = 116$), and lines represent the fittest model (table 1).

body mass should reflect temperatures experienced during some two-month interval up to five months before sampling (i.e. the estimated lifespan of *R. ovulum* in the field). Hence, temperature variables were computed for time intervals of 0–60, 30–90, 60–120 and 90–150 days before sampling, and a separate model was built for each.

All models were ranked according to Akaike's Information Criterion corrected for sample size (AICc), and models with a difference of two units or less relative to the lowest AICc were favoured. Model explanatory power was assessed as the squared correlation between observed and predicted values (R^2), and mean per cent change in body mass per °C was calculated as $(\exp^{(\text{slope})} - 1) \times 100$ [7]. All analyses were performed in R 3.3.2 [15].

3. Results

A single model was clearly supported over the alternatives: *R. ovulum*'s body mass decreased with increasing daily maximum temperature between 0 and 60 days before sampling, with average reduction in body mass being higher in riparian than in non-riparian forest (table 1, figure 1); random-factor variance was negligible (2.6% of the total variance). This conclusion was unaffected by exclusion of potential outliers

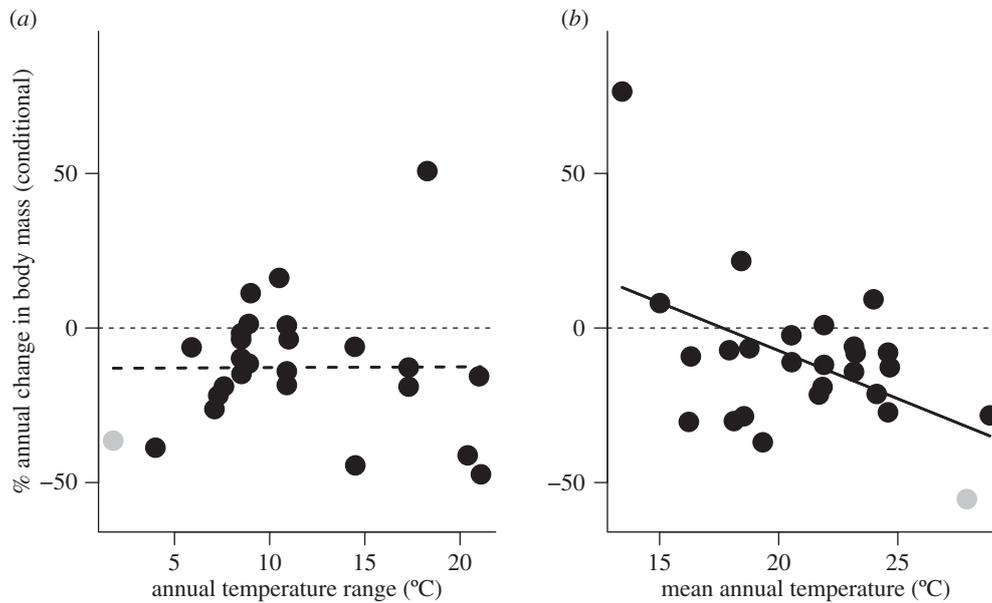


Figure 2. Conditional effects of (a) annual temperature range and (b) mean annual temperature on the strength of the seasonal TSR across terrestrial arthropod species ($n = 26$). Black circles, dataset from [7]; grey circles, *R. ovulum* (this study). Dashed and solid lines represent non-significant and marginally significant effects, respectively.

(electronic supplementary material, appendix S2, figures S1 and S2, table S3). For each 1°C increase in maximum temperature, average body mass decreased by 9.72% in non-riparian forest, but by 38.85% in riparian forest.

4. Discussion

Our results confirm that strength of the seasonal TSR varies naturally within species, depending on local habitat. The TSR has been generally discussed either as a non-adaptive consequence of ontogenetic thermal dependencies, or as an adaptive response to fitness costs signalled by temperature. For instance, developmental rates are generally more sensitive to temperature than growth rates, which should cause adult size to shrink with warming [1]. Likewise, variation in such sensitivities could change the TSR. However, assuming that selection buffers adult size (and thus fitness) from environmental perturbations [1], it is unclear why such sensitivities should vary, especially between habitats with similar thermal regimes, as studied here.

By contrast, adaptive hypotheses explicitly predict the strength of the TSR to change with environmental factors, particularly oxygen and resource levels. For instance, warming increases the ratio of oxygen demand to supply through body fluids, which should favour size reduction to maintain aerobic scope [2,16]. Indeed, the TSR is generally stronger in aquatic than in terrestrial habitats, consistent with the former's lower oxygen diffusion rate [6,7]. Our results agree with this idea in that TSR was stronger in riparian forests, which are periodically flooded by hypoxic waters [9]. However, habitat thermal responses were crossed, and the largest individuals also occurred in riparian forest (figure 1). Thus, either oxygen limitation was not the driving mechanism, or some other, interfering factor caused between-habitat differences in absolute size.

Alternatively, as temperature increases, so does mass-specific demand for resources; for a constant resource supply, resource use should be optimized by reducing size [5]. Yet, the fitness gains of growing larger as resource

supply increases should weaken the TSR [5]. Accordingly, improved nutritional conditions have been shown to reduce the thermal dependence of growth rate [17], as well as the strength of the TSR [3,18]. In riparian forests, *R. ovulum* experiences lower litter inputs of poorer nutritional quality than in uplands [9]. Thus, the stronger TSR in riparian forests is consistent with nutritional limitation. Further support comes from the fact that changes in nutritional conditions have been shown to cause crossed thermal responses as observed here [3], whereas this is not expected from changing oxygen levels [2,4,16].

More generally, habitat-specific TSR could reflect either phenotypic plasticity by widely distributed genotypes, habitat-specific genotypes with divergent reaction norms or some combination thereof [8]. Parthenogenetic oribatid mites produce clonal offspring [19], suggesting high potential for local genetic differentiation. Yet, soil arthropods generally lack genetic structure at local spatial extents due to passive dispersal [20]. Clarifying this issue will require genetic data and/or common garden experiments.

A latitudinal gradient in the strength of the TSR may occur, e.g. if warmer environments favour optimal resource allocation through the TSR [1] or magnify the discrepancy between oxygen demand and supply [16]. A recent meta-analysis on arthropods found no evidence for such a gradient [7], but low-latitude species were lacking. Therefore, we collated our results to this dataset and tested simultaneously for effects of annual temperature range and mean annual temperature on the seasonal TSR in terrestrial arthropods (electronic supplementary material, appendix S2). We found that the former had no effect ($p = 0.98$), but species inhabiting hotter sites did experience generally stronger seasonal TSR ($p = 0.06$; $R^2 = 0.26$) (figure 2). Thus, our study suggests that size thermal dependence varies predictably with the environment both locally and globally. Minimizing geographical bias in TSR research will likely provide novel insights into this widespread phenomenon.

Ethics. This study complied with local legal requirements; no special licence was required for this kind of research.

Data accessibility. The datasets supporting this article have been uploaded as part of the electronic supplementary material.

Authors' contributions. P.A.C.L.P., E.F., R.A.N. and J.W.M. conceived and designed the study. P.A.C.L.P. acquired and analysed the data. All authors interpreted the data. P.A.C.L.P. drafted the manuscript, and E.F., R.A.N. and J.W.M. revised it critically. All authors approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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