Review Article

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Features of the Modeling Masked in Situ Temperature-Size Rule in Large Sample Array of Carabus Granulatus L. (Coleoptera: Carabidae)

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ABSTRACT

The study investigates the manifestation of the Temperature-Size Rule in the carabid beetle Carabus granulatus across a large geographic range. TSR is a phenomenon where warmer temperatures result in smaller adult body sizes in ectothermic organisms. Using a dataset of 10172 individuals from 15 regions, we performed regression analysis to explore the relationship between body size (elytral length) and climatic variables. Initial simple regressions showed no clear evidence of TSR. However, more complex models incorporating interactions between precipitation, maximum and average temperature revealed masked Temperature-Size Rule effects. The study emphasizes that TSR can be obscured by other environmental factors and their interactions. The results suggest that temperature-dependent size changes may become apparent only under specific environmental conditions, particularly when precipitation levels are low. These findings highlight the importance of using large sample sizes and considering complex interactions when studying ecological rules like TSR in natural populations.

Keywords: Temperature-Size Rule, Linear Regression, Body Size, Precipitation, Insects, Carabus Granulatus

Introduction

Temperature-size rule (TSR) is a tendency, observed in invertebrates. According to it, imago has smaller size when reared in warmer temperatures [1]. Nevertheless, this rule has been shown clearly for laboratory studies [2], while studies on animal sizes in situ reveal contradictory results [3]. It is proposed that TSR can be found on interspecific level, while on intraspecific level its manifestation varies. Also, Tseng et al. suggest that the tendency of TSR can be strongly blurred by a great number of factors, which also affect animal size. Therefore, we challenged ourselves to find traces of TSR for a species where it was clearly violated in situ: Carabus granulatus. Our advantages were large sample size along with wide geographic representation. Such characteristics of the samples allow us to uncover subtle trends, while including interactions in the model doesn't lower the quality.

Problem Formulation

Carabus granulatus L. 1758 is a spring breeder carabid beetle. Its range extends across Eurasia, and the life cycle of C. granulatus can adapt in different regions, but for all the regions involved in the analysis, its life cycle remains a one-year univoltine with

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larvae maturing during summer months [4,5].
In order to reveal TSR we performed a regression analysis.

We analyzed elytral length of 10172 individuals from 71 plots in 15 regions, including Russian Federation, Republic of Belarus, Republic of Bulgaria, Slovak Republic, republic of Poland, Italian Republic and Czech Republic. Geographically, the sampling plots extend from 42.8911 to 56.85 °N and from 7.70111 to 86.186 °E (table 1). As predictors for regression models, we used global bioclimatic variables, including annual temperature and precipitation, as well as the same variables for the warmest and wettest quarters and for July, because it is the month, when C. granulatus is matures in all regions [6,7].

Before analyzing, outliers were removed from the data using 1.5 IQR method [8]: in total, 100 measurements. P-levels of coefficients were calculated with robust method.

For modeling we used R software [9]. For calculating p-levels we used libraries “sandwich” and “lmtest” [10-12].

Large sample size allows us to treat results of the linear regressions as consistent despite possible deviations of the residuals from homoscedasticity and normal distribution, because in large samples tests on these characteristics become too sensitive.

Problem Solution
Linear regression of elytral length on annual temperature, temperature of the warmest quarter (summer months) and wettest quarter (usually, spring-summer months) as well as maximum temperature of the warmest month (mostly, July) showed statistically significant ($p<0.001$) positive coefficients for females. The reaction of males differed significantly from that of females only for annual temperature, where it was more pronounced. Hence, C. granulatus seemingly does not follow TSR within simple regression.

Assuming that TSR is masked, we built linear regressions using the interaction of various temperature variables with precipitation (table 1). The results partially reveal Temperature-Size Rule, but inconsistently: sometimes the coefficients of the temperature factor become negative, and sometimes the interaction is negative.

Table 1: Estimated Coefficients of Linear Regression of Elytral Length on Various Temperature and Precipitation Variables. Sexual Differences were Part of the Model, but Without Interaction. All Coefficients have P-Level < 0.0001. R2 of the Models Varies from 0.35 to 0.38

Model	Temperature factor coefficient	Precipitation factor coefficient	Interaction
Annual Temperature×Annual Precipitation	-0.18	-0.007	0.0005
Max temperature of warmest month×Precipitation of warmest quarter	-0.22	-0.04	0.002
Avg. temperature of warmest quarter×Precipitation of warmest quarter	+1.26	+0.07	-0.004
Avg. temperature of wettest quarter×Precipitation of wettest quarter	+1.88	+0.15	-0.009

It can be seen that annual and maximum temperatures interact differently with the precipitation factor than average temperature. Considering that correlations between factors may blur true relations, we decided to use temperature and precipitation data of July, when larvae are maturing. Based on the results of table 3, we used both average and maximum temperature, because they could act as different factors. We modeled interactions of average temperature with precipitation in July and maximum temperature with precipitation in July, and added an interaction between maximum and average temperature to avoid the correlation effect. Sex was added in the formula to take sexual dimorphism of the beetles into consideration, but without interaction, since we assume that TSR affects both males and females equally. The coefficients of the regression are presented in Table 2. Predictors were transformed into z-scores since they vary in different ranges. Maximum temperature in the interaction with precipitation was squared due to higher p-levels of the factor.

Table 2: Coefficients of the Regression of Elytral Length of C. Granulatus on Precipitation (Prec), Average (Tavg) and Maximum Temperatures (Tmax) of July with their Interactions. Estimates, Standard Errors and p-levels are Displayed. R2 of the Model is 0.389

Coefficient	Estimate	Std. error	p-level
Intercept	12.095	0.017	<0.0001
Tmax	-0.260	0.029	<0.0001
Tavg	0.222	0.027	<0.0001
Prec	-0.219	0.018	<0.0001
Sex	-1.037	0.016	<0.0001
Tmax^2×Prec	0.019	0.004	<0.0001
Tavg×Prec	-0.046	0.021	0.035
Tmax×Tavg	0.057	0.008	<0.0001

Results show that maximum temperature reveals Temperature-Size Rule in a straightforward way, while average temperature acts through the interaction, reducing positive effect of precipitation level. Interactions between temperature factors and precipitation are displayed in figures 1 and 2.

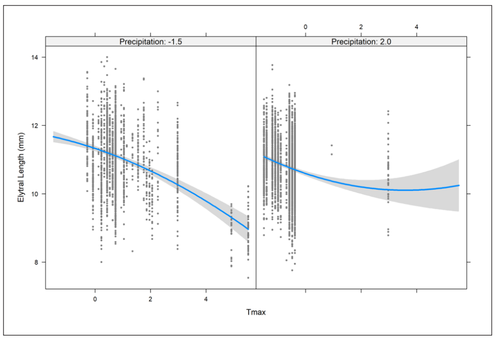

Figure 1: Regression of Elytral Length of C. Granulatus on Maximum Temperature of July within 1st and 99th Percentiles of Precipitation Levels

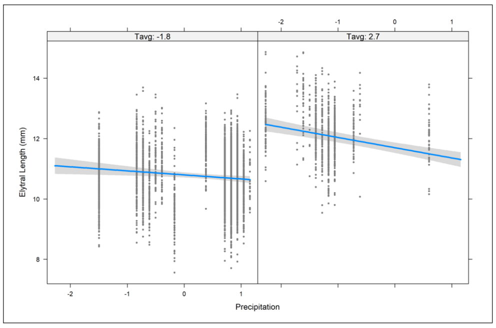

Figure 2: Regression of Elytral Length of C. Granulatus on Precipitation of July within 1st and 99th Percentiles of Average July Temperature Levels

Conclusion

Despite the apparent violation of the TSR in C. granulatus, a more complex regression model points out, that it can be masked within interactions. An increase in maximum temperature has a more pronounced effect on body size under conditions of low precipitation levels. Average temperature doesn't show TSR trends itself, but it lowers the positive influence of precipitation, operating through interaction. Close results were published for Asellus aquaticus L. [13]: the level of oxygen can modulate the expression of TSR, and it reveals itself under conditions of low oxygen. Based on this, we can speculate, that temperature effect on size of ectotherms arises under extreme conditions. Under normal conditions it is masked by myriad other factors and may affect only as a minor interaction.

As for modeling such an inconsistent rule, we underscore the importance of sample size and the consideration of more complex interactions to reveal underlying trends. Nevertheless, linear regression is a descriptive a posteriori method useful for the first approach. Subsequent studies may include such methods as Bayesian statistics and other a priori models, where more precise coefficients can be adjusted.

Contribution of Individual Authors to the Creation of a Scientific Article (Ghostwriting Policy)

R.P. Gorbunov was responsible for statistical analysis and writing.
S.L. Luzyanin, V.V. Aleksanov, C. Ferracini, I.A. Solodovnikov, A.B. Ruchin, T.M. Teofilova, V. Langraf, A.G. Borisovskiy, D. Stoĉes, A.L. Anciferov, A.A. Maksimovich provided material.
A.A. Saveliev performed data and analysis validation.
R.A. Sukhodolskaya managed the workflow and verified the draft of the paper.

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