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THE LOCAL INTERSPECIFIC ABUNDANCE − BODY WEIGHT RELATIONSHIP OF GROUND BEETLES: A COUNTEREXAMPLE TO THE COMMON PATTERN

ABSTRACT: The interspecific abundance – body weight relationship (AWR) is generally believed to follow a power function with a negative slope. Here we report on the AWR of two local assemblages of ground beetles in northern Poland spanning more than three orders of magnitude in body weight. Both assemblages showed significant positive AWR slopes in raw and grouped data plots even after controlling for phylogenetic and sampling effects. We conclude that ground beetles might be an exception from the overall AWR pattern.

KEY WORDS: Carabidae, poplars, metabolic theory, allometry

One of the best documented patterns in macroecology is the inverse correlation of species abundance with species body weight, the abundance – body weight relationship (AWR) (Cotgreave 1993, Blackburn and Gaston 1997, Hendriks 1999, Gaston and Blackburn 2000, Brown *et al.* 2004). The negative AWR (in particular with a slope of –0.75) is basic to many recent macroecological and eco-metabolic theories (Damuth 1987, Currie 1993, Brown *et al.* 2004).

Current theory holds that this relationship should be a power function with a negative slope. Blackburn and Gaston (1997) compiled over 291 published quantitative AWRs and found 253 of these to have the predicted negative slope. Hence, about 13% of the slopes were positive. However, positive slopes occurred only at small differences of body size (less than four orders in magnitude) and had always low coefficients of determination. The reason for this can be seen in Fig. 1. Taking small parts of an overall strong negative AWR gives (due to the high variance in abundance) much lesser coefficients of correlation and lower slope values. Such plots will in many cases even show positive slopes, although most often with low and statistically not significant R^2 values. This is exactly the pattern Blackburn and Gaston found.

However, above a size range of four orders of magnitude all to date published AWRs had a negative slope and the regression frequently explained more than 50% of variance in abundance (Blackburn and Gaston 1997, Hendriks 1999, Gaston and Blackburn 2000). Further, the use of geometric mean abundance and size classes to reduce the total variability reduces also the size range effect in Fig. 1 and results even at small size difference in negative slopes. We are not aware of any study dealing with size

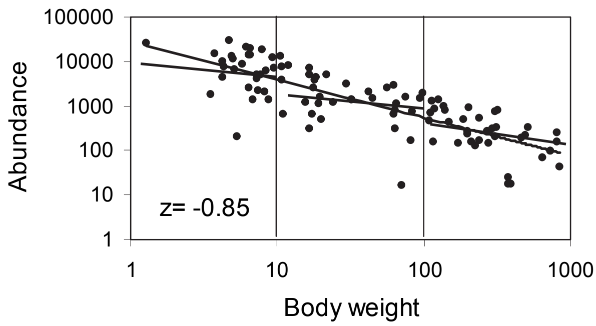

Fig. 1: A typical abundance – body weight relationship over three $\log_{10}$ weight classes with a slope of z = –0.85. Using the same data points but regarding only single $\log_{10}$ weight classes would result in much less significant relationships and shallower slopes.

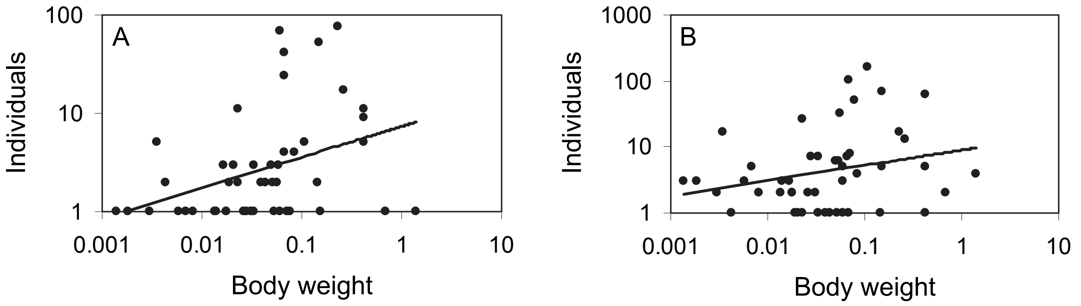

Fig. 2: Abundance (number of individuals + 1) – body weight (W in gram) plots of the ground beetles trapped. A: poplar plantation; N = (12 ± 1.5) $W^{(0.43 \pm 0.13)}$, R^2 = 0.24, P(t) = 0.002. B: field; N = (2.1 ± 0.5) $W^{(0.22 \pm 0.14)}$, R^2 = 0.05, P(t) = 0.11.

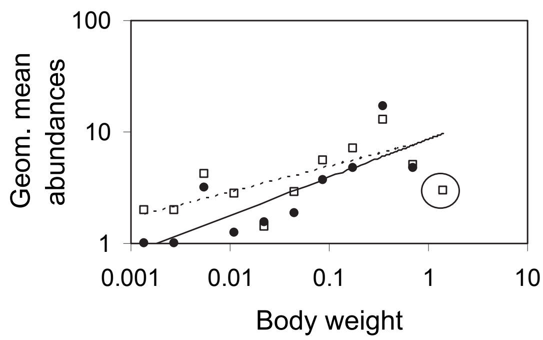

Fig. 3: Geometric mean number of individuals – body weight class [g] relationship of the ground beetles trapped. Black circles: Poplar plantation, open squares: field. Leaving the uppermost weight class aside that is made up by three individuals of *Carabus coriaceus* trapped only at the field site (marked by the oval) gives for both study sites significant power function relationships. Plantation: R^2 = 0.66; z = 0.34 ± 0.09; P(t) = 0.004. Field: R^2 = 0.53; z = 0.23 ± 0.08; P(t) = 0.02.

classes that reported an AWR with a significantly positive slope.

The vast majority of AWRs was inferred from vertebrates, particularly from birds and mammals. Much less is known about the AWRs of arthropods. Nevertheless, the existing evidence also points to generally negative AWRs although the slope values seem to be somewhat lower than for vertebrates (Hendriks 1999, Ulrich 2001). Here we report on the AWD of two ground beetle communities spanning both more than three orders of magnitude in body weight. Both communities deviate from the common AWR in having significantly positive slopes even after grouping into size classes.

Two ca 60 years old Poplar (*Populus canescens*) plantations (Ostromecko [13 ha] and Wierzbiczany [11 ha]) and two adjacent winter wheat fields (Wierzbiczany [8 ha]: Ostromecko [6 ha]) near Bydgoszcz in Northern Poland were sampled in 2001 with standard Barber traps (Work *et al.* 2002) with an opening diameter of 7 cm. Cyzmann (2002) classified the sites as a *Ficario-Ulmetum campestris* (Ostromecko) and as a *Tiliocaroinetum stachyetosum* (Wierzbiczany). They are situated in the Vistula lowland and are characterized by rather high levels of groundwater that cause infrequent flooding of both poplar plantations. At each of the four sites we run 15 traps in form of a transect for one week each in May, June, July, and September. Ulrich *et al.* (2004) give detailed descriptions of the study sites and the trapping program.

In total we trapped 994 individuals out of 52 species (species list and species abundances in Ulrich *et al.* 2004). Because at all sites identical numbers of traps were used we constructed AWR plots on the basis of the total number of animals trapped per site. Body weight data stem from mean species body lengths as given in Hurka (1996) using the regression of Szujecki *et al.* (1983): W [g] = 0.000133 L [mm]$^{2.555}$. Nonlinear regression functions and associated standard errors were computed with the nonlinear estimation module of Statistica 5 (Statsoft 1997) using ordinary least squares regression.

The ground beetle AWRs of both study sites followed allometric functions with a positive slope (Fig. 2). This pattern remained when using mean abundances and binary body weight classes instead of raw data (Fig. 3). The regressions explained 24% (plantation) and 5% (field) of the variance in the raw data and 72% and 56%, respectively, in the grouped data. They were in all four cases significant at the 5% error level (Figs. 2, 3).

Simple regressions as above might be influenced by three types of errors. First, the data points might not be independent due to phylogenetic constraints. In the present case species of the same genus are of similar size and the positive correlation between abundance and size might stem from similar constraints acting upon the similar sized species of a genus. There is still no unequivocal phylogenetic system of ground beetles available (Madison *et al.* 1999); hence we were unable to compute phylogenetic contrasts at the genus level (Felsenstein 2004). To account at least in part for this possible source of errors we computed the abundance – body weight regression upon total abundances per genera (25 genera in total) using mean body weights per genus. Surprisingly, this procedure retained the significant positive correlation between log abundance and log body weight for the plantation ($R^2 = 0.17$; $P = 0.04$) and strengthened even the positive regression for the field although the latter was less significant due to the lower number of data points ($R^2 = 0.11$; $P = 0.09$; data not shown).

A second source of errors might be an unequal distribution of data points along the body weight axis, which might result in an overproportional influence of outliners. To test for this we applied the ratio test of Strong *et al.* (1979) and tested for a non-random distribution of body weights along the weight axis using the variance of absolute differences in weight of the ordered sequence of species. The expected variance was inferred from 1000 random assignments of body weights (using linear random numbers) inside the observed range (cf. Ulrich 2005 for details of the applied null model). The observed body weight distribution did not deviate from a random expectation ($P > 0.1$).

A third source of errors might be an unequal trapping of species with different body size. It is widely believed that larger species have higher velocities and travel longer distances (Ebenman *et al.* 1995, but see Halsall and Wratten 1988 for a contrasting view). If these differences cause uneven trapping probabilities a bias towards larger species might result (Luff 1975, Baars 1979, Spence and Niemelä 1994). Indeed Luff (1975), Spence and Niemelä (1994) and Ulyshen *et al.* (2005) found some evidence that too small traps catch lower proportions of very small beetles below 5 mm body length. Our seven cm traps were at the lower level of opening diameters used and recommended (Work *et al.* 2002). Hence, a small- species effect might cause the positive AWR of Figs 2 and 3. To test for this we run the regression in a stepwise manner leaving out step by step the smallest species. To our surprise the elimination of species below 5 mm body length (8 species) even strengthened the positive AWR pattern ($z_{plantation} = 0.52$, $P(t) < 0.001$; $z_{field} = 0.44$, $P(t) < 0.01$). The regressions for both habitats remained positive until only species above 10 mm body length were included, although these regressions were not significant (at $P < 0.05$) for species above 8 mm body length (probably due to the reduced number of species included). Additionally, for the positive AWR slope being solely a sample artefact, the larger species above 50 mg would have to be oversampled by one to two orders of magnitude (Figs 2, 3). We are not aware of any study reporting such a bias in sampling efficiency between larger and smaller species and feel therefore that a potential body size effect of trapping efficiency should not influence our main result of a positive AWR. Nevertheless further studies using an *a priori* correction for possible sample biases have to establish the exact AWR shape.

To our knowledge explicit abundance weight distributions of ground beetles were only reported by Ulrich and Zalewski (2005) who also found a significant positive AWR for ground beetle assemblages on lake islands in northern Poland ($z = 0.44$; $P(t) < 0.01$). The reconstruction of the AWR from the data of Gutierrez *et al.* (2004) on Spanish ground beetles also implies a positive AWR with an exponent of $z = 0.33$ ($P(t) < 0.01$). Hence, a positive AWR might be a general feature of carabid communities irrespective of habitat or geographic location.

The positive AWR might be explained by the different life history strategies of large and small bodied ground-beetles. While both groups are mainly predacious prey types are very different and the larger beetles, being top predators, might have fewer competitors. If therefore resource availability limits beetle occurrences metabolic theory (Brown *et al.* 2004) seems not applicable and AWRs with positive slopes might arise.

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