# Body size and host range in herbivorous beetles on different geographical scales

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## Synopsis

The positive relation between body size and host range in phytophages may be explained by at least three hypotheses: (1) Widely distributed phytophagous species may use more hosts than phytophages with a narrow geographic range (geographic hypothesis). The distributional range of an animal is positively correlated with body size. Hence, host range should increase with body size. (2) Size-dependent energetic constraints may affect the host range: while relative energy use decreases with body size, energy requirement per unit area increases with decreasing body size, thus favouring specialization in small species. (3) The relation between host range and body size may be due to sampling artifacts.

We tested these hypotheses in phytophagous beetles feeding on Cardueae and Brassicaceae. In a regional study on Cardueae we obtained a marginally significant positive correlation of body size with host range which is best explained by the geographic hypothesis. In a local study dealing with Brassicaceae, the raw data showed a marginally significant negative correlation which can be explained by sampling artifacts. Correcting the relationship in Brassicaceae for the sampling effort, the correlation becomes positive. However, there is no simple linear relationship, but a triangular pattern.


*Body size, abundance, Brassicaceae, Cardueae*

## 1 Introduction

Body size influences physiology, abundance and distribution of species (PETERS 1983). Processes such as energy turnover, competition, predation, extinction and colonization depend on body size (PETERS 1983; PETERS & WASSENBERG 1983; BROWN 1995). By analyzing patterns of body sizes one may get deep insights in the general ecological rules that underpin the endless lists of animal species. Thus, »for the same reasons the journalists report people's ages, ecologists record body size: no single number is so informative and it is easily measured« (NEE & LAWTON 1996).

Many studies analyzing body size patterns, however, concentrate on mammals and birds (reviewed in BROWN 1995), because these two groups are well investigated. As long as body size patterns are mostly done by vertebrate ecologists, our view of nature is biased. Especially phytophagous insects pose a number of intriguing problems about diversity, density and host range patterns. There is now a growing body of evidence about a positive relationship between body size and host range in insects (WASSERMANN & MITTER 1978; NIEMELÄ & al. 1981; GASTON & LAWTON 1988; LINDSTRÖM & al. 1994). In the present note, we extract host ranges of phytophagous beetles on Cardueae and Brassicaceae to test the generality of this pattern.

There are at least three hypotheses that may generate a correlation between body size and host range. (1) By tracking the resources, widely distributed species may use more hosts than species with a narrow geographic range. Since distribution is positively correlated with body size, host range should increase with body size. (2) BROWN & MAURER (1989) argue that specialization of vertebrates should be influenced by size-dependent energetic reasons: relative energy use decreases with body size, whereas energy requirement per unit area increases with decreasing body size. Furthermore, the home range of an organism is positively correlated with its body size. Thus small organisms need to collect much high-quality food within a small home range, which leads to specialization. (3) Finally, the relation between body size and host range may be influenced by sampling, because in a survey of host plants large (rare) insect species will become detected at few hosts, while small (abundant or rare) species may be detected at few or many hosts.

## 2 Material and Methods

We used two published studies on insect-plant relationships to extract host range data of phytophagous beetles feeding endophytic or external on plant tissues. Beetles feeding on nectar or pollen were not included. During a local study in Poland phytophagous insects were sampled from Brassicaceae (LIPA & al. 1977), and in a more regional study ZWÖLFER (1965) sampled phytophagous insects from Cardueae throughout Europe. We restricted the analysis on

| Coleoptera | Brassicaceae (LIPA & al. 1977) | | Cardueae (ZWÖLFER 1965) |
|---|---|---|---|
| | n species | n specimen | n species |
| Curculionidae | 33 | 1856 | 44 |
| Chrysomelidae | 22 | 3261 | 13 |
| Nitidulidae | 8 | 2137 | 0 |
| Mordellidae | 0 | 0 | 5 |
| Elateridae | 4 | 45 | 0 |
| Cerambycidae | 0 | 0 | 3 |
| Coccinellidae | 2 | 343 | 0 |
| Σ | 69 | 7642 | 65 |

Table 1
**List of beetle families and associated phytophagous species sampled on either host plant taxon and number of specimen collected on Brassicaceae.**

phytophagous species of the families listed in table 1. Beetles are a main component of the fauna of Brassicaceae and Cardueae and comprise more than one quarter of all phytophagous species found by LIPA & al. (1977) and ZWÖLFER (1965). Body size of adult beetles was extracted from FREUDE, HARDE & LOHSE (1966–1983) and HOFFMANN (1950, 1954, 1958), using the mid point between minimum and maximum length (in millimetres) as a measure of body size. ZWÖLFER & BRANDL (1989) compared own measurements in Cerambycidae and Curculionidae with the size-range given in the literature and demonstrated that the latter is a reliable measure for body size.

LIPA & al. (1977) investigated 132 plant species and 8 subspecies within 56 genera (14266 samples), including even alien species and cultivars. Besides host range data the lists allowed to extract the number of sampled beetle individuals as a relative measure of abundance. We summed up all individuals sampled by sweeping, shaking and picking. LIPA & al. (1977) sampled their plants mainly in especially designed collection gardens on few sites in Poland. Thus this study has a local perspective.

ZWÖLFER (1965) surveyed 59 species within 14 genera of Cardueae throughout Europe (1354 samples). Thus this study has a regional perspective. For each phytophage we counted the number of plant species where it was recorded by ZWÖLFER. Due to the sample size it was not possible to extract a relative measure of abundance of each species.

Statistical analysis was done with log-transformed data of host plant numbers, abundance and body size of beetles using simple correlation analysis. The raw data are available from the internet (http://www.ufz.de/spb/bioz).

## 3 Results

Analyzing the data of the beetle fauna of Cardueae (Fig. 1A; $n=52$), the correlation between body size and the number of hosts is marginally significant ($p=0.07$). To decrease errors caused by different sampling effort on host plants, we restricted our analysis on hosts where 10 populations were examined at least. The correlation of the fauna of Cardueae is consistant with the predicted positive relationship of body size and host range. However, using the data of phytophagous beetles on Brassicaceae, we found a marginally significant negative correlation between the same parameters (Fig. 1B; $n=69$; $p=0.08$). The two correlation coefficients are different ($p<0.01$). Note that in the case of Brassicaceae the relationship seems to be triangular: large species have a low host range whereas small species have a low or large host range.

This pattern is repeated in detail by plotting body size versus relative abundance of beetle species on Brassicaceae (Fig 2A). Large species are rare, whereas small species may be rare or abundant. This leads to a strong correlation between the relative abundance and the number of hosts. Thus, the pattern in the plot of body size versus host range (Fig. 1B) is in part a sampling artifact.

To test the combined impact of body size and relative abundance on host range we performed in a first step a multiple regression. Relative abundance explained about 87% of the variance in host range, which increases by only one percent if body size is included. Nevertheless, this increase is marginally significant ($p=0.06$). After correcting for relative abundance, the relationship between body size and host range becomes positive.

In the next step, we constructed a null-model to calculate the expected number of hosts if individuals were randomly distributed among hosts. For each beetle species we distributed individuals randomly across 139 host species. This process was repeated 100 times for 1 to 1650 individuals. Afterwards the

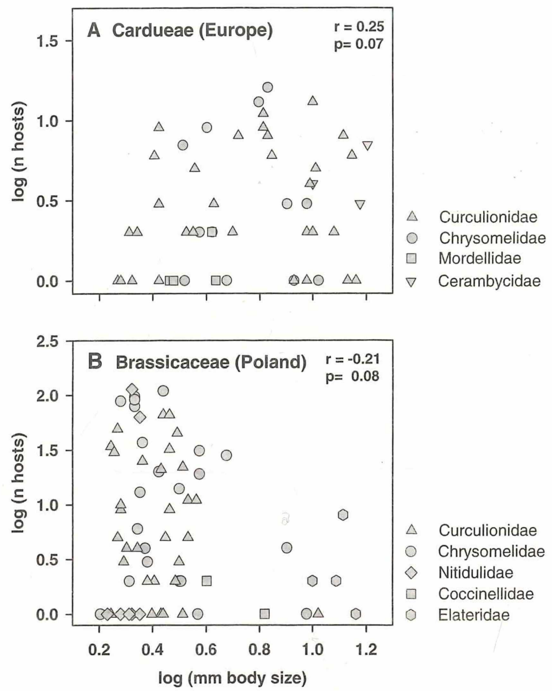


Fig. 1
**The correlation between body size of phytophagous beetles and number of host plant species in (A) Cardueae in Europe and (B) Brassicaceae in Poland.**

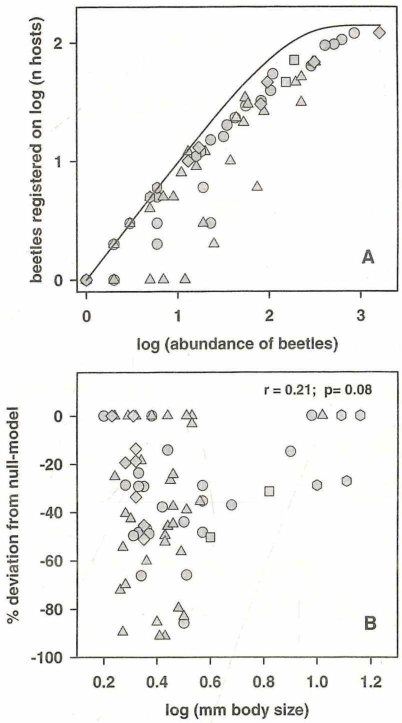


Fig. 2
**(A) The correlation between abundance and host range of phytophagous beetles on Brassicaceae in Poland. The line represents the results of a null-model where individuals were randomly distributed across 139 plant species. (B) Plot of body size versus deviations (in %) from the null-model.**

mean number of hosts was plotted (Fig. 2A, bold line). Although this null-model makes a number of unrealistic assumptions (i.e. all plant species have the same abundance and suitability for insects), the results may be used as a reference point to interprete our data. If the deviation (in %) of each species from the null-model is plotted against body size, the correlation becomes again positive (Fig. 2B). However, a simple correlation fails to describe the pattern of Figure 1B: large species are specialists, whereas small species are specialists or generalists, resulting in a triangular pattern.

## 4 Discussion

As described in the introduction, there are at least three hypothesis operating on different spatial scales which generate a relationship between body size and host range: (1) the geographic range hypothesis (large scale and species level), (2) the host range hypothesis of BROWN & MAURER (1989) (local scale and individual level) and (3) the sampling hypothesis (all scales, population level)

Hypothesis 1: As a consequence of regional host shifts, widely distributed species may have more hosts than geographically restricted species (WIKLUND 1982; ROMSTÖCK 1986; ZWÖLFER 1988). Body size is correlated to geographic range size (GASTON & BLACKBURN 1996), which leads to a positive correlation between body size and host range. ZWÖLFER (1965) studied phytophages on Cardueae on a geographic scale, covering a wide range of European provinces. Thus this study fits the scale of the geographic hypothesis, relating body size with host range. However, the relationship between body size and geographic range is more complex than a simple linear relationship (JOHST & BRANDL 1996). In short, the relationship is approximatly triangular with small species covering small or large geographical ranges and large species covering large ranges. This would lead to a triangular pattern of body size versus host range. However, such a pattern is not apparent in the data of ZWÖLFER (1965; Fig. 1A).

Hypothesis 2: Contrary to the geographic scale, physiological mechanisms may influence the correlation of body size and host range on a local scale. Comparing the relationship between body size and home range as well as body size and daily energy requirement, BROWN & MAURER (1989) argue that small species should be more specialized than large species. In a similar vein WASSERMAN & MITTER (1978) argue that large body size serves to buffer a generalist against physiological stress. According to the idea that general feeders are »jacks of all trades«, but »masters of none«, they are expected to experience stressful conditions more frequently than their smaller specialized counterparts. Hence generalists should be large. LIPA & al. (1977) collected the data in collection gardens where the host species were grown side by side. The pattern in the data of insects on Brassicaceae were best explained by physiological constraints. However, contrary to the simple versions of the physiological hypothesis which predicts a linear relationship, we found a triangular pattern after correcting for abundance.

Hypothesis 3: Large species are rarer than small species which may be rare or common (BROWN & MAURER 1989; GRIFFITHS 1992). If species are sampled according to their abundance, than sample size varies with body size which leads to a bias in the estimation of the host range correlated with body size. The data of insects on Brassicaceae are clearly influenced by sampling. However, after correcting for sample size by using a relative measure of abundance, the relationship between body size and host range fits the basic pattern predicted by hypothesis two.

In conclusion, the data of Cardueae and Brassicaceae suggest that the relationship between host range and body size occurs across spatial scales. The processes generating this pattern, however, differ between spatial scales. But we have to make two cautionary remarks: (1) Although the patterns are in a rough agreement with the predictions of the hypotheses, there are some inconsistencies in the details. (2) In our chain of arguments we have to rely on general macroecological patterns (e.g. the correlation of body size and distribution). It is not clear whether these patterns hold across all spatial scales and across different taxa.

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