

Body size changes in ground beetle assemblages – a reanalysis of Braun *et al.* (2004)'s data

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Abstract. 1. Data in Braun *et al.*'s (2004) recent paper on size trends in ground beetles (Carabidae) are re-analysed, after re-classifying the species according to feeding categories.

2. When ground beetles are classified as predatory species, mixed feeders or herbivores, and evaluated separately, the size trends indicate group-specific differences. Most of these do not support the efficiency-specialisation hypothesis.

3. Taxonomic groups rarely fit into one ecological category and ecological analyses should explicitly consider this hurdle.

Key words. Body size, Carabidae, disturbance, feeding type, life history, pollution.

Introduction

Size has a significant, substantial impact on ecological interactions (Peters, 1983). It modulates resource use, the outcome of species interactions (Peters, 1983), and more indirectly, the periods of activity, habitat suitability, and numerous other parameters. The study of size relationships and their role in shaping interactions is an active research area in ecology (Peters, 1983; Brown, 1995).

Changes in either the size in individual species, or the size distribution of the species in a habitat are also parameters potentially indicating environmental stress (McGeoch, 1998). Recently, Braun *et al.* (2004) used this approach to analyse species size trends in ground beetles (Carabidae) at an abandoned fertiliser factory in Germany. Using the mean size (estimated biovolume) of beetles present, they found that the average species size decreased over time (16 years), in parallel with a decrease in habitat contamination caused by the former fertiliser factory. Based on these results, they speculated about the validity of two conflicting hypotheses of resource use distribution within the family of ground beetles (Carabidae). In Braun *et al.*'s study (2004) ground beetles were used as a taxonomic (and predatory) group; no consideration was made of the various feeding strategies that are found within the group.

In the present contribution the results by Braun *et al.* (2004) are reconsidered and their data were subjected to an evaluation

that considered feeding habits of the species. The main motivation for this was that an important assumption, the uniform feeding type of ground beetles, is not correct. Neither all ground beetles, nor even the majority of them can be considered predatory. In the European fauna, there are many species that are herbivores, or mixed feeders (Lövei and Sunderland, 1996). A final point is that one of the hypotheses evaluated by Braun *et al.* (2004) and attributed to Blake *et al.* (1994), in fact was suggested earlier by Szyszko (1983).

Materials and methods

Data presented in Braun *et al.* (2004) were re-analysed after resorting their species list into three adult feeding categories: predatory species, mixed feeders, and herbivores. This categorisation was based on work by Larochelle (1990), Hürka (1996), and Lindroth (1985, 1986). We then re-analysed size change trends using the same methods as Braun *et al.* (2004) but chose a different graphical representation.

Size trends were analysed using ANOVA, followed by Tukey tests if significant differences were found. Calculations were done using the SPSS statistical software (SPSS, 2000).

Results

Size trends of all species

Considering all carabids together (regardless of their feeding categories), the mean size in the 90s was significantly smaller

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than that in the 80s for all the studied areas (Fig. 1 and Table 1; see also fig. 3 and table 2 in Braun *et al.*, 2004). This picture changed when the species in the different feeding categories were considered separately.

Analysis by feeding categories

Carnivore species. In the severely polluted area, body size was smallest in 1991, significantly smaller than either in 1980 and 1996 (but not 1990). The other three body size values did not significantly differ from each other, although 1981 was smaller than either 1980 or 1996 (Fig. 1 and Table 1).

In the moderately polluted area, there is a decreasing trend, but this consists only of a drop from the first year's higher value to a lower level in the following year. Ten years later, this level is somewhat lower, now becoming significantly smaller than the corresponding value for 1980 (but not the more variable 1981). This level shows virtually no difference 5 years later (Fig. 1 and Table 1).

In the lightly polluted area, there are no significant time trends. The mean size in 1980 was somewhat larger than in the other 3 years (Fig. 1 and Table 1).

Herbivore species. There were few herbivorous species. The size trend in the severely polluted area showed a zigzag pattern, with some significant differences in the middle years. The initial and final years did not differ. The same appeared in the other two areas, at a somewhat lower level (Fig. 1 and Table 1).

Mixed feeder species. The largest number of species were classified as mixed feeders, and, consequently, this group should contribute considerably to the overall trend. In fact, the trends shown by the mixed feeders were similar to that of 'all species'. This group shows no significant size difference among the dif-

ferently polluted areas in 1980 or 1981. Severely and moderately polluted areas seem to support assemblages that became progressively smaller, more in the severely polluted than in the moderately polluted area. There was no decreasing trend in the lightly polluted area, except a smaller assemblage in 1991 (Fig. 1 and Table 1).

Discussion

This re-analysis further developed the conclusions of Braun *et al.* (2004). Most of the support for the role of the increasing specialisation hypothesis in the organisation of ground beetle assemblages disappears when the feeding behaviour of the species is taken into account.

Our analysis underlines the notion that taxonomic units rarely correspond to ecological units, and it is rarely justified to consider them as such. Considering the mean size of ground beetles in general may give rise to a statistical artefact. This is due to the oversimplified classification of the family as predators. Considering natural history is essential for the correct ecological interpretation of patterns in nature. Carabids can conveniently be collected by a single method as most of the species, at least in the northern temperate region (but not in the tropics, see Erwin, 1979), have surface-active adults. Traditionally, carabids have been considered predators, but even Thiele (1977) stressed that this can be a misleading simplification. Results published since the early 70s fully support this suggestion (Lövei and Sunderland, 1996; Toft and Bilde, 2002). Consequently, the approach followed by Braun *et al.* (2004) is of limited value, and in need of further development. The different feeding types of ground beetles should be considered separately and it was demonstrated that this indeed changed the time-size relationship. It is ecologically more valid to consider the changes in size and the assumed resource partitioning with at least

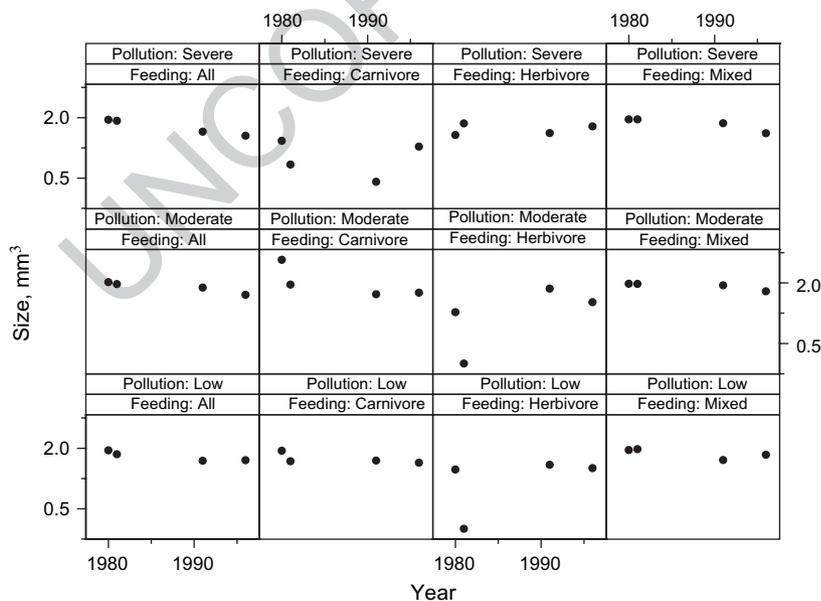


Fig. 1. Size trends (biovolume, mm^3) of ground beetle species captured in three areas under different pollution levels near a fertiliser factory, Germany, in 4 years between 1980 and 1996. Data from Braun *et al.* (2004).

Table 1. Results of the one-way ANOVA for the ground beetle species collected in the severely, moderately, and lightly polluted areas in 1980, 1981, 1991, and 1996, near a fertiliser factory, Germany. Data from Braun *et al.* (2004)

Source	SS	d.f.	MS	F	P	Tukey-test
All species, severely polluted area						
Year	79.855	3	26.618	93.023	< 0.001	1980 = 1981 > 1991 > 1996
Error	1092.223	3817	0.286			
Total	11937.437	3821				
All species, moderately polluted area						
Year	7.279	3	2.426	15.992	< 0.001	1980 = 1981 = 1991 > 1996
Error	71.312	470	0.152			
Total	1647.199	474				
All species, lightly polluted area						
Year	4.588	3	1.529	9.386	< 0.001	1980 > 1991; 1980 > 1996
Error	118.786	729	0.163			
Total	2311.356	733				
Carnivore species, severely polluted area						
Year	68.275	3	22.758	56.302	< 0.001	1980 > 1991; 1996 > 1991
Error	191.194	473	0.404			
Total	794.861	477				
Carnivore species, moderately polluted area						
Year	4.069	3	1.356	3.976	0.009	1980 > 1991; 1980 > 1996
Error	48.440	142	0.341			
Total	521.016	146				
Carnivore species, lightly polluted area						
Year	0.942	3	0.314	1.465	0.224	
Error	66.863	312	0.214			
Total	956.640	316				
Herbivore species, severely polluted area						
Year	4.155	3	1.385	24.174	< 0.001	1996 > 1991
Error	50.995	890	0.057			
Total	2497.278	894				
Herbivore species, moderately polluted area						
Year	4.923	3	1.641	30.136	< 0.001	1991 > 1996
Error	4.847	89	0.054			
Total	249.327	93				
Herbivore species, lightly polluted area						
Year	2.430	3	0.810	12.819	< 0.001	not performed*
Error	4.423	70	0.063			
Total	175.991	74				
Mixed feeding species, severely polluted area						
Year	51.720	3	17.240	72.583	< 0.001	1980 > 1991; 1980 > 1996, 1981 > 1996, 1991 > 1996
Error	580.979	2446	0.238			
Total	8645.298	2450				
Mixed feeding species, moderately polluted area						
Year	1.447	3	0.482	9.555	< 0.001	1980 = 1981 = 1991 > 1996
Error	11.713	232	0.050			
Total	876.856	236				
Mixed feeding species, lightly polluted area						
Year	3.370	3	1.123	9.220	< 0.001	1980 = 1981 = 1996 > 1991
Error	41.419	340	0.122			
Total	1178.725	344				

*Too few individuals in 1980 and 1981.

the different feeding types separately. The assumptions of feeding categories are crucial, and future studies refining these categories (for example, the extent of carrion feeding in carabids, which currently is not well understood, Lövei and Sunderland, 1996) might lead to still different results.

When seeking explanations for assemblage organisation, single-group studies can lead to spurious results. In the case of carabids, spiders and ants should be considered, as they have a significant impact on ground beetles (Thiele, 1977; Lövei and Sunderland, 1996).

A further, modulating influence on assemblage organisation is the permanence of species in a habitat. Species presence is often taken as an indication that the species can find all its needs and survive in the habitat. The presence of non-resident species, termed tourists, transient or occasional species in ecological communities, however, is frequent (Magurran, 2003). Such species do not have sufficiently tight links to the habitat where found, and even though their ratio can be high (Novotny and Missa, 2000), they are not legitimate members of the ecological community. Considering all species captured as integral components of the ecosystem is debatable. Species presence is not necessarily permanent, and community organisation could be better understood if permanent and transient species are identified and separated (Magurran and Henderson, 2003). The latter may have little explanatory power in the search for assembly and resource distribution patterns (Magurran, 2003). Size trends could be different also in this case if we could separate permanent from temporary species in the present case but this is not possible due to the non-continuous sampling.

Braun *et al.* (2004) termed the hypothesis that increasing disturbance causes the average size of ground beetles to decrease in a habitat as 'Blake *et al.* hypothesis'. The same idea, although formulated a little differently, was suggested in 1983 by Jan Szyszko, who studied the possibility of characterising pine forest regeneration by using an index of 'mean individual biomass' (Szyszko, 1983). His hypothesis, while formulated as 'decreasing disturbance allows greater average body size', is essentially the same as in Blake *et al.* (1994). Therefore, in accordance with scientific priority, we suggest that this hypothesis should be termed the 'Szyszko-hypothesis', or 'increasing average size hypothesis'.

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