Predators are rare even when they are small

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A recent review of published studies revealed that predators generally have lower population densities than non-predators in a variety of communities. We report here similar results for a highly replicated study of macroinvertebrates that colonized very uniform detrital microcosms in an old field. This pattern persisted even though predators usually were smaller than non-predators, as determined by body length and volume.

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One tenet of animal ecology is that the number of individuals at a given trophic level will decrease with an increase in trophic rank because energy that is conserved through each link is minimal (Whittaker 1970). This leads to the expectation that predators should be rare or less abundant than non-predators in community assemblages. Spencer (2000) examined the issue of rarity among predators by analyzing published data for a variety of invertebrate communities. He found that predators make up a small proportion of individuals in most communities, but they comprise a higher proportion of species than expected from the observed number of predatory individuals. This was anticipated for plant-based communities because of the bottom-up effects exerted by antiherbivore defenses of plants on the abundance-frequency distributions of herbivore guilds (Maierana and Van Valen 1991). But Spencer (2000) also found this community-wide pattern for predators and non-predators in detritus-based ecosystems in which the primary energy source (dead organic matter) is relatively undefended.

When structuring food webs within communities, predator-prey relationships are often determined by size. Diets of predators are often restricted by the size of their prey. The cascade model put forth a hierarchical, predator-prey based food web, and it was later proposed that this hierarchy is mediated by body size (Warren and Lawton 1987, Cohen et al. 1990). However, exceptions to this rule exist, as in the case of parasites. But if predators are indeed rare and the amount of energy conserved from one trophic link to the next is minimal, then it would follow that predators should also comprise less biomass or energy in a community than non-predators. Spencer (2000) recently developed a model that predicts the proportion of predatory species will probably be higher than the proportion of predatory individuals if the size of predators is equal to or larger than their prey.

However, if predators in a detritus-based community tended to be smaller than their prey, then under certain circumstances predators might not be rare, according to Spencer’s (2000) model. Our long-term studies of leaf litter invertebrates found in Missouri’s Ozark forest ecosystems suggest that predators may often be smaller than their prey in nature (J. Carrel and J. Weaver unpubl.). We decided to test this hypothesis using macroinvertebrates present in detrital microcosms because this approach allows precise control over environmental variables and ease of replication in a semi-natural setting (Fraser and Keddy 1997).
Methods

Detrital microcosms

We sampled communities of macroinvertebrates in this study from a subset of a large array of detrital microcosms \((N = 400)\) established 2 yr earlier for teaching and research purposes in a common plot outside the Botany Research Greenhouse at the Univ. of Missouri. Each microcosm was assembled in a 2-L polycarbonate plastic beverage bottle after we cut off the top and drilled three small holes into the bottom for drainage. In July 1998, to each bottle we added 0.5 L of soil made by thoroughly mixing equal parts of dry Freeburg silt loam, which we scraped from the upper 5 cm in a nearby plowed field, and dry Missouri River sand. Subsequently we added 0.5 L of composted mulch, prepared from yard wastes by the City of Columbia Public Works Dept, to each bottle before placing all of the bottles upright, side-by-side in a fenced field undergoing secondary succession to a savannah habitat. Once in place, the bottles were topped up in July and again in October, 1998 with \(\sim 1\) L of grass clippings and newly fallen tree leaves, respectively. The microcosms were exposed to the same weather conditions for 2 yr in the field, but they were not treated or disturbed by anyone until we retrieved them. As a control, we inspected the contents of some bottles \((N = 24)\) after they had been in place for only 1 d in the field and found that the microcosms were devoid of macroinvertebrates \((<1\) individual/bottle). Hence, all animals subsequently found in a microcosm were the product of colonization.

Macroinvertebrates

On 29–30 August 2000, we brought 24 microcosms from the field to our lab where we manually sorted through the contents of each and removed large worms, crickets, beetles, and isopods. Then we separated the leaf litter from the soil in each sample and extracted the remainder of the invertebrates in Tullgren funnels using a standardized procedure (Weaver 1995, Weaver and Heyman 1997). We preserved all invertebrates in 70% ethanol and sorted them to morpho-species within each sample. For identification purposes we used various keys and the extensive collection of leaf litter arthropods \((\sim 900\) morpho-species represented by \(>500000\) individuals) assembled by the Missouri Forest Ecosystem Project (J. Weaver, PI), which is housed in our lab.

For practicality purposes, we counted only animals larger than 1 mm in this study. In addition, ants were not included because of the difficulty in determining what constitutes an “individual” since one worker is not capable of reproducing and could not survive long on its own. For all other species, we counted the number of individuals and determined their trophic habits from published sources. Using this information, we categorized each species as either a predator or non-predator. As given by Spencer (2000), we defined a predator as “any species feeding primarily on living metazoa”. Accordingly, we regarded parasites as predators in the samples in which they appeared.

Data analysis

Using the raw data, we calculated the average \((X \pm SEM)\) number of individuals and morpho-species per microcosm. We also measured body length (from tip of the head to tip of the abdomen) and body width (the widest part of the head, thorax, or abdomen) of macroinvertebrates to the nearest 1 mm. For each morpho-species, if there were more than ten individuals in a sample, then we measured a representative subsample of ten individuals. But if there were ten or fewer individuals, we measured all animals in the sample. We calculated body volume of animals assuming for all intents and purposes that each individual had a cylindrical shape. The proportions of individuals and species for the predators among the samples were then compared as well as the mean body lengths and volumes of the predators and non-predators. We used the Mann-Whitney and the Wilcoxon test to determine significance (Zar 1974), and each sample was treated as an individual data point. Because both statistical tests gave similar results, for simplicity we report here only the Mann-Whitney values.

Spencer (2000) argued mathematically that if the mean body mass of predators \((W_p)\) generally is equal to or greater than that of non-predators \((W_n)\), then one might expect the proportion of predatory species \([p/(1 + p)]\) to be greater than the proportion of predatory individuals \([N_p/(N_p + N_n)]\). Using Spencer’s notation, \(r\) is the number of different size fractions of detritus, \(n\) is the number of non-predator species that can coexist on one size fraction of detritus, \(n\) is the number of non-predator individuals, and \(p\) is the number of predator species that can coexist on one species of non-predator. Therefore, there are \(rn\) species of non-predators and \(rnp\) species of predators. Altogether then, the total number of invertebrates is \(rn + rnp\) and \(rnp/(rn + rnp)\) is the proportion of predator species. In addition, \(N_p\) is the number of predator individuals and \(N_n\) is the number of non-predator individuals. His equation is: \(p \geq e(W_p/W_n)^k\), wherein \(e\) is the trophic transfer efficiency \((\sim 0.1)\) and \(k\) is the size/metabolism scaling constant for invertebrates \((\sim 0.3)\). We wished to evaluate this relationship in cases where predators are generally smaller in size than non-predators. Furthermore, we reasoned that body volume \((V)\) for invertebrates should be approximately an arithmetic function of their body mass \((W)\), assuming for all intents and purposes that the density of invertebrates is...
Table 1. Taxonomic diversity of macroinvertebrates present in detrital microcosms. The number of morpho-species in each order is listed in parentheses.

<table>
<thead>
<tr>
<th>Phylum</th>
<th>Class</th>
<th>Order (Spp.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mollusca</td>
<td>Gastropoda</td>
<td>Pulmonata (1)</td>
</tr>
<tr>
<td>Annelida</td>
<td>Oligochaeta</td>
<td>Opisthobranchi (3)</td>
</tr>
<tr>
<td>Arthropoda</td>
<td>Chilopoda</td>
<td>Geophilomorpha (2)</td>
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<tr>
<td></td>
<td>Diplopoda</td>
<td>Polydesmida (4)</td>
</tr>
<tr>
<td></td>
<td>Symphyla</td>
<td>(unknown) (1)</td>
</tr>
<tr>
<td></td>
<td>Crustacea</td>
<td>Isopoda (2)</td>
</tr>
<tr>
<td></td>
<td>Insecta</td>
<td>Diplopoda (1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Colembola (6)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Orthoptera (2)</td>
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<td></td>
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<td>Blattoidea (2)</td>
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<td></td>
<td></td>
<td>Psocoptera (2)</td>
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<td></td>
<td></td>
<td>Hemiptera (3)</td>
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<tr>
<td></td>
<td></td>
<td>Coleoptera Diptera (3)</td>
</tr>
<tr>
<td>Arachnida</td>
<td>Araneae</td>
<td>Araneae (11)</td>
</tr>
<tr>
<td></td>
<td>Acarina</td>
<td>Pseudoscorpionida (1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Opiliones (3)</td>
</tr>
</tbody>
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constant. Hence, we simply substituted body volume ($V_p$) for body mass ($W_p$) in the aforementioned equation, as follows: $p \geq 0.1(V_p/V_n)^{-0.7}$. We used this equation to calculate the expected proportion of predators for each sample [$p/(1+p)$], and we compared these values with the observed proportion of predators for each microcosm using the Mann-Whitney test or the Wilcoxon test (Zar 1974).

Results

As indicated in Table 1, we found many different kinds of macroinvertebrates among the 24 microcosms. A total of three phyla, eight classes, 19 orders, and 62 morpho-species were represented in our samples. As one might expect, insects were the dominant taxon both in numbers of individuals and in numbers of morpho-species. Because two microcosms lacked any predatory species, we eliminated them from further consideration. On average we found $54.0 \pm 6.3$ [range: 16–137] macroinvertebrates belonging to $10.1 \pm 0.66$ morpho-species [range: 3–14] in a microcosm ($\bar{X} \pm$ SEM).

In the remaining 22 detrital microcosms, as shown in Fig. 1, the proportion of predatory species was significantly higher than the proportion of predatory individuals ($Z = 4.75, P < 0.001$). All of the points lie considerably below the $x = y$ line in Fig. 1. The mean proportion of predatory individuals was 0.09, whereas the mean proportion of predatory species was 0.28.

In our study, predators usually were significantly smaller than non-predators. For example, as shown in Fig. 2, mean body length in predators (5.78 mm overall) in a microcosm was less than the mean length of non-predators (8.76 mm overall) in 16 out of 22 cases ($Z = 2.66, P < 0.01$). This pattern was maintained (see Fig. 3) when we compared the volume of predators and non-predators (33.7 mm$^3$ versus 72.9 mm$^3$ overall) ($Z = 3.25, P < 0.001$).

We found that the average expected proportion of predatory species based on their volume was $0.347 \pm 0.058$ (range: 0.044–0.866). This was not significantly different ($Z = 0.223, P > 0.8$) from the mean proportion of predatory species we found in our samples ($0.278 \pm 0.025$, range: 0.091–0.444). Hence, when predatory species are small in size relative to non-predators in detrital microcosms, on experimental grounds one would expect that predators will be rare, but on theoretical grounds one would expect that the proportion of predatory species would be similar to the proportion of non-predatory species.

Discussion

Our data reflect the same trend reported by Spencer (2000): the proportion of predatory species was higher than the proportion of predatory individuals. This was true in all samples, and it seems to further support the generality that predators are rare. Spencer (2000) suggests one reason for the low abundance of individuals per species for predators is that animals with ‘‘different morphological, biochemical, and behavioral character-
Fig. 2. Mean body length of predators and non-predators in 22 detrital microcosms. The mean body length of all predators (5.78 mm, standard error 0.84 mm) was significantly smaller than the mean body length of all non-predators (8.76 mm, standard error 0.86 mm): Mann-Whitney test, \( Z = 2.664, P < 0.01 \). The line shows equal body lengths of predatory species and non-predatory species.

Fig. 3. Mean body volume of predators and non-predators in 22 detrital microcosms. The mean body volume of all predators (33.7 mm\(^3\), standard error 11.2 mm\(^3\)) was significantly smaller than the mean body volume of all non-predators (72.9 mm\(^3\), standard error 13.4 mm\(^3\)): Mann-Whitney test, \( Z = 3.251, P < 0.001 \). The line shows equal body volumes of predatory species and non-predatory species.

characteristics may . . . evolve to specialize on different kinds of prey\(^4\). In other words, predators will become specialized to feed on certain prey-types causing lower proportions of individuals than species. Special dietary needs along with a low transfer of energy between trophic links (\( e \sim 10\% \)) could account for the biggest reasons explaining the rarity among predators.

On the other hand, the results from the rest of our study indicate that increasing body size with increasing trophic rank may not be a good reason as to why predators are rare. The trends seen in Figs 2 and 3 contradict what has been previously shown with predator versus prey size. Non-predators showed significantly longer body lengths than predators, and this same trend was even more pronounced for the body volumes of the non-predators. The data points in Fig. 2 are clustered around the \( y \)-axis showing that the mean body volume of the predators was very low. The size relationships of predators and prey are usually compared in a pairwise manner. Cohen et al. (1993) compared the body weights and lengths of predators with their respective prey and found that predators are in most cases longer or heavier than their prey. But when the overall lengths, widths, or volumes of predators and non-predators are compared, as in our study, species that may not actually be in the same food web are being compared to each other, potentially skewing the pair-wise trend. Although our data are contrary to the idea that predators are usually larger than their prey, they do suggest that predators are rare in two ways: not only do they have low proportions of individuals per species, but they also comprise less body volume or energy in the ecosystem than non-predators.

In our analysis with Spencer (2000) model, we used the arithmetic mean of the \( V_p \) and \( V_n \) in place of \( W_p \) and \( W_n \), respectively, without weighting these values by the proportion of available energy captured by each species. (We had no empirical data on which to base such species-specific weightings.) This procedure might have introduced an artifact into our calculations that resulted in our theoretical proportions of predators and non-predators being small and not significantly different from the experimental proportions.

One might wonder about the influence of dispersal of macroinvertebrates between microcosms on the outcome of our analyses. Although we did not study this phenomenon, two lines of evidence suggest that intermicrocosm dispersal was limited for most macroinvertebrates. First, as the detritus settled and decayed after we established the microcosms, within six months there emerged a 5–10 cm high wall of smooth plastic at the top of each bottle which served as a barrier to migration for most macroinvertebrates. Second, previous studies of several hundred comparable microcosms side-by-side in a “common garden” array revealed that
neighboring microcosms were as different in community structure as any two microcosms separated by 1–2 m (J. Carrel unpubl.). If dispersal rates were moderate, then one might expect nearest neighboring microcosms to contain a similar assemblage of morpho-species.

Overall, our data indicate that predators have a low abundance of individuals per species and that predators comprise a small amount of the body volume of animals in our detritus communities. Spencer (2000) argues that diet, energy flow, and body size patterns may be sufficient to account for the rarity of predators, and our results seem to agree with this statement except for the trends he points to with respect to body size. In our case, the trend for size is the opposite. The mean body sizes of predators in our communities were smaller than the mean body sizes of the non-predators; this showed a tendency for overall body size to decrease with an increase in trophic rank. However, we reached the same conclusion as Spencer (2000): predators are rare in abundance and energy.

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