BODY SIZE DISTRIBUTION IN PREDATORY LADYBIRD BEETLES REFLECTS THAT OF THEIR PREY

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Abstract. The size distribution of the species of a wide range of plants, herbivores, and carnivores is similar in form, i.e., right skewed when size is plotted logarithmically. In addition to differential extinction and speciation rates, it is argued that allometric constraints determine the efficiency with which resources are converted into offspring, which in turn determines the frequency of species of different body sizes. In looking for a general explanation for the size distribution shown by all organisms, theorists currently tend to favor explanations based on physiological rather than ecological constraints. Of the body size distributions of predatory ladybird beetles in the Palearctic, Nearctic, Ethiopian, and Australian regions, only that for the Nearctic is significantly right skewed. Even within the Palearctic, the form of the distribution differs among countries, with that for Japan significantly right skewed and that for Central Europe significantly left skewed. An analysis of the prey of ladybirds indicates that increasing ladybird size is associated with increase in size and/or mobility of their prey. The smallest species feed on mites, and the largest on caterpillars and beetle larvae. In addition, the ratio of the numbers of species of aphidophagous to coccidophagous ladybirds in the Nearctic and Palearctic regions reflects the ratio of the numbers of species of aphids to coccids in these two regions. The relationships between egg and adult volumes for 61 species, and egg and adult masses for 26 species both indicate that large species lay larger eggs than small species. In particular, the predators of large and/or active prey lay larger eggs than the predators of small and/or slow moving prey. The relevance of these findings to our understanding of the factors that have shaped body size frequency distributions is discussed. In the case of predatory ladybirds it is concluded that the shape of their body size distribution curves is determined by the nature and the relative abundance of their prey, that is, by ecological rather than physiological constraints.

Key words: adult size; body size distribution; coccinellids; egg size; ladybird beetles; prey size.

INTRODUCTION

Most species of ladybird beetles are predatory and feed on insects and mites; the rest feed on higher plants and fungi. Of the predatory species, those that feed on aphids, although very different in size, are similar in shape and appear to partition their resources between soma and gonads similarly (Stewart et al. 1991). That is, they conform to a basic design. Less is known about ladybirds that eat prey other than aphids, but some belong to the same genera and are generally similar in shape to the aphidophagous species. Assuming that all predatory ladybirds share the same basic design, then it is not unreasonable to ask what has determined the shape of the size diversity curve of the predatory species in this taxon.

Although the factors that determine the size of organisms are poorly understood (Haldane 1927) their size is correlated with other attributes such as longevity, reproductive rate, and resource use (Peters 1983, Calder 1984, Harvey and Pagel 1991). Thus, a knowledge of the distribution of body sizes within taxa might indicate differences in overall resource availability or differences in the ways in which resources are partitioned among species (Pagel et al. 1991).

The diversity of body sizes in organisms is thought to be a consequence of a random multiplicative speciation process (Maurer et al. 1992), which can be described by a log normal distribution. The size distributions of the species of a wide range of plants, herbivores, and carnivores are similar in form, i.e., log right skewed (cf. Blackburn and Gaston 1994). This skewness argues against accounting for the distributions purely in terms of speciation and extinction rates (Gould 1988), and stresses the importance of directional changes (Maurer et al. 1992).

Empiricists have tended to view size as optimum for the niche a species occupies (Stanley 1973). In terms of functional biology, the size of phytophagous and predatory organisms is thought to reflect the size of their host plants and prey, respectively; or the structural complexity of habitats acts as a selective filter, allowing the establishment of more small species in more complex habitats (e.g., Elton 1927, Davidson 1977, Kirk 1991, Dixon et al. 1995, Kaspari 1996, Polo and Car-
rascal 1999). Theorists have used the fractal structure of habitats or energetics to explain the evolution of body size distributions. The explanation based on fractal structure (e.g., Morse et al. 1985) only offers a partial explanation as in none of the body size distributions presented does the smallest class contain the most species. Blackburn and Gaston (1994) have championed the energetic model proposed by Brown et al. (1993) to account for the right-skewed size distributions observed in mammals. They argue that allometric constraints determine the efficiency with which resources are converted into offspring, which in turn determines the frequency of species of different body sizes. The peak in the body size distribution is thought to coincide with the body size that is most efficient (100 g), given the additional constraints of energy availability and interspecific competition. Recent studies on the optimum body sizes for bats and insectivores (Jones and Purvis 1997, Symonds 1999), however, do not show the relationships between life history variables and body size predicted by their model. As the evidence for this energy conversion hypothesis is not convincing, Blackburn and Gaston (1996) proposed one extension to this idea and noted an alternative hypothesis already in the literature. Species that show the optimum size are those whose populations are likely to control the greatest proportion of the available energy (“energy control hypothesis”) or the energy controlled should be summed across the total of all the populations of the species of a particular size (“individual energy control hypothesis”). Recently, Kołowski and Weiner (1997) have proposed a model of life history evolution for animals that stop growing when they reach reproductive maturity, in which it is assumed that the rates of energy assimilation, respiration, and mortality scale with body size according to simple power laws. Interestingly, although two of the six ecological parameters in this model are assumed to be normally distributed among species, the model predicts that the distribution of optimal body sizes should be skewed to the right even when body size is logarithmically transformed. The other four ecological parameters were represented by means. If these are varied then most of the predicted body size distributions are still skewed to the right; but a few are now either not significantly skewed or are even significantly skewed to the left (Kindlmann et al. 1999). However, the underlying assumption remains; the important feature is energy conversion. That is, body size distributions are determined more by physiological than ecological constraints. Although most of the size distributions that have been published are right skewed, it is of interest to know how general this is. In addition, the relevance of the energetic model to poikilothermic organisms needs to be established.

In this paper, the size distribution curves for the predatory ladybirds for the four best studied biogeographic regions are presented, i.e., the Palearctic, Nearctic, Ethiopian, and Australian. The analysis is also performed at several geographic scales within the Palearctic. The hypothesis that their size is correlated with the size and/or mobility of their prey, and thus determined more by ecological constraints, is also tested.

**Methods**

**Source of ladybird beetle sizes for regions and countries**

The average body length (size) of each of the species of predatory ladybirds in the Palearctic was obtained from Mader 1926–1955; Belgium from van Goethem 1975; France from Portevin 1931 and Goureau 1974; Portugal from Raimundo and Alves 1986 and Raimundo 1992; Britain from Pope 1953; Central Europe from Fürsch 1967; and Japan from Sasaji 1971. Similar data for the Nearctic were obtained from Gordon 1976, 1985, and for the Ethiopian region from Mader 1941, 1950, 1954. The sizes of the Australian predatory ladybirds were obtained from Crotch 1874, Pope 1989, and R. D. Pope, personal communication. The prey of ladybirds was obtained from the summary in Schilder and Schilder (1928), and compiled from the following sources in the literature: Mader 1926–1937, 1955; Iwata 1932; McKenzie 1932; Collyer 1953; Kamiya 1961a, b, 1965, 1966; Sasaji 1967a, 1968; Hodek 1973; Goureau 1974; and Iablokoff-Khazhorian 1982.

**Egg and adult sizes**

The lengths and breadths of the eggs and adults of ladybirds were obtained from the following sources in the literature: Palmer 1914; Simanton 1916; Davidson 1923; Wille 1926; Iwata 1932; McKenzie 1932; Vesey-Fitzgerald 1940; Bodenheimer 1951; Delucchi 1954; Tawfik 1962; Brettell 1964; Keston 1969; Tranfaglia and Viggiani 1972; Quezada and DeBaCh 1973; Tawfik and Nasr 1973; Maelzer 1978; Chateau 1981; Nsiama She et al. 1984; Longo and Benfatto 1987; Ginting et al. 1992; Vandenberg 1992; and Singh et al. 1993.

In addition, the masses of eggs and adults of 26 species kept in culture at 20°C were obtained by weighing them to an accuracy of ±0.1 mg on a microbalance (Sartorius Supermicro S4, Sartorius AG, Goettingen, Germany).

**Analysis**

The sizes of the predatory ladybirds of four biogeographic regions (the Palearctic, Nearctic, Ethiopian, and Australian) were logarithmically transformed, and the normality, uniformity, and skewness of the size distributions tested (Pearson and Hartley 1966, Dagnelie 1975, Wilkinson et al. 1992). A median test (Siegel 1956) was also applied to determine whether the four data sets differ in their central tendencies.

The logarithms of the sizes were then grouped in six classes of equal interval to determine whether the proportions of species in each size class differed in the four biogeographic regions. The size distribution for
the Palearctic was used as the standard because the coccinellid fauna of this region is the best known. The proportion of ladybird species of different sizes in the Nearctic, Ethiopian, and Australian regions were compared with those for the Palearctic by means of a \( G \) test (Sokal and Rohlf 1995). The size distribution for several countries within the Palearctic was similarly tested. To determine whether the grouping chosen affects the outcome, the four closed size classes used in the analyses were each divided in half; thereby, giving a total of 10 size classes, eight closed and two open. The analyses with this increased number of size classes gave very similar results to those presented. Further division resulted in some size classes having few or no species in them, which confounds further statistical analysis.

**Table 1.** Characteristics of the body-size distribution curves of ladybird species in four biogeographic regions.

<table>
<thead>
<tr>
<th>Region</th>
<th>Number of species</th>
<th>Pearson coefficient of skewness</th>
<th>Median</th>
<th>Kolmogorov-Smirnov test</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palearctic</td>
<td>609</td>
<td>0.0045</td>
<td>0.50</td>
<td>0.52** 0.19**</td>
</tr>
<tr>
<td>Nearctic</td>
<td>424</td>
<td>0.3527**</td>
<td>0.38</td>
<td>0.50** 0.17**</td>
</tr>
<tr>
<td>Ethiopian</td>
<td>379</td>
<td>0.0408</td>
<td>0.54</td>
<td>0.55** 0.17**</td>
</tr>
<tr>
<td>Australian</td>
<td>269</td>
<td>0.0272</td>
<td>0.48</td>
<td>0.52** 0.18**</td>
</tr>
</tbody>
</table>

**Results**

**Size diversity of predatory ladybirds**

*Regional differences.*—The total numbers of species of predatory ladybirds in the Palearctic, Nearctic, Ethiopian, and Australian regions grouped according to size are given in Fig. 1. None of these distributions are normally or uniformly distributed. Those for the Nearctic and Australian regions are weakly right skewed, but only that for the Nearctic is significantly so (Table 1). In contrast, the distributions for the Ethiopian and Palearctic regions are weakly skewed to the left, but not significantly so. That is, the size distributions of predatory ladybirds, although not normally distributed, differ from that of many other organisms in not being significantly right skewed except in the Nearctic. In addition, the value of the median for the Nearctic is significantly the lowest value (Median test: \( \chi^2 = 91.6, \) 3 df, \( P < 0.001 \)). In the Nearctic there are proportionally more small species in the smallest size classes than in the Palearctic, and in the Australian region there are more species in the size category 0.32–0.51, than in the Palearctic. In contrast, it is the number of species in the larger size categories in the Ethiopian region that is greater than in the Palearctic (Table 2). Summarizing, the size diversity curves for predatory ladybirds differ significantly among regions and, although not normally distributed, only that for the Nearctic is significantly right skewed. The Australian and Nearctic regions have

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**Fig. 1.** The size diversity curves for the predaceous ladybirds in four biogeographic regions. Body lengths were originally measured in millimeters.
proportionally more small species, and the Ethiopian region proportionally more large species than the Palearctic region.

**Differences within regions.**—The size diversity curves for six countries within the Palearctic region (Fig. 2) are not normally distributed, and in the case of four countries, not uniformly distributed. More importantly, the distribution for Japan is significantly right skewed and that for Central Europe significantly left skewed. The distribution for Japan also has a significantly lower median (Median test: \( \chi^2 = 12.2, 5 \text{ df}, P < 0.05 \) (Table 3), and compared with the Palearctic, has proportionally more small species (Table 4). That is, the form of the distribution is not similar throughout the Palearctic.

**Prey of ladybirds**

For this analysis, those species of ladybirds for which the prey has been recorded were assigned to one of three body size classes, and the percentages in each size category that feed mainly on mites, coccids, aphids, and chrysomelid and lepidopterous larvae were calculated (Fig. 3). Both this data set and that of Schilder and Schilder (1928) showed the same trend. A greater percentage of the small species, like *Stethorus* and *Scymnus*, feed on mites than of the large species; and similarly for the large species, such as *Ailocaria* and *Pseudosynonychia*, a greater percentage are recorded feeding on chrysomelid and lepidopterous larvae. If the prey of a ladybird is recorded, it is usually only the group to which the prey belongs (mites, aphids, etc.). Therefore, it is difficult to determine the actual size range of the prey in most cases, which is particularly so for aphids and coccids. Another factor is the mobility of the prey. Aphids generally are more mobile than coccids, and large species of ladybirds move faster than small species (Dixon and Stewart 1991). Coccidophagous species of ladybird are, on average, smaller than aphidophagous species (data from Gordon 1976, 1985: \( \bar{x}_{\text{coccid}} = 2.6 \text{ mm}, \bar{x}_{\text{aphid}} = 4.8 \text{ mm}; t = 4.8, 37 \text{ df}, P < 0.01 \)). Therefore, the increasing trend in the percentage of prey made up of aphids with increasing ladybird size (Fig. 3b) is possibly a consequence of both the mobility and the size of the prey.

An examination of the more extensively documented faunas of the Palearctic and Nearctic regions reveals that the ratios of aphid to coccid species in these two regions are significantly different (Table 5: \( \chi^2 = 15.6, 1 \text{ df}, P < 0.01 \)). Although the ratio of aphidophagous to coccidophagous ladybirds in the two regions do not differ significantly, they appear to reflect the prey ratio in the respective regions (Table 5). That is, the difference in the aphid to coccid ratios in the two regions, through its affect on the size of their predators, may account in part for the overall size distributions of the ladybirds in the two regions.

**Relationship between adult and offspring size**

What evidence is there that the offspring of aphidophagous species are larger at birth than those of coccidophagous species? Although the mass of adults and eggs are rarely recorded, the linear dimensions of these stages have been recorded for several species. The values for the volumes (length \times breadth squared) of the eggs and adults of 61 species of ladybirds are plotted in Fig. 4a. The relationship between egg mass and adult mass, based on data for 26 species, is given in Fig. 4b. Both aphidophagous and coccidophagous species appear to follow the same relationship, with large species laying larger eggs than small species. The slopes \( b \) of the relationships in Fig. 4 are similar (\( b_{\text{volume}} = 0.664 \) and \( b_{\text{mass}} = 0.778; t = 0.9127, 83 \text{ df}, P < 0.05 \), and both significantly less than one (\( t_{\text{volume}} = 7.67, 59 \text{ df}, P < 0.001; t_{\text{mass}} = 2.64, 24 \text{ df}, P < 0.05 \) using a \( t \) test. Therefore, both sets of data indicate that the large species lay smaller eggs relative to their size.

**DISCUSSION**

In the search for a general explanation of the shape of size diversity curves, two models have been very seductive. The first is based on the fractal structure of habitats (Morse et al. 1985) and the second on energetics (Brown et al. 1993). The relatively low numbers of small species in well researched groups questions the credibility of the first explanation. The energetics-based model developed for mammals, or a variant of it, is seen as offering the best potential for a realistic description of the forces structuring body size distributions (Blackburn and Gaston 1994, 1996). If it is to be the basis of a general explanation it has to be shown to apply to mammals, birds, and especially to poikilothermic organisms. However, analyses of empirical data for two groups of mammals do not support the prediction of Brown et al. (1993) that the regression of life history variables on body mass will have different slopes on either side of the optimum body mass (100 g), or any other body size. A constraint to testing this model of Brown et al. is the availability for other organisms of measures of acquisition and conversion of energy to reproduction, comparable to those avail-

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**Table 2.** Numbers of ladybird species in six size classes in the Nearctic, Ethiopian, and Australian regions. Each frequency distribution is compared with that from the distribution observed in the Palearctic (\( G \) test).

<table>
<thead>
<tr>
<th>Size class</th>
<th>Expected</th>
<th>Observed</th>
<th>Expected</th>
<th>Observed</th>
<th>Expected</th>
<th>Observed</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \leq 0.14 )</td>
<td>19.5</td>
<td>24</td>
<td>17.4</td>
<td>6</td>
<td>12.4</td>
<td>13</td>
</tr>
<tr>
<td>0.15–0.31</td>
<td>92.6</td>
<td>112</td>
<td>82.8</td>
<td>61</td>
<td>58.7</td>
<td>47</td>
</tr>
<tr>
<td>0.32–0.51</td>
<td>103.0</td>
<td>164</td>
<td>92.1</td>
<td>92</td>
<td>65.4</td>
<td>113</td>
</tr>
<tr>
<td>0.52–0.70</td>
<td>135.1</td>
<td>80</td>
<td>120.7</td>
<td>140</td>
<td>85.7</td>
<td>65</td>
</tr>
<tr>
<td>0.71–0.90</td>
<td>61.9</td>
<td>39</td>
<td>55.4</td>
<td>68</td>
<td>39.3</td>
<td>29</td>
</tr>
<tr>
<td>( \geq 0.91 )</td>
<td>11.8</td>
<td>5</td>
<td>10.6</td>
<td>12</td>
<td>7.5</td>
<td>2</td>
</tr>
</tbody>
</table>

\( (P < 0.001) \)
Table 3. Characteristics of the body size distribution curves of ladybird species in six countries of the Palearctic region.

<table>
<thead>
<tr>
<th>Country</th>
<th>Number of species</th>
<th>Coefficient of skewness</th>
<th>Median</th>
<th>Normality</th>
<th>Uniformity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Portugal</td>
<td>62</td>
<td>-0.0537</td>
<td>0.52</td>
<td>0.53**</td>
<td>0.18*</td>
</tr>
<tr>
<td>France</td>
<td>86</td>
<td>-0.0085</td>
<td>0.46</td>
<td>0.54**</td>
<td>0.16*</td>
</tr>
<tr>
<td>UK</td>
<td>41</td>
<td>-0.1516</td>
<td>0.54</td>
<td>0.52**</td>
<td>0.18 NS</td>
</tr>
<tr>
<td>Belgium</td>
<td>54</td>
<td>-0.2522</td>
<td>0.56</td>
<td>0.54**</td>
<td>0.17 NS</td>
</tr>
<tr>
<td>Japan</td>
<td>146</td>
<td>0.6027**</td>
<td>0.36</td>
<td>0.52**</td>
<td>0.20**</td>
</tr>
<tr>
<td>Central Europe</td>
<td>91</td>
<td>-0.1993*</td>
<td>0.52</td>
<td>0.53**</td>
<td>0.17**</td>
</tr>
</tbody>
</table>

* P < 0.05; ** P < 0.01; NS = Not significant.

Fig. 2. The size diversity curves for the predaceous ladybirds in six countries within the Palearctic region. Body lengths were originally measured in millimeters.

Kozlowski and Weiner’s (1997) model similarly predicts that the distribution of body sizes should be skewed to the right. However, when all the ecological parameters in their model are varied, the predicted body size distributions can be skewed to the right, not significantly skewed, or skewed to the left (Kindlmann et al. 1999) as is observed in ladybird beetles. That the shapes of the size diversity curves for predatory ladybirds vary both within and between regions, however, argues against an explanation in terms of energetics. The energetics-based model does not rule out the possibility that the distributions of body sizes in

able for mammals. An attempt to use this model to predict the optimum body size for aphids, for which the appropriate energetic values exist, gave a very unrealistic value (P. Kindlmann and A. F. G. Dixon, unpublished data).
TABLE 4. The observed (Obs.) and expected (Exp.) frequencies of ladybird species in six size classes in six countries. Each frequency distribution is compared with that expected from the distribution observed in the Palearctic (G test).

<table>
<thead>
<tr>
<th>Country</th>
<th>Size classes</th>
<th>0.15–</th>
<th>0.32–</th>
<th>0.52–</th>
<th>0.71–</th>
<th>0.90</th>
<th>≥0.91</th>
<th>G test</th>
</tr>
</thead>
<tbody>
<tr>
<td>Portugal</td>
<td>Obs.</td>
<td>5</td>
<td>14</td>
<td>12</td>
<td>22</td>
<td>8</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Exp.</td>
<td>2.8</td>
<td>13.5</td>
<td>15.1</td>
<td>19.7</td>
<td>9.1</td>
<td>1.7</td>
<td>2.74  NS</td>
</tr>
<tr>
<td>France</td>
<td>Obs.</td>
<td>1</td>
<td>23</td>
<td>26</td>
<td>27</td>
<td>13</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Exp.</td>
<td>4.2</td>
<td>20.1</td>
<td>22.4</td>
<td>29.3</td>
<td>13.4</td>
<td>2.6</td>
<td>4.48  NS</td>
</tr>
<tr>
<td>Belgium</td>
<td>Obs.</td>
<td>3</td>
<td>8</td>
<td>8</td>
<td>15</td>
<td>6</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Exp.</td>
<td>1.9</td>
<td>8.9</td>
<td>10.0</td>
<td>13.1</td>
<td>6.0</td>
<td>1.1</td>
<td>1.37  NS</td>
</tr>
<tr>
<td>Japan</td>
<td>Obs.</td>
<td>7</td>
<td>55</td>
<td>30</td>
<td>31</td>
<td>19</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Exp.</td>
<td>6.7</td>
<td>31.9</td>
<td>35.5</td>
<td>46.5</td>
<td>31.3</td>
<td>4.1</td>
<td>20.78  ***</td>
</tr>
<tr>
<td>Central Europe</td>
<td>Obs.</td>
<td>4</td>
<td>16</td>
<td>24</td>
<td>32</td>
<td>13</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Exp.</td>
<td>4.2</td>
<td>19.9</td>
<td>22.1</td>
<td>29.0</td>
<td>13.3</td>
<td>2.5</td>
<td>1.41  NS</td>
</tr>
</tbody>
</table>

*** P < 0.001.

groups like ladybirds are dependent on that of the organisms on which they feed. The same is predicted by the Kozlowski and Weiner (1997) model if the assimilatory, respiratory, and mortality rates of the predator

![Fig. 3](image-url)

**Fig. 3.** The percentage of prey consisting of mites, coccids, aphids, and chrysomelids and lepidopterous larvae for species of ladybirds whose adult body lengths, on a logarithmic scale, are <0.2, >0.2 ≤ 0.5, or >0.5. (A) Data from Schilder and Schilder 1928; \( \chi^2 = 38.32, P < 0.001 \). (B) Data compiled from the literature; \( \chi^2 = 74.2, P < 0.001 \). Body lengths were originally measured in millimeters.

![Fig. 4](image-url)

**Fig. 4.** The relationships between (a) the logarithm of the egg volume and that of adult volume for 52 species, and (b) the logarithm of egg mass and that of adult mass for 22 species.
siderably lower than those of similarly sized aphidophagous species. Similarly, if one assumes that the abundance of aphidophagous and coccidophagous ladybird beetles changes little from year to year, and accepts that the fecundity of the latter is lower than that of the former, then the mortality rate of coccidophagous species is also likely to be less than that of aphidophagous species (Dixon 2000). If all the rates which according to Kozlowski and Wiener (1997) determine body size are lower in coccidophagous than in similarly sized aphidophagous species, then their model cannot account for body size distribution in ladybirds. However, more data of this sort needs to be collected with the specific objective of testing the assumptions made by Kozlowski and Wiener (1997).

In the absence of a general model, there is a tendency to seek the directional process that has shaped the size diversity curve of a particular group of organisms. What evidence there is tends to support the idea that each predator only eats prey of a limited range of body sizes (Elton 1927, Sabelis 1992). Elton (1927) saw communities as having a limited membership. This concept was developed further by Hutchinson (1959) who argued that the average body size of two species corresponds to the average size of their prey. That is, there is a partitioning of resources, and empirical data indicated a ratio of 1:1.3 between consecutive sizes. Theoretical analyses of this concept (MacArthur and Levins 1967, May and MacArthur 1972, May 1974) confirmed that a minimum difference in body size (utilization function) is needed for coexistence but no “universal constant” emerged that corresponded to the value of 1.3. That is, in some species morphological traits, including size, accurately reflect differences in resource utilization (Lack 1947, Hutchinson 1959, Peters 1983, Calder 1984). In the case of aphids, the optimum adult size for maximizing the rate of population increase is approximately 15 times the birth size, which is correlated with the depth to which an aphid has to probe specific plant tissues in order to locate phloem elements. That is, the shape of the size diversity curve for aphids is thought to reflect the relative surface area of specific plant structures; i.e., the abundance and structure of their host plants (Dixon and Kindlmann 1994, Dixon et al. 1995).

The size diversity curves for ladybirds are not all right skewed and vary significantly in shape both within and between biogeographic regions. Similarly, the slope of the body size classes above the modal size class must also differ. Compared to the Palearctic, the coccinellid fauna of the Ethiopian region has a greater proportion of large species, while the reverse is true of the Nearctic and Australian regions. How can these differences be explained? Approximately constant ratios of numbers of species of predator to number of species of prey have been recorded for several communities (Jeffries and Lawton 1985, Pimm 1991, Hall and Raffaelli 1993, Begon et al. 1996). That is, the number of prey species determines, in some way, the number of predator species (Pimm 1991). Of our data sets, the Palearctic and Nearctic are the most extensively and reliably documented. In these two regions, the ratios of the numbers of aphids to aphidophagous ladybirds and of coccids to coccidophagous ladybirds are similar (Table 5). As coccidophagous species of ladybird are usually smaller than aphidophagous species, the differences in the ratios of aphids to coccids in the two regions may in part account for the difference in the body size distributions of the ladybirds in the two regions.

In addition to the correlation between type of prey and body size in ladybirds (with mites the prey of mainly the smallest species, and chrysomelid and lepidopterous larvae the prey of mainly the largest species), large species of ladybirds lay significantly larger eggs than small species. Large eggs give rise to large larvae, which move faster and are capable of catching larger and more active prey than small larvae (Dixon 1958, Glen 1973, Sabelis 1992). Life history theory predicts that organisms should optimize the trade-off between number and size of offspring. Thus, the positive interspecific relationship between adult size and offspring size argues for size being adaptive and determined by the need to pursue and subdue their prey. That is, as for aphids, the shape of the body size distribution curve for predatory ladybirds appears to be dependent on the nature and relative abundance of their food resources.

How does this study of predatory ladybirds affect our understanding of the body size frequency distribution? It challenges the notion of the existence of a general relationship, which came from the observation that the frequency distribution for species in body sizes (linear) above the modal size class could be fitted by a straight line with a slope of approximately −2; i.e., a 10-fold increase in size is accompanied by a 100-fold decrease in species number (May 1978). This has stimulated, and continues to stimulate, a lot of interest (cf. Loder et al. 1997), but the results are not supportive of a general relationship in terms of skewness or slope. Similarly, there appears to be little to support an explanation based on energetics. Like ecological efficiency (Slobodkin 1972), the study of the shape of the frequency distribution of animal body sizes appeared to bring the application of more rigorous scientific thinking to ecology. Although body size frequency distributions are undoubtedly interesting, the seeking after generality appears disappointingly and increasingly likely to suffer the fate of ecological efficiency. Therefore, it may be time to ask: what is wrong with accepting that the study of body size frequency distributions indicates the way resources are partitioned among species, and accepting that features of resources other than space and energetics could be important? Explanations in terms of the structure of the trophic level on which organisms depend for food, however, are perceived as less satisfying because they concede
that the structure of communities is governed by a multiplicity of assembly rules rather than by one rule.

This debate was initiated by May (1978) fitting lines to the slopes of body size distributions “more for entertainment than from any sense of conviction.” The generality he was seeking has been slow in coming. Is it not time, therefore, to change the emphasis and consider that generality for many organisms could be in size, with large organisms feeding on large organisms and vice versa? That is, rather than continue with the current trend of focusing on physiological constraints, more attention should be given to looking for the generality in terms of ecological constraints (cf. Witting 1998).

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