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Predator-prey ratios: a special case of a general pattern?

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SUMMARY

Approximately constant ratios between numbers of predator and non-predator ('prey') species have been observed in both community and food web data. However, only a limited set of explanations for the pattern have been considered, and interpretation is complicated by the non-equivalence of the two data types. Analysis of predator-prey ratios for a large and heterogeneous set of community data, drawn from freshwater, marine and terrestrial systems, shows that predator richness is almost, though not exactly, proportional to prey richness across and within habitats, with some suggestion that ratios differ between habitat types. Three existing, and two new, explanations for this result are considered: random draw (influence of the species pool); prey niches (more prey types provide more niches for predators); enemy-free space (the number of prey coexisting with a predator is limited by apparent competition); energy ratios (richness is proportional to available energy at each trophic level); and common determinants of diversity (factors influencing diversity act similarly on predators and prey). Separating these is not straightforward, but the latter two hypotheses have high generality, and component parts of each are supported by available evidence. We suggest that a hierarchy of processes, each of predominant importance at different scales from patches to regions, produces the observed pattern of predator-prey ratios and that, in view of these explanations, predator-prey ratios should be considered as a special case of the general problem of guild structure.

1. INTRODUCTION

Various studies of trophic structure have suggested that numbers of predator species and numbers of prey species are approximately proportional across a range of different communities. Alternatively, the predator-prey species ratio is roughly constant (Evans & Murdoch 1968; Cohen 1977; Briand & Cohen 1984; Jeffries & Lawton 1985; Lockwood *et al*. 1990). Such a pattern, or variants upon it, have been reported both from food web data (Cohen 1977; Briand & Cohen 1984; Sugihara *et al*. 1989); from faunal lists where species can be classified *a posteriori* by trophic habit (Jeffries & Lawton 1985); and from guild structure analyses (Evans & Murdoch 1968; Teraguchi *et al*. 1977, 1981; Moran & Southwood 1982; West 1986; Stork 1987). Although the results from these different data are not necessarily equivalent (a point discussed below), the apparent ubiquity of the observation implies that predator-prey proportionality is a fundamental feature of natural communities and may reflect important functional aspects of such systems. Predator-prey ratios are one of the patterns used to quantify trophic structure with a view to understanding the functioning of food webs (Cohen 1989*a*; Lawton 1989; Sugihara *et al*. 1989), and may be useful in addressing other fundamental issues such as estimating the magnitude of global species richness (May 1988).

Evidence for a correlation between predator and prey species richness has come to date from a few rather disparate data sets, and explanations for the pattern have been discussed more or less independently of each other, with no clear agreement on the most plausible proposal (Cohen 1989*a*; Lawton 1989; Pimm *et al*. 1991). Such work raises two main questions. Firstly, is the pattern consistent across different types of system, sampled at differing spatial and temporal scales; or are the values of the predator-prey ratios system- or scale-dependent? Secondly, what processes might account for the pattern?

Our purpose here is to assess the relation between predator and prey species numbers, using a combination of new and previously reported data for a range of ecosystems, and examining both the overall and within-habitat patterns. We then review three existing hypotheses proposed to account for the pattern, suggest two alternative, or complementary, explanations, and evaluate the predictions of all these ideas with respect to available data. First, however, it is necessary to briefly discuss definitions and data.

(*a*) *Definitions*

Although they are generally cited together, distinction must be drawn between predator-prey ratios derived from food web data and those derived from

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faunal lists or guild analyses (see also Closs 1991). They are neither the same, nor directly comparable. The 'prey' in food web analyses are basal resources (e.g. producers, detritus) plus any consumer species, predatory or non-predatory, which themselves are fed upon by one or more other species in the web (Cohen 1977). 'Prey', thus defined, potentially includes plants, detritus, detritivores, herbivores and carnivores. This contrasts with the definition used in faunal list and guild studies where 'prey' are simply non-carnivore consumers (Jeffries & Lawton 1985). Obviously the definitions of a predator must be correspondingly different: 'predators' in food webs include all consumers; in faunal lists and guild studies they are carnivores only (typically including parasites and parasitoids). These definitions result in fundamental differences in the data. In food webs, species can be both predator and prey (Cohen 1977), and the designation of a species may change as a result of the presence or absence of another species in the web. For example, the addition to a web of a carnivore that feeds on an existing top predator in the web will mean that the latter predator also becomes a prey species. A three-level classification of species as 'basal' (those that feed on no others), 'intermediate' (those that feed upon, and are fed upon by, others) and 'top' (those that feed upon, but are not fed upon, by others) removes the problem of species being both predator and prey (Briand & Cohen 1984). However, species designations still depend upon others (e.g. top species may become intermediate species by the addition to the community of a consumer feeding upon them). Moreover, top and intermediate species cannot necessarily be equated with predator and prey as defined in faunal list or guild studies (e.g. a herbivore may be a top species), and these kinds of studies do not include basal species at all. An additional complication is that many food web analyses actually deal in trophic 'species' (an aggregate of taxonomic species having identical predators and resources), whereas other studies follow a more conventional, taxonomic definition of species.

A further point of definition is that the term 'constant' as widely used in discussions of predator-prey ratios, generally means scale invariant (i.e. independent of total species number) and does not imply any formal measure of the variance of the ratio.

2. EMPIRICAL PATTERNS

(*a*) *Data and Methods*

As predator-prey species ratios derived from food web analyses are not equivalent to those derived from faunal lists, we restrict our analyses to data from the latter source. We follow precedent for such studies (Jeffries & Lawton 1985) in defining predators as species that feed predominantly on living metazoa, and prey (or more properly, non-predators) as those species feeding upon dead or non-metazoan resources (i.e. plants, detritus and associated microbial flora). Data were drawn from a variety of published and unpublished species lists and analyses of guild structure, for habitats ranging from ponds and streams to tropical and temperate forest canopies (see Appendix 1). Studies were restricted to those where most taxa were identified to species level, or OTUs; where higher levels of classification occurred in otherwise good lists the taxon was counted as two species unless there was explicit indication that only one species was present (following Jeffries & Lawton 1985).

Where possible, the data were taken from sources where predators and non-predators were classified as such in the original study; however, for freshwater invertebrates, where trophic habits are relatively well known, we were able to classify predators and non-predators directly from species lists, using information from various sources (e.g. Merritt & Cummins 1978). Species generally recorded as omnivores (in the sense of feeding on both plant and living animal material) were treated as non-predators, unless the literature suggested that their principal food habit was predatory. Most of the studies we have used focus on invertebrates and consequently either ignore or only inconsistently record the presence of vertebrates. Because of this, and the small numbers of vertebrates involved, we have excluded them from the analyses. For similar reasons microinvertebrates, such as rotifers and protozoa in freshwaters, have also been excluded from the few studies that recorded them. The data represent communities sampled on a variety of temporal and spatial scales from single samples to cumulative species lists over many sites and dates. We have divided the data into two groups: summary data, cumulative lists over several different types of site in an area and over several dates; and non-summary data, samples from a single site, or single habitat type within an area, on one, or sometimes more than one, sample date.

Data were also classified according to habitat. Although we found data for terrestrial, freshwater and marine systems, the representation of habitats within those types is far from balanced. Freshwaters provide the widest range of systems, further classified as flowing or still waters; the bulk of these are temperate. Terrestrial systems are represented predominantly by communities from trees, both temperate and tropical. Marine systems, with the exception of one tropical intertidal community, are from temperate, shallow water benthic habitats.

Evidence of predator-prey proportionality has generally come from observation of a linear relation between predator and prey species numbers (e.g. Cohen 1977; Jeffries & Lawton 1985; Jenkins & Kitching 1990). Determination of the form of such a relation by means of ordinary least squares regression may, however, be inappropriate as there are undoubtedly errors associated with both variables, and neither is obviously the independent variable. This problem has been treated in various ways in predator-prey ratio studies (e.g. Jeffries & Lawton 1985; Lockwood *et al.* 1990). McArdle (1988), in a comparative study of methods for estimating the 'structural' relation between two variables, suggests that where error variances on both variables are (as here) unknown but likely to be similar, or in proportion to the underlying

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variances, the reduced major axis or geometric mean regression (Ricker 1973) may be the most appropriate technique, as it is reasonably insensitive to violation of assumptions about error structure.

Another question in the interpretation of a linear relation (and in particular a 'constant' ratio) between predator and prey species numbers concerns the intercept of the line. It has been suggested that the relation should pass through the origin and that any deviation in the intercept is an indication of bias due to behavioural, population dynamic or sampling effects (Lockwood *et al.* 1990). However, we see no compelling reason why this should necessarily be so. Although communities of predators without prey may be unreasonable (aeolian and other 'tourist-fed' communities aside), small communities of prey without predators are quite possible (e.g. Kitching & Pimm 1985). Even if the relation is linear, if the y-intercept is non-zero the ratio (predator:prey species) estimated from such a relation will not be scale invariant; at low species numbers it will be dominated by the effect of the intercept. Thus, scale invariance of the predator-prey ratio may be affected either by a genuine lack of proportionality (i.e. a curvilinear predator species against prey species relation), or by a non-zero intercept. Untangling these two possibilities, which have rather different biological implications, is not easy.

Given these considerations we assessed the strengths of relations using correlations and the slopes using reduced major axes (Ricker 1973; Clarke 1980; McArdle 1988). Because the reduced major axis is equivalent to the first principal component of the correlation matrix of the data (McArdle 1988), the pattern of 'residuals' (in this case perpendicular deviations) about the line was obtained from the scores on the second principal component of such an analysis. A logarithmic transformation ($\ln[n+1]$) was used to counter both skew and heteroscedasticity in the predator and prey data; the effect of the (+1) correction for zeros should be minimal, given the values of most of the data. The use of a log transformation does not, however, imply that the original, arithmetic, relation was expected to be curvilinear.

(*b*) *Results: the basic patterns*

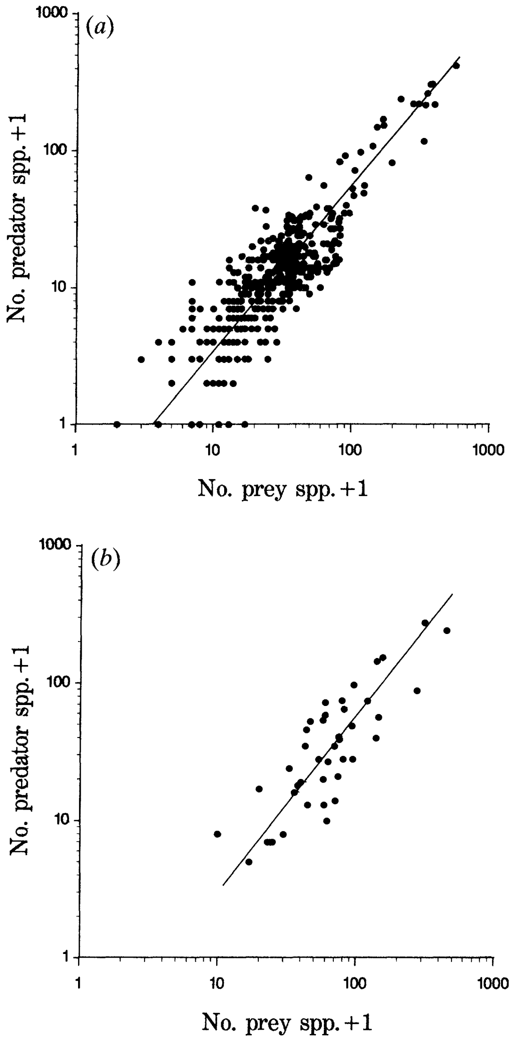

Figure 1. The relation between $\log(x+1)$ predator richness and $\log(x+1)$ prey richness with fitted reduced major axes (RMA) for (*a*) all non-summary data ($b_{[\mathrm{RMA}]} = 1.22$, $r = 0.85$, $n = 389$, $p < 0.0001$); (*b*) all summary data ($b_{[\mathrm{RMA}]} = 1.29$, $r = 0.83$, $n = 42$, $p < 0{\cdot}0001$).

The relation between predator and prey species number, across all habitats, is shown in figure 1. Despite the diversity of studies from which the data are drawn, the relation between log (predator species + 1) and log (prey species + 1) is remarkably good and is described reasonably well by a single straight line (figure 1). Because many of the studies contributed several observations, the data points are not wholly independent, hence significance levels are overestimates. However, five analyses of the same relation, using in each case randomly selected single observations from each study, yielded a range of values entirely consistent with those from the full data set ($b_{[\mathrm{RMA}]} = 1.19$ to 1.37; $r = 0.82$ to 0.89, $n = 35$, $p < 0.001$). The slopes of the reduced major axes in both summary and non-summary data are slightly, and significantly, greater than 1, again with the proviso that there is some non-independence in the data (non-summary data: $T = 7.4$, d.f. $= 286$, $p < 0.001$; summary data: $T = 2.9$, d.f. $= 31$, $p < 0.01$ (Clark 1980; McArdle 1988)).

The mean predator: prey ratio is 0.46 (s.d. = 0.27), i.e. roughly 31% of animal species in the community are predatory. However, as the slope of the fitted line suggests, proportions of predators are not entirely constant. Values range from a mean of 0.24 (s.d. = 0.14) for species-poor communities (fewer than 21 species (the lower quartile)) to 0.33 (s.d. = 0.1) for species-rich systems (more than 61 species (the upper quartile)); and in the most species-rich communities (number of species > 200) the proportion of predators averages 0.46 (s.d. = 0.07). This pattern, interestingly, contrasts with Jeffries & Lawton's (1985) observation for freshwater communities of a slight decrease in the proportion of predators in larger communities.

The data can also be examined by habitat. Predator and prey richness are significantly correlated in each habitat type (figure 2*a*,*b*). The slopes of the

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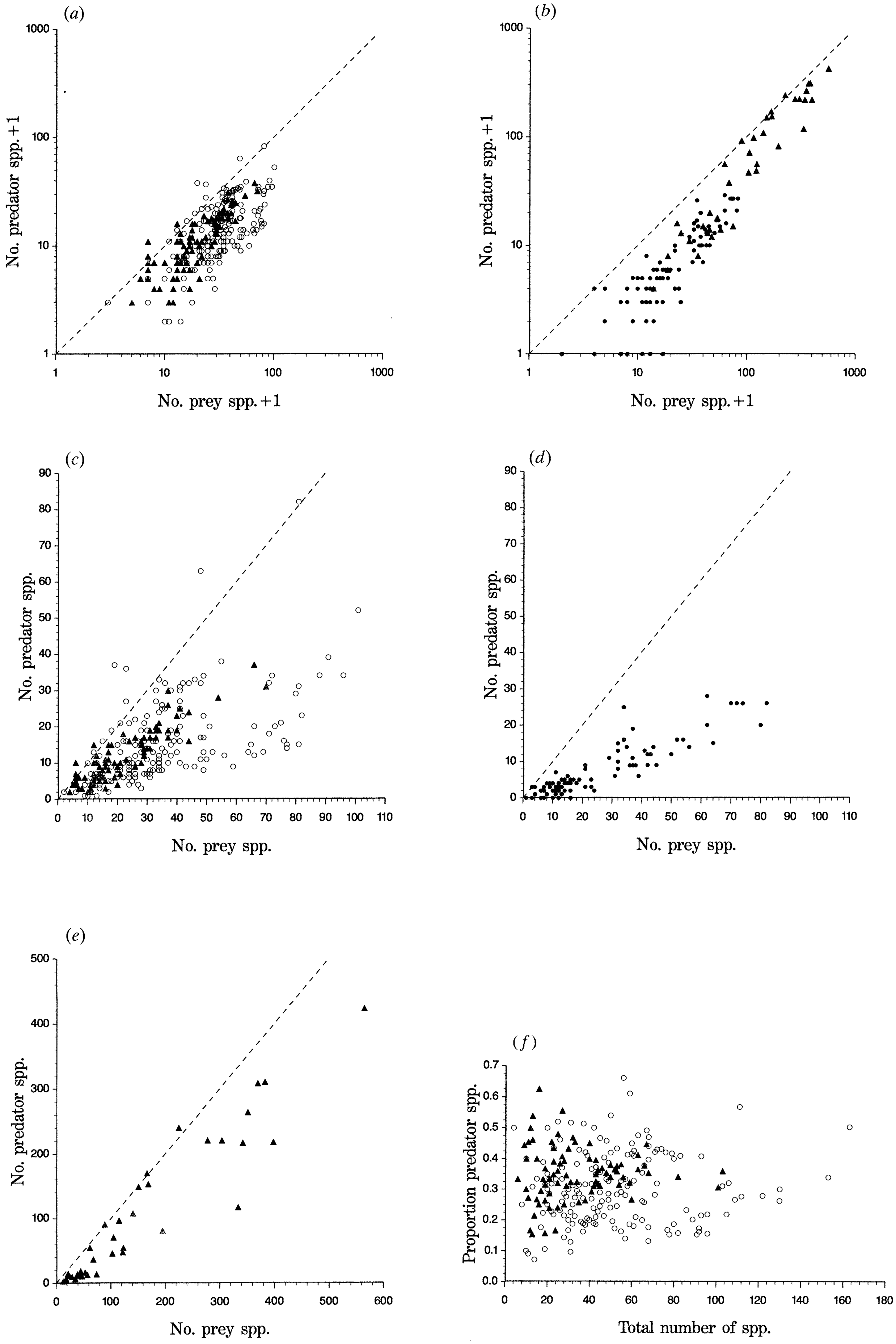

Figure 2(*a*–*f*)

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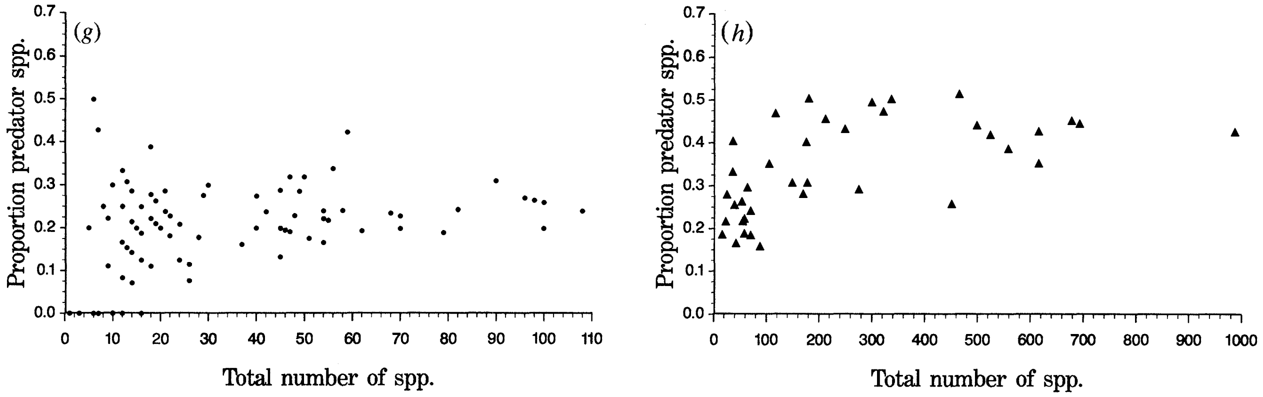

Figure 2. The relation between predator and prey richness on logarithmic ($\log[x+1]$) axes (*a*,*b*) and arithmetic axes (*c*–*e*) and between the proportion of species that are predators and total species richness (*f*–*h*). (*a*,*c*,*f*) freshwaters (solid triangles, still water; open circles, flowing water); (*b*) marine (solid circles), terrestrial (triangles); (*d*,*g*) marine; (*e*,*h*) terrestrial. (The broken lines in (*a*–*e*) indicate equal predator and prey richness.)

reduced major axes are again slightly higher than one; significantly so in the case of lotic systems ($b_{[\mathrm{RMA}]} = 1.18$, $T = 2.85$, d.f. = 139, $p < 0.01$), marine systems ($b_{[\mathrm{RMA}]} = 1.18$, $T = 2.89$, d.f. = 69, $p < 0.01$), and terrestrial systems ($b_{[\mathrm{RMA}]} = 1.35$, $T = 6.5$, d.f. = 27, $p < 0.001$), but not in the case of lentic systems ($b_{[\mathrm{RMA}]} = 1.04$, $T = 0.69$, d.f. = 66, $p > 0.05$).

These results suggest that predator richness increases slightly faster than prey richness, i.e. that predator and prey species numbers are close to, but not strictly, proportional.

As already mentioned, such a result could be generated most simply by either a continuously curvilinear predator species against prey species relation or by a linear relation which does not intercept the y axis at zero. The arithmetic plots of predator against prey species numbers (figure 2*c*,*d*,*e*) do not suggest clear curvilinearity in any of the habitat types, but there is some tendency for small communities to have prey but few or no predators. Reduced major axes of the arithmetic plots have negative y-axis intercepts in all cases, and lentic systems, which have a slope not significantly different from one, have an intercept closest to zero. Simple plots of the proportion of species that are predatory against total numbers of species (figure 2*f*–*h*) show that proportions of predatory species are scale invariant over much of the range, but there is a tendency for small communities within each habitat type to have lower proportions of predators (again with the exception of lentic systems).

We conclude that, for this data, predator and prey species richness are close to, but not exactly proportional; predator richness increases slightly faster with total species numbers than does prey richness. The effect appears mainly due to a marked tendency for smaller communities to have few predator species, and the proportion of predators being roughly scale invariant in larger systems.

It is apparent from figure 2 that there may be differences in the patterns of predator-prey richness between different habitat types. The highest predator-prey ratios occur in freshwater systems, which also have the greatest variation. Marine communities appear to be consistently more prey dominated than freshwater or terrestrial ones (figure 2*c*,*d*) . Comparison of flowing and standing freshwaters (figure 2*a*,*c*) indicates that standing waters have quite a good correlation of predator and prey species, and tend to have a high proportion of predators; flowing waters are much more variable, from rather more predator rich to considerably less. As already discussed, standing waters appear to have the most scale-invariant predator-prey ratios, by virtue of the smaller communities from such habitats not showing a decline in predator richness. The mean 'residuals' (see Methods) from the reduced major axis for data in the range in which at least two habitats occur are shown in figure 3. If the data are treated as independent points the differences in mean residuals are significant (ANOVA: $F_{[3,356]} = 11.7$, $p < 0.001$), but using the sets of randomly chosen independent points, when subdivided by habitat, gives very small sample sizes, and only one of the five data sets yields a significant effect of habitat ($F_{[3,28]} = 3.07$, $p < 0.05$). The appropriate level of independence must lie somewhere between the two extremes, but at this stage we can only say that the data suggest some systematic differences in the predator-prey ratios between habitats.

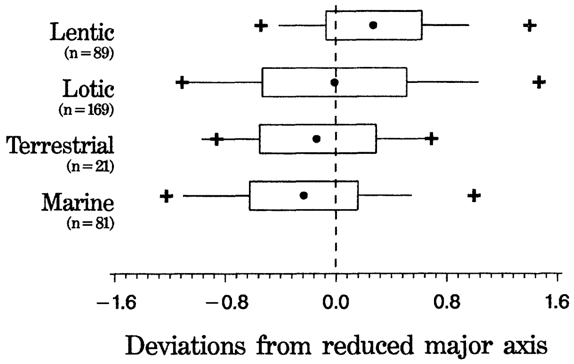

Figure 3. The mean deviations (solid circles) of each major habitat type from the RMA (measured as the second principal component score) for all non-summary data for the range in which at least two habitats overlap (from figure 1*a*) (box, 1 standard deviation; whisker, 2 standard deviations; cross, maximum or minimum). Positive deviations indicate more predator-dominated systems.

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A final point we would note about the relation in figures 1 and 2 is that the upper bounds of the data for all habitats correspond closely to the line of equal predator and prey richness. Although there is considerable scatter in the data below this line, very rarely are there more predator species than prey.

3. EXPLANATIONS

(*a*) *Existing hypotheses*

With respect to data deriving from species lists, or guild studies, we are aware of three ideas that have been proposed to account for predator-prey correlation. These are summarized below. We also note the relation between Cohen & Newman's (1985) 'cascade model' of food webs and explanations of the predator-prey relation.

(*i*) *Random draw*

Cole (1980) suggested that the apparent constancy in the proportions of predatory (entomophagous) and non-predatory (herbivorous) species of grassland arthropods through a season, observed by Evans & Murdoch (1968), need not result from trophic constraints, but might instead reflect the structure of the species pool from which the species were drawn. The 'random draw hypothesis' essentially suggests that predictable patterns of trophic (or other) structure may arise because the pool of available colonists itself has certain characteristics (e.g. a particular ratio of predator to prey species) and, irrespective of interactions within the community, even a random sample of species from that pool will reflect something of this structure. One problem with this explanation is that it assumes constancy in the characteristics of the species pool from which species are drawn, but leaves unanswered the question of what determines that constancy (Van Valen 1982).

(*ii*) *Predator food niches*

Types of prey are one niche axis along which predator species may be arranged; where prey 'types' are groups of prey with similar sets of general characteristics (such as size, colour, habitat use, etc.). More prey types may result in more predator types either by reducing competition (by allowing predators to become more specialized and thus reducing niche overlap) or simply by the provision of resource types not previously present, allowing predators dependent on these resources to enter the system. Arnold's (1972) analyses of predatory snakes and their prey showed that predator species richness seemed to be related most strongly to the richness of the particular prey types upon which they depended, from which he concluded that snake diversity was largely determined by the diversity of prey. A variant on this hypothesis (Tilman 1986) suggests that the proportionality of basal, intermediate and top species in food web data may result from the interplay of competition and predation; the number of predators being determined by the number of prey types and the number of prey types coexisting on one resource being determined by the number of predators, through predator mediation of competition. This balance requires particular relations between competitive ability and predation vulnerability in the species concerned.

(*iii*) *Competition for enemy-free space*

Jeffries & Lawton (1984, 1985) proposed that, although the number of predator species may be influenced by the number of prey types, strong correlations between predator and prey species would be expected only if the number of prey species coexisting with each predator species was in some way limited. This could result from polyphagous predators causing 'apparent competition' (Holt 1977) for enemy-free space among prey species (Jeffries & Lawton 1984, 1985). In other words, prey species of dissimilar types to those already in the community will tend to establish more successfully because they are less likely to be vulnerable to attack from established predators.

Mithen & Lawton (1986) have examined this hypothesis using models of communities with two trophic levels. Their simulations of community assembly with such models do indeed produce correlated predator-prey richnesses and, equally critically for the hypothesis, the successful invaders are less similar to the prey species already in the community than are those that fail to invade (Mithen & Lawton 1986).

(*iv*) *Cascade model*

The stochastic 'cascade model' of food webs (Cohen & Newman 1985) appears to account reasonably well for the proportionality of basal, intermediate and top species in food webs (see, for example, Cohen *et al.* 1985; Cohen 1989*a*; Warren 1989). This raises the question: does it make any predictions about predator-prey proportionality in other data? Although, for the reasons discussed earlier, the conclusions relating to food web data do not necessarily imply the same results in species list or guild data, the cascade model does, at first sight, appear to predict proportionality in the latter also. The model is based on two assumptions: a trophic hierarchy where species can be arranged in a sequence such that they can only feed on (any) others below them in that sequence; and a fixed probability of a feeding link between any two species (see Cohen & Newman 1985; Cohen 1989*a*; Lawton 1989). As basal resources tend to occur towards the bottom of the hierarchy then, on average, animals close to the bottom of the hierarchy are more likely to have feeding links to basal resources (i.e. to be prey) and those at the top more likely to have links to prey than to basal resources (i.e. to be predators) as a large proportion of the species below them are prey. Thus, the probability of a species being predator or prey is determined by its rank in the hierarchy (for a given connectance level) and so proportions of predator and prey species are likely to remain roughly constant in different models. However, as the probability of a species being predator or prey is dependent on its position in the hierarchy, and the hierarchy is assumed, this is equivalent to drawing species from a pool in which there are fixed proportions of predators

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and prey; this explanation is thus more or less equivalent to hypothesis (i), though is perhaps a weaker constraint.

(*b*) *Additional hypotheses*

In addition to the hypotheses above we suggest two further potential explanations which as far as we are aware have not been proposed with respect to predator-prey ratios.

(*i*) *Energetic/population density ratios*

The trophic explanations proposed so far (hypotheses (ii) and (iii), above) have been based on a niche oriented view of communities. However, a rather different trophic explanation can be suggested based on energy availability. Although the value of the trophic level concept as a description of community function is a matter of debate (see Peters 1977; Cousins 1987; Burns 1989), in the simple case with which we are concerned here its application is unambiguous. Prey are all those species feeding on basal resources ('level 2') and predators feed upon prey (or other predators) ('levels 3+'), forming two mutually exclusive sets. Within any community there will be more energy available to the prey level than the predator level and this difference in energy might be expected to be manifest in the biomass or total abundance of organisms at each of the two levels. The nature of the difference in biomass or abundance will depend on generation times or biomass turnover rates at each level, however, 'predators' and 'prey' in most communities represent heterogeneous sets of taxa of varying, and often overlapping, generation times, body sizes etc. whose collective biomass turnover rates will therefore tend away from the extreme high or low values of particular taxa, though differences may occur between particular types of system. Assuming some generality in the magnitude of energy loss between the levels the result will be an approximate proportionality between biomass or total number of individuals at prey and predator levels. If higher energy availability allows more populations of viable size (Lawton 1990) (i.e. more species), and energy ratios between trophic levels are roughly constant, we might expect to see an approximate proportionality of predator and prey species richness.

There is theoretical and empirical support for a positive (though not necessarily linear) relation between the number of individuals and number of species in a community and, to a lesser extent, across communities (Preston 1948, 1962; Yount 1956; Williams 1964; May 1975; Southwood *et al.* 1982; Stork 1991). The exact form of the relation depends on the distribution of species' relative abundances, for which a variety of models, some with a biological basis, others purely statistical, have been proposed (see reviews in May 1975; Hughes 1986; Gray 1987; Magurran 1988; Tokeshi 1990). One well established derivation from such species-abundance models is the species-area relation; the number of species expected in an area can be predicted from a particular species abundance model (usually the lognormal or log series distribution) with the assumption that the total number of individuals in the community is proportional to the area (Preston 1962; May 1975; Diamond & May 1981; Wright 1988). One can make a similar argument for predator-prey ratios by assuming similar species-abundance distributions for both predators and prey and substituting energy for area, an equivalence suggested elsewhere (Wright 1983). Energy-richness relations, explained in terms of more energy leading to more individuals and hence more species, have been discussed and documented for various taxa within trophic levels (see Turner *et al.* 1987, 1988; Owen 1988; Lawton 1990; Currie 1991); we are proposing that the energy ratios between levels result in corresponding species richness ratios between those levels.

(*ii*) *Common determinants of diversity*

The observation of a pattern in trophic structure begs, most obviously, an explanation in terms of trophic mechanisms. Observation of a scale-invariant predator-prey species ratio tends to generate explanations in terms of the direct influence of the presence of prey species on their predators, and the converse. However, prey species, or types, are just one dimension of a predator's niche and predation just one factor in the ecology of prey species. Species richness may be influenced by a variety of factors such as available energy or production (Brown & Davidson 1977; Schall & Pianka 1978; Abramsky & Rosenzweig 1983; Wright 1983; Turner *et al.* 1987, 1988; Currie & Paquin 1987; Owen 1988; Adams & Woodward 1989; Currie 1991); area (MacArthur & Wilson 1967; Williamson 1988); habitat heterogeneity and structure (Pianka 1967; Harman 1972; Kohn & Levitan 1976; Southwood *et al.* 1979; Moran 1980; Boomsma & van Loon 1982; Tonn & Magnuson 1982; Strong *et al.* 1984; Leather 1986; Friday 1987); rates of immigration (MacArthur & Wilson 1967; Schoener & Schoener 1983; Robinson & Dickerson 1987); disturbance (Connell 1978; Hildrew & Townsend 1987; Petraitis *et al.* 1989); and time, both evolutionary and ecological (Kennedy & Southwood 1984; Beaver 1985; Leather 1986; Ricklefs 1987; Brown & Southwood 1987). These effects, though in some cases observed in entire communities, have been more commonly noted from assemblages, guilds or other subsets of communities. It follows that we might expect these factors to influence both predator and prey species in rather similar ways and, hence, the richness of the two groups to be correlated. Or, to invert the proposition, it would be rather surprising if the diversity of two broad subsets of a community responded consistently in completely different ways to the spatial, temporal and energetic characteristics of their environment.

(*c*) *Assumptions, predictions and tests*

All the above hypotheses make the same general prediction: the number of predator species will be correlated with the number of prey species across a range of communities. Are there additional predic-

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tions specific to any of the hypotheses which will enable us to evaluate which are most applicable?

(*i*) *Random draw*

Under this hypothesis the pool of potential colonists from which the species are drawn should have the same predator-prey ratio as individual communities. However, it is rarely straightforward to define the species pool. At its simplest, it is the list of species available to colonize a site, but availability for colonization depends on a number of factors including the local abundances and dispersal characteristics of taxa. Consequently, the species pool may not be readily defined geographically. For the most part, however, the best data available are either local or regional species checklists or cumulative data from samples for a series of sites or over a period of time (see Terborgh & Faaborg 1980; Cornell 1985*a*,*b*; Ricklefs 1987; Compton *et al.* 1989; Lawton 1990; Tonn *et al.* 1990). A second problem is that even if the species pool has the same structure as individual communities, it is hard to tell whether the former is a consequence of the latter or vice versa (for example see Cole 1980; Van Valen 1982). If individual communities have internally determined predator-prey ratios then, assuming that the average turnover of species (β-diversity) is the same for predators and prey (itself an interesting point), the sum of the individual communities should produce a species pool with the same predator-prey species ratio. Despite the difficulties of establishing causality, a lack of correspondence between the ratio in the species pool and that in individual communities would suggest that the composition of the species pool was having little effect on the trophic structure of those communities (although, bearing in mind the difficulties of defining a species pool outlined above, it would not constitute a critical test). British freshwater invertebrates provide one data set where such regional against local comparisons can be made.

Figure 4 shows the predator-prey species relation for data from freshwater communities at British sites only. Invertebrates from a regional species list (for the area around Sheffield, S. Yorkshire; (Zasada & Smith 1981)) and the British national list (Maitland 1977) were classified in the same way as for the community data (excluding all vertebrates, and species not normally recorded in freshwater community studies: Protozoa, Rotifera, etc.). As is evident from figure 4, the ratios for the freshwater community data correspond remarkably well to the two regional data points. The proportions of species that are predatory are 0.34 and 0.37 for the Sheffield region and British list respectively, this compares with 0.31 ± 0.022 (95% confidence interial) and 0.35 ± 0.018 for mean proportions in flowing and standing water systems. In other words the predator-prey ratio of the species pool, crudely defined, at two scales corresponds reasonably well to the ratios in samples from actual communities, with the suggestion that the regional pools may be slightly more predator rich than individual communities. In addition to real community data, figure 4 has data from two artificial 'communities' assembled by randomly selecting two species from each of 15 still-water sites in the Sheffield area and experimentally determining the feeding interactions within each 'community'. The predator-prey ratios for both 'communities' are similar and correspond closely to that from other freshwater communities. Clearly, on this evidence, we cannot reject the idea that the composition of available species influences the structure of local communities, indeed it would perhaps be rather surprising if it did not. However, although demonstration of similar ratios in local communities and their respective species pools is interesting, it is clearly not sufficient to disentangle the random draw from other explanations.

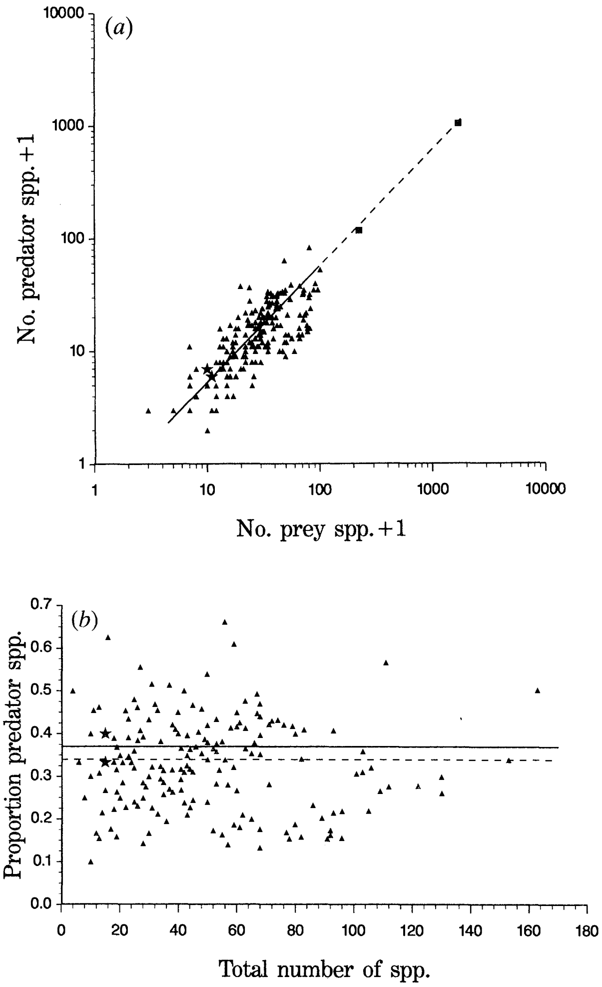

Figure 4. (*a*) The relation between log (predator richness + 1) and log (prey richness + 1) for British freshwater, non-summary, data (triangles) with the reduced major axis for that data ($b_{[\mathrm{RMA}]} = 1.03$, $r = 0.73$, $n = 190$). Additional points are: squares, (lower) Sheffield regional fauna, (upper) U.K. national list; stars, artificially assembled pond 'communities' (see text for details). (*b*) The proportion of total species that are predators for the same data: symbols as above except regional values are shown by: solid line, U.K. national list; broken line, Sheffield regional fauna.

A further possible prediction from the random draw is that if, for energetic reasons, prey species typically have larger local populations than predators, prey will have a greater probability of colonizing a habitat (or being rescued from local extinction by immigration),

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resulting in local communities that are more prey biased than the regional pool, as the data here seem to suggest.

As a final point it is noteworthy that the influence of the species pool will be most pronounced when the number of species in a community is a significant proportion of the total number available. In this situation the predator-prey ratio must tend toward that of the pool. Jenkins & Kitching's (1990) study of food web reassembly in tree-hole communities in Australia appears to provide a good example of this effect.

(*ii*) *Predator food niches and competition for enemy-free space*

If the number of predator species in a system depends simply on the number of prey types then, as recognized by Jeffries & Lawton (1985), it does not necessarily follow that there will be a tight correlation between predator and prey species. If the range of types of organisms that can occur in a community is finite, then as species richness increases the rate of addition of new types will decrease and consequently the predator-prey species ratio should decrease, a result noted in their data by Jeffries & Lawton (1985). If such an effect occurs we should expect both to see it within a particular type of system, and for it to be most pronounced in systems of generalist feeders, such as freshwater invertebrate communities, where predators feed on a wide range of prey (i.e. a 'type' may include many species). In more specialist systems (e.g. host-parasitoid), where species and types correspond much more closely, the ratio might be expected to be more constant. Plotting data for each study (from single habitats or community types) for which there are several data points (ten or more) yields a wide range of correlations, but no cases where the untransformed data suggest anything other than a linear relation. The prediction above is a fairly weak one, there being several possible counter-effects (e.g. resource fragmentation may prevent the richness of specialist predators from keeping pace with that of their prey, and may even cause a reduction in predator species at high prey richness; (Janzen 1981)). However, it does lead to a secondary prediction that more specialist-dominated systems should have more predators per prey: addition of a new prey species is likely to provide a new niche, an uncompeted-for resource. Classification of communities as specialist or generalist dominated is not unequivocal, but it seems reasonable to suggest that terrestrial, plant-associated arthropod systems contain a higher proportion of specialist predators than do aquatic systems; however, although our data do suggest some differences between habitats, (see: Results; figures 2 and 3) these do not provide any clear support for the prediction. Finally, running counter to the first of the above predictions, because predators may themselves be resource types for other predators, the predator food niche explanation does suggest that predator richness might increase slightly faster than that of prey, as suggested by the data.

Jeffries & Lawton's (1984) addition of the idea that apparent competition for enemy-free space restricts the number of prey that can coexist with each predator is very hard to test. The explanation is based on the prevalence of strong top-down effects of predators on their prey assemblages but there is much debate about the relative importance of top-down and bottom-up control in food webs (Carpenter 1987; Hildrew & Townsend 1987; Lawton 1989) and, although such strong interactions do undoubtedly occur, it is not clear how prevalent such effects are across, or indeed within, communities (see Paine 1992). A second point relating to the role of predators is that, although the effect of polyphagous predators may be to exclude some species from a community, they may also promote coexistence of potential competitors through an overall reduction of the abundance of prey (Paine 1966; Glasser 1979, 1983). Although there will be advantages to exploiting enemy-free space, these may be countered to some extent by the advantages of competitor-free space, resulting in more abundant resources and hence allowing specialization among prey (Glasser 1979, 1983). Mithen & Lawton's (1986) simulations involve prey that are basal species, which in the model are self-limiting and do not compete with each other, the model therefore does not (and was not intended to) examine this aspect of predator impact.

One prediction of the enemy-free space model is that predator-prey ratios will vary depending on the biology of species in the community. For example, increasing connectance (proportion of predator-prey links realized) tends to increase the predator-prey ratio (Mithen & Lawton 1986). From the arguments above, it seems reasonable to suppose that less-specialist systems (i.e. marine and freshwater benthic communities) will have higher trophic connectance (Warren 1990), and thus, the model predicts, generally higher predator-prey ratios. The evidence in figures 2 and 3 is, again, equivocal; freshwaters do have some of the highest ratios, but marine systems are consistently low, trees somewhere in between.

In general the predator niche/enemy-free space mechanism does not appear to make any clearly unique predictions amenable to non-experimental testing; the weak predictions examined here find little support in our data.

(*iii*) *Energetic/population density ratios*

This hypothesis rests on three main assumptions: there is more energy available to the prey than to the predator fractions of communities; the total number of individuals is related to available energy; and the number of species is related to the number of individuals. The first is a logical necessity given the mutually exclusive definitions of predator and prey used here. Whether the difference will be apparent in terms of biomass or abundance will depend on production (i.e. the standing crop of a resource could be less than that of its consumers; e.g. phytoplankton and grazing zooplankton in some aquatic systems (Greze 1970)). However, it seems unlikely that such effects will be characteristic of the data analysed here which relate to animals only and in which predators and prey overlap substantially in life-history features

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such as generation time. A wide range of studies, particularly in aquatic systems, show that production, biomass and total numbers of individuals tend to decrease through successive trophic levels (see Greze 1970; Petipa *et al.* 1970; Krebs 1978; Dunbar 1979; Begon *et al.* 1990).

Positive relations (or proportionality) between productivities, biomasses or abundances across trophic levels have been theoretically predicted (see Kerr 1974; Ardeti *et al.* 1991) and empirically demonstrated in a variety of natural systems. McNaughton *et al.* (1989) show that herbivore consumption, production and biomass are all positively related to net (above ground) primary productivity in terrestrial grassland, and they speculate that such relations should hold for the rest of the food web. Similar relations have been shown between primary and secondary production (see Brylinsky 1980; Morgan *et al.* 1980; Begon *et al.* 1990); basal resource and primary consumer biomasses (see Egglishaw 1964, 1968; Kirchner 1977; McCavley & Kalff 1981; Paloheimo *et al.* 1984; Hanson & Peters 1984); between basal resource biomass or abundance and primary consumer abundance or diversity (see Cameron 1972; Egglishaw 1964, 1968; Kirchner 1977; Minshall & Minshall 1977; Hawkins & Sedell 1981; Southwood *et al.* 1982; Barmuta 1988; Lightfoot & Whitford 1991); between prey and predator biomass (see Hijii 1986, 1989); and between prey and predator abundance (or diversity) (Cameron 1972; Hawkins & Sedell 1981; Dudgeon 1984; Hijii 1986; Barmuta 1988). Figure 5 shows the correlation between predator and prey species densities or total abundances for some of the studies from which species data used in the previous plots were derived, suggesting a general tendency for the two to be related, even across a very diverse set of communities. It seems reasonable to suggest that the relative energy available to predators and prey may in some way set bounds on the relative abundances of organisms in each group.

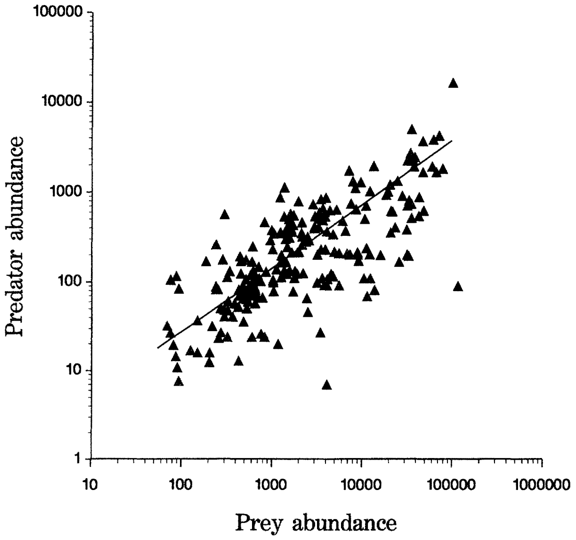

Figure 5. Relation between log predator density and log prey density for a range of aquatic and terrestrial habitats ($r = 0.74$, $n = 226$, $p < 0.0001$).

The third assumption is that total abundance is related to species number. As already mentioned this idea has been widely utilized in the derivation of species-area relations from the commonly used models of species-abundance distributions, and empirically numbers of individuals may be a better predictor of number of species than is area (see Angemeier & Schlosser 1989). We do not, for the most part, have data to satisfactorily examine the species-abundance relations for the communities in our data set, but for those where it is possible, the distributions are reasonably well described by a lognormal or logseries model. The individuals-species relation has been examined empirically rather rarely, except in the context of sample effort curves; most studies show a roughly linear relation between species number and abundance (sometimes biomass) or their logarithms (see Yount 1956; Southwood *et al.* 1982; Wolda 1987; Angermeier & Schlosser 1989; Stork 1991). Hendrix *et al.* (1988) suggest that the abundance-richness relation is sufficiently good to allow inference of patterns in richness from patterns in abundance for arthropod guilds.

There is, it seems, reasonable evidence for each of the component arguments of the hypothesis. But does the hypothesis as a whole make any testable predictions? If the total abundance of individuals is related to number of species for both predator and prey then we might expect variation in the proportion of species that are predators (or variation about predator species – prey species relation) to be related to the percentage of the total individuals that are predators. For the data for which we have information on both species and numbers of individuals this is indeed the case; the 'residuals' from the reduced major axis of the predator-prey species richness relation (for all data where predator and prey richness and total abundances were recorded) are significantly correlated with the proportion of the total number of individuals that are predators ($r = 0.5$, $n = 97$, $p < 0.001$), though as before some studies contributed several points. It should be noted that this is a rather weak test of the relation because the abundance data are in many cases densities rather than total numbers, whereas the species data represent the totals for the habitat or samples. Energetics may also, directly or indirectly, lead to a decrease in proportions of predators in small communities. If increasing energy availability allows longer food chains (a matter of debate: see Pimm 1982; Yodzis 1984; Lawton 1989; Pimm *et al.* 1991) then the species added will be predominantly predators. This effect is most likely to be apparent in the transition from very low energy systems to moderate energy systems, and might thus produce increases in the predator-prey ratio in relatively species-poor communities. At a trivial level the observation that predators cannot occur without prey, but prey-only communities are possible, is a manifestation of energetic constraints.

Energetic constraints to the predator-prey species relation also suggest that we should see a relatively hard upper limit to the scatter of points in figures 1 and 2, with points generally lying below the line of

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equal predator and prey diversity. The actual pattern observed conforms to this expectation.

(*iv*) *Common determinants of diversity*

The hypothesis that factors influencing diversity act similarly across both predator and prey species seems obvious, and intuitively reasonable. It also makes two specific predictions. Firstly, groups of trophically unrelated species within a system should show correlations of richness similar to that seen in trophically related groups like predators and prey. Secondly, within a taxonomic group that contains both predators and prey (and in which the latter are not substantially fed upon by the former), predator-prey correlation should also occur. To test the first prediction we examined the correlations between species richness in each pair of guilds for all the data for arboreal arthropods (for which a standard set of guilds have been used). The results are given in table 1. It is readily apparent that many pairs of trophic guilds which have no obvious direct trophic connection with each other (e.g. epiphytic grazers and phytophages; epiphyte grazers and scavengers; phytophages and tourists; tourists and predators) show similarly strong correlations to those pairs for which direct linkage can be postulated (e.g. phytophages and parasitoids, phytophages and predators). The data for aquatic systems are less straightforward – species numbers are much lower and cover very limited ranges, most of the freshwater studies do not give species richness by guild and so sample sizes are small – however, they are included for completeness. In freshwaters, correlations between richnesses of the main guilds (= functional groups (Cummins 1973)) do occur, but are generally weak (table 1), although the strongest relations are between predators and two potential prey groups (gatherers and filterers). In marine systems, combining data from three studies and pooling guilds to produce as far as possible comparable data (accepting that there may be inconsistencies in guild allocation (Maurer *et al.* 1979)) significant correlations occur between the richness of suspension feeders, deposit feeders and predators (table 1).

In summary, the richness of pairs of trophic groups other than predators and non-predators can show significant correlations; however, it is worth noting that in most cases the strongest relations are between predators and their actual, or potential, prey. This is consistent with the idea that energy supply is an important determinant of guild structure. Guilds, such as 'deposit feeders', 'epiphyte grazers' and 'shredders', are defined in terms of, and may vary with respect to, different energy sources. Factors influencing diversity may act similarly on species in all guilds in a system, but the energy available to a guild (epiphytic algae, coarse particulate organic matter, etc.) will limit the extent to which within-guild diversity can increase.

Consequently, if the energy sources of a pair of guilds are linked, their richnesses are more likely to be correlated; guilds whose energy inputs vary independently, whatever the common determinants of diversity, should correlate less closely. Although guilds that are apparently trophically independent of each other may not be entirely so, any interdependence is likely to come via effects on energy flow rather than niche constraints. For example, herbivore abundance may

Table 1. *Correlations of species richness ($\log[x+1]$) between guilds in samples from trees ($n = 33$), freshwaters ($n = 18$) and marine benthic habitats ($n = 43$)*

(Significance levels, which for reasons of non-independence of data points (see Methods) and of tests provide rough guidance only, are given in parentheses only where $p > 0.001$.)

trees	phytophages	epiphyte grazers	scavengers	predators[a]	parasitoids[a]	ants
epiphyte grazers	0.88	—	—	—	—	—
scavengers	0.82	0.87	—	—	—	—
predators	0.94	0.89	0.83	—	—	—
parasitoids	0.89	0.87	0.78	0.93	—	—
ants	0.60	0.56	0.75 (0.004)	0.49 (0.01)	0.44	—
tourists	0.91	0.85	0.82	0.96	0.94 (0.007)	0.46

freshwater	shredders	scrapers	predators	gatherers
scrapers	−0.60 (0.009)	—	—	—
predators	−0.41 (0.09)	0.17 (0.5)	—	—
gatherers	0.07 (0.78)	−0.10 (0.68)	0.69 (0.0014)	—
filterers	−0.49 (0.039)	0.29 (0.28)	0.67 (0.003)	0.53 (0.024)

marine benthic habitats	predators	suspension feeders
suspension feeders	0.64	—
deposit feeders	0.80	0.57

[a] In the main analyses, predators and parasitoids are treated as predators.

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be related to scavenger abundance (with consequent species correlation) because of the correlation of each with the provision of, respectively, living autotrophic tissue and dead, unconsumed material, both of which ultimately depend upon primary productivity.

The second prediction, predator-prey species correlation within a taxonomic subset of a community, has been examined for the Coleoptera (Gaston *et al.* 1992) with the conclusion that a correlation exists between numbers of predatory and non-predatory beetles in samples from a wide range of different habitats, in both temperate and tropical regions. This pattern is evident even though beetles comprise only a subset (albeit a substantial one) of the community, and although predatory beetles as a group are not feeding entirely, or even extensively, on non-predatory beetles. Related results for guilds of birds on West Indian islands (Faaborg 1985) and in four tropical forests (Karr *et al.* 1990) suggest that the numbers of bird species in different trophic guilds form approximately constant proportions of the total bird faunas. Lockwood *et al.* (1990) showed that, in sagebrush arthropod communities, predator-prey richness (and density) ratios differed little between insects, arachnids, or all arthropods, suggesting that this was due to the effect of common ecological processes.

4. DISCUSSION

Numbers of predator and prey species are correlated in combined data from terrestrial and aquatic systems. There is some evidence that different types of system may have consistently different predator-prey ratios, but a strong general correlation, across all scales, emerges as a dominant result. Predator and prey richnesses are close to proportional, but the data suggest that predator richness increases slightly faster than prey richness, especially in small communities. The predator-prey ratio, although roughly scale invariant over much of the range of species numbers, is rather variable, predators constituting anywhere from 0% to almost 70% of the species in a community. At least five different hypotheses predict a correlation between predator and prey richness and three of these, the random draw, predator feeding niches and energy ratio hypotheses do, at least in some circumstances, predict similar variation in the predator-prey ratio to that apparent in the data. In the following sections we discuss whether a single explanation is sufficient, and the consequences of combining theories; the significance of variation in predator-prey ratios; and the relation of predator-prey ratios to the wider issue of guild structure.

(*a*) *Evaluating the explanations*

To this point we have considered the proposed explanations for predator-prey proportionality more or less separately. The consistency of the pattern, across a variety of communities and scales, requires explanation, but any single explanation must have wide generality to apply to such diverse data. On the evidence presented above, the random draw gives the greatest degree of scale independence; the energy ratios and common determinants of diversity hypotheses have high generality and find reasonable independent empirical support for their assumptions and, in the case of the latter, for additional predictions. The two other hypotheses, although based on the proximate consequences of direct trophic interactions, are not without support in a broader context. Arnold's (1972) analysis is based on data for species occurring in large (several square miles) areas compiled from distributional information, and so represents a relatively large spatial and temporal scale. Similarly, many of the examples of the moulding of species niches by natural enemies appear to represent evolutionary responses (Jeffries & Lawton 1984), implying again large-scale consequences of community-level interactions.

These observations draw us inevitably to the conclusion that it is inappropriate to seek a single explanation for the observed patterns of predator-prey proportionality. Rather, given that all the explanations make similar predictions in this respect, the question should be inverted: under what circumstances would we predict the absence of a correlation between predator and non-predator species numbers? In other words, if all the explanations were potentially applicable (and we should note that none appear to be exclusive of any of the others) then our basis for selecting an explanation – does it explain the result at all levels? – becomes redundant; rather, the critical question is, under what circumstances might none of the explanations apply and predator-prey proportionality hence break down? There seem likely to be few circumstances in which one or another of the proposed hypotheses would not provide bounds to the predator-prey species relation, although such bounds will be statistical rather than absolute.

Assuming the plausibility, at least in some circumstances, of each mechanism, their interactions will also be important. For example, as mentioned above, 'energy ratios' and 'common determinants of diversity' combine to predict predator-prey proportionality better in combination than either alone. In common with many other areas of biological organization we suggest that the pattern results from a hierarchy of processes (O'Neill *et al.* 1986) although there may be feedback between levels. At large scales (very large communities or sets of communities in a region) the composition of the pool of available species determines the pattern (although it is still not clear what sets this structure). Within that, total predator and prey abundances must be limited by relative energy availability; this applies at a variety of scales, within individual communities and across groups of communities. Within the framework set by energy, the division of the total number of individuals among species will be influenced by a variety of, non-trophic, factors acting commonly on both predators and prey (generally within individual communities). From the level of individual communities down to the level of particular patches within a community, there are more direct effects of trophic interactions. The number and relative abundance of prey types (itself

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presumably linked to the number of basal resources ('energy types') as well as other non-trophic factors) defines the number of ways in which energy is available to predators and so, paralleling the process at a higher level, the potential abundance of predators on that prey type. How these abundances are translated into species will depend on the dynamics of the interaction – how many competitors can coexist on the resource – and on non-trophic influences on diversity. Where predator effects are strong (and probably at the smallest scales) the number of prey species coexisting within a prey type may be determined by apparent competition for enemy-free space. It is interesting to note the recurrence of processes, and their interaction at more than one level (particularly energetic constraints and non-trophic determinants of richness). Whether the idea extends to the species pool – with energy (abundance or biomass) setting the potential for rates of speciation or geographic spread (see Glazier 1987, Brown & Maurer 1987, Maurer & Brown 1988) and the pattern or frequency of such speciation events or spread being determined by mainly non-trophic factors (topography, microclimate etc.) – is a speculation beyond the scope of this study.

(*b*) *Variation in predator-prey ratios*

If predator-prey correlation is the consequence of a combination of the possible mechanisms discussed above, then it could be argued that the significance is not so much in the pattern itself but in the systematic deviations from it. Such deviations may or may not have functional significance. For example, there is the suggestion in the data presented here that some types of community may have consistently more predators per prey than others (figure 3); Briand (1983) gives related observations from food web data. Do these reflect differences in species' biologies, or structural features of food webs consequent upon species characteristics (e.g. connectance) as predicted by Mithen & Lawton's (1986) model? Alternatively, is it a product of different sampling techniques? There is evidence that sampling methods can influence observed predator-prey ratios, possibly due to the microhabitats they sample, or to the effect of species mobility or the capture success with different methods (see Gaston *et al.* 1992). Is it a consequence of ignoring particular taxa (e.g. fish, birds, meiofauna, parasites) which may be of varying importance in different community types? Finally, can the differences be explained in terms of any of the processes postulated above? For example, different taxa probably have different characteristic ratios of production to biomass: high production: biomass ratios in prey might support more predators. Or predator-prey size relations might be very disparate between systems: for a given prey biomass, larger predators will be comparatively less abundant and consequently there may be fewer viable predator populations in communities predominantly composed of such species.

Other intriguing variations in predator-prey richness ratios that have been noted are the apparently higher proportions of predators (in some taxa) on islands (Becker 1975; Janzen 1973), in arid habitats (Wagner & Graetz 1981, and references therein), and with decreasing latitude (Pianka 1966). Whether this reflects general changes in other aspects of food web structure with latitude (e.g. phytotelmata webs, (Kitching & Beaver 1990) is not clear.

Little experimental work has been done on predator-prey ratios, but Lockwood *et al.* (1990) demonstrated that the prey-predator richness and density ratios in sagebrush arthropod communities initially decreased following mowing and herbicide application, although richness ratios subsequently recovered. Although the mechanisms are unclear, this suggests that ratios may be affected by habitat conditions and that in this case the effect seems likely to have been through interference with the resource base depressing prey densities and richness (Lockwood *et al.* 1990). Jenkins & Kitching (1990) show that reassembly of tree-hole communities following disturbance results in a gradually increasing predator-prey ratio; presumably frequently disturbed systems would generally be found in the early stages of reassembly and would therefore exhibit lower ratios than those less frequently disturbed.

(*c*) *A special case of constancy in guild structure?*

So far we have deliberately considered predator-prey species correlation as a distinct pattern, in keeping with much of the literature. However, it becomes apparent, when explanations other than those based on the direct species-species effects of predators on prey are considered, that the pattern is no different from the more general observation of roughly constant species proportions in various guilds from many different systems; a general, although not universal, observation (Cornell & Kahn 1989; Hawkins & MacMahon 1989). The guild structure of communities has been the subject of much interest in ecology (Terborgh & Robinson 1986; Hawkins & MacMahon 1989), both as a way of examining the supposed functional structure of communities and (following Root (1967)) as a means of identifying subsets of species between which strong interactions (especially competition) might be expected to occur. Guild structure has been put to particular use in analysing the functional organization of aquatic communities; it forms the basis of the River Continuum Concept (Vannote *et al.* 1980) and has been used in a similar way to look at structure in marine benthic systems (Pearson & Rosenberg 1987). These analyses generally focus on the total abundance of guilds, rather than species numbers, with the implicit recognition that guild abundance is related to rate of food supply. Thus, the basis for much guild structure analysis is the same as that for the energy ratio hypothesis discussed above.

On these grounds it seems evident that predator-prey ratios are a special case of the general problem of constancy of guild structure, and should not necessarily be treated in isolation. The way in which explanations for each or any of the patterns overlap and interact may vary from one particular guild to

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another, but the applicability of processes postulated here is not limited to predator-prey ratios. Consideration of these processes also emphasizes the gaps in our understanding. In particular, the fundamental question of how resources are divided up between species, i.e. what factors determine the species-abundance distribution, is central to linking the functional patterns in ecosystems to classification and description based on species composition. In a pertinent comment on McNaughton *et al.* (1989), Cohen (1989*b*) notes the potential for developing links between the structural 'anatomy' of communities (in that case species proportionality in food webs) and the functional aspects of systems implied by McNaughton *et al.*'s results. The fields of tropho-dynamics and energy flow and those of species diversity and niche theory have often followed rather separate paths (Brown 1981); however, it seems increasingly likely that many clues to understanding community structure lie in their synthesis. We are some way from rigorously establishing such links, but it seems an important goal.

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APPENDIX 1. SOURCES OF DATA (SEE METHODS)

Main species analyses: Benke *et al.* (1984), Cameron (1972), Canton & Chadwick (1983), Dudgeon (1984), Edmonds (1974), Friday (1987), Gaines *et al.* (1989), Gore (1979), Griffiths (1973), Harrel & Dorris (1968), Hawkins *et al.* (1982), Heatwole & Levins (1972), Hildrew *et al.* (1984, 1985), Hynes (1961), Jeffries (1989), Jeffries & Lawton (1985; 12 studies), Jones (1940, 1941, 1943, 1948, 1949*a,b*, 1951), Laurie (1942), Lubchenco *et al.* (1984), Malmqvist & Bronmark (1985), Maurer *et al.* (1979), Miller (1985), Moran & Southwood (1982), Pearson (1971), Percival & Whitehead (1930), Perry & Schaeffer (1987), Pimentel (1961), Pimentel & Wheeler (1973), Rosenberg (1973), Smock (1985), Stork (1987 and personal communication), Teraguchi *et al.* (1981), Warren (1989), West (1986).

Numbers of individuals analyses: Benke *et al.* (1984), Bunn (1986), Cummins *et al.* (1981), Fedra (1977), Gaines *et al.* (1989), Gore (1979), Harrel & Dorris (1968), Hartley (1984), Hawkins *et al.* (1982), Hijii (1986, 1989), Hildrew *et al.* (1984), Hynes (1961), Lake & Doeg (1985), Maitland (1964), Marchant *et al.* (1985), Minshall (1981), Minshall *et al.* (1982), Moran & Southwood (1982), Odum (1971), Perry & Schaeffer (1987), Pimentel (1961), Rosenberg (1973), Scott & Osborne (1981), Stork (1987 and personal communication).

Guild/functional group analyses: Bunn (1986), Lake & Doeg (1985), Canton & Chadwick (1983), Dudgeon (1984), Maurer *et al.* (1979), Moran & Southwood (1982), Pearson (1971), Perry & Schaeffer (1987), Rosenberg (1973), Stork (1987 and personal communication), West (1986).

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