

Predators, parasitoids and pathogens: species richness, trophic generality and body sizes in a natural food web

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Summary

1. A food web is presented which describes trophic interactions among the herbivores, parasitoids, predators and pathogens associated with broom, *Cytisus scoparius* (L.) Link. The data come from published work on the community at a single site. The web comprises a total of 154 taxa: one plant, 19 herbivores, 66 parasitoids, 60 predators, five omnivores and three pathogens. There are 370 trophic links between these taxa in the web. The taxa form 82 functionally distinct groups, called trophic species.
2. Predators consumed significantly more species than did parasitoids: a median of two prey species per species of predator (range = 1–9), compared to a median of one host species per species of parasitoid (range = 1–4). Significant differences in the number of species consumed were also found among the five predator groups: birds (median = 4), spiders (median = 5), Coleoptera (median = 1), Diptera (median = 2) and Hemiptera (median = 7).
3. Vulnerability, measured by numbers of consumer species, was significantly affected by the herbivores' feeding styles: externally feeding herbivores were most vulnerable and the concealed herbivores were least vulnerable. Miners were vulnerable to the most parasitoid species and externally feeding herbivores were the most vulnerable to predators.
4. Resource species had a median vulnerability of 13 consumer species, a figure far higher than that in most published food webs. No significant relationship was found between species' vulnerability to predators and vulnerability to parasitoids. However, there was a strong negative relationship between the percentage mortality due to predation and percentage mortality due to parasitism.
5. The broom food web contains nine orders of insects, a figure higher than previously recorded. The web also contains vertebrates, arachnids, bacteria and fungi. Most of the interactions between the orders were weak. Connectance was calculated for the complete web, the parasitoid sub-web and the predator sub-web. The connectance of the predator sub-web, a value of 0.0364, was more than an order of magnitude larger than the connectance of the entire web (0.0156) or the parasitoid sub-web (0.018).
6. The body lengths of 52 species in the food web were estimated from field guides or museum specimens. Larger predators consumed smaller prey in 93% of predator–prey interactions. Smaller parasitoids consumed larger hosts in 79% of parasitoid–host interactions. Parasitoids were significantly smaller than predators.
7. The 52 species were arranged in order of increasing body length along the columns and down the rows of a food web matrix. The predator sub-web was predominantly upper triangular with 8% of non-zero elements falling below the leading diagonal. The parasitoid sub-web was predominantly lower triangular with 21%

non-zero elements falling above the leading diagonal. The entire web contains entries both above and below the main diagonal and thus violates a central assumption of the cascade model.

Key-words: broom, cascade model, connectance, source web, trophic species.

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Introduction

An attraction of food webs is that they cut across the narrow habitat and taxonomic divisions that are still a powerful, restricting force in the development of ecological theory (Lawton 1995). Ideally, food webs could fulfil this goal by representing a random sample of all species found in natural communities. Far from this ideal, ecologists typically ignore parasites and diseases and restrict their study to either parasitoid–host communities or predator–prey communities (Lawton 1989; Marcogliese & Cone 1997). Consequently, habitat and taxonomic divisions still restrict ecological theory. For example, many terrestrial projects have looked at the parasitoid species richness of different host insects and plants (e.g. Askew 1961; Askew & Shaw 1986; Hawkins & Lawton 1987; Memmott, Godfray & Gould 1994; Muller *et al.* 1999) while ignoring predator species richness or pathogen species richness within the same communities. In contrast, numerous freshwater food webs almost exclusively describe predators while ignoring parasitic and pathogenic trophic interactions (e.g. Winemiller 1990; Martinez 1991; 1993a; Havens 1993).

These discrepancies are largely due to the relative ease of observing trophic interactions in these different habitats. Quantifying parasitoid species richness for a terrestrial herbivore is relatively simple. The herbivore is simply collected from the field and parasitoids reared out in the laboratory. However, it can be extraordinarily difficult to determine predator–prey interactions. The hit-and-run style of insect predation makes it easy to miss a predator–prey interaction. It is also rare for clear evidence to remain of who ate whom, after predation occurs, which further compounds the problem. In aquatic habitats, the trophic resources of predators and herbivores such as fish and zooplankton that engulf their prey whole are relatively easy to observe in gut contents. Beyond ease of observation, divergent sub-disciplinary conventions (e.g. terrestrial vs. aquatic ecology) also maintain the appearance of empirical discrepancies between habitat types (May 1983). One of the few trophic hypotheses that bridge predator and parasitoid-biased studies is the assertion that the host ranges of parasitoids are more specialized than those of predators because parasitoid life histories are more intimately tied to their hosts (Price 1980). Here, we present one of the few studies

that compares the generality of parasitoid–host and predator–prey interactions in the field.

Hawkins & Lawton (1987) and Hawkins (1988) have demonstrated that herbivore feeding strategy affects vulnerability as measured by the species richness of parasitoids that consume the herbivore. They proposed that the pattern could be explained by differences in the ease with which parasitoids locate hosts in different feeding niches and the degree to which the hosts are protected from predation. Hawkins, Cornell & Hochberg (1997) investigated the mortality factors of 78 species of insect and their data suggest that herbivore feeding biology affected pathogens, predators and parasitoids differently. Although the characteristics that influence the vulnerability of herbivores to parasitoids have received considerable attention, interactions among parasitoids and predators have been much more sporadically studied and it is not clear how mortality due to different types of consumers covary (Hawkins *et al.* 1997). How and where a herbivore feeds undoubtedly influences its predators (Hawkins & Lawton 1987), but it is not clear whether herbivores escape one type of enemy only to be consumed by another type of enemy.

Herbivore feeding style is one of many factors that affect trophic interactions in insect communities. Body size is also important. For example, large predators eat prey with a wider range of body sizes than do smaller predators (Cohen *et al.* 1993a). Body size is one of the most obvious features of any organism and one of the most easily measured. One approach to studying the relationship between size and trophic relationships is to measure the ratios of weight or body-length of consumers and their trophic resources in a particular community. This approach has not previously been used on a large insect food web.

In their work on the cascade model, Cohen & Newman (1985) demonstrated that statistically assembled food web matrices, constrained to be upper triangular, generate several of the patterns found in food webs. The cascade model assumes that species can be arranged into a cascade or hierarchy such that a given species can feed only on species below it and itself can be fed on only by species above it in the hierarchy (Pimm, Lawton & Cohen 1991). The original work on the model did not provide an explanation for the proposed trophic cascade, but subsequently body size has been suggested

as a likely candidate (Warren & Lawton 1987 and independently by Cohen 1989b). Thus, predators are typically larger than their prey (Vezina 1985) and parasitoids are typically smaller than their prey (Elton 1927). Published food webs largely conform to the assumptions of the cascade model, based on a hierarchy of body sizes. For example, Cohen *et al.* (1993b) found that about 90% of feeding links involve a larger predator feeding on a smaller prey. However, this is not because there are no exceptions to these generalizations, but because nobody has really studied them (Lawton 1989). Thus, parasitoid sub-webs support the cascade model, as do predator sub-webs, but the body size interpretation of the cascade model has not been tested against a web containing predators, parasitoids and pathogens.

In this paper, we describe a community centred on Scotch broom, *Cytisus scoparius*, at a field site in England. The data are presented as a food web describing the trophic relations in a community of 154 species: one plant, 19 herbivores, five omnivores, 66 parasitoids, 60 predators, and three pathogens. The data come from published work on these organisms at a single field site. We use the food web to answer five questions: (1) Is the trophic generality of predators greater than that of parasitoids? (2) Does herbivore feeding style affect herbivore vulnerability to predator, parasitoid, hyperparasitoid and pathogen species to the same degree? (3) Does mortality due to predators and parasitoids covary? (4) Does analysing parts of food webs (i.e. webs missing entire groups of consumers) bias estimates of food web statistics? (5) Does a food web containing predators, parasitoids and pathogens conform to the assumptions of the cascade model?

Materials and methods

THE FIELD SITE

The data are from Silwood Park, Berkshire in southern England (51°24'N, 0°34'W). At the time of the study, the field site was 97 hectares in size and the insects were collected from broom growing in six areas of the site. These study sites are described in detail in Waloff (1968).

THE DATA

The information used to construct the food web was collected over an intensive 12-year research programme investigating the ecology of Scotch broom and its associated fauna. The data were collected by N. Waloff, O. W. Richards, J. P. Dempster and their students between 1956 and 1968. Most of the data were collected in projects of a 3-year duration. The unifying factor in the work lies in the environment provided by the host plant (Waloff 1968).

Most of the data presented here are from Waloff (1968), a paper which collates the data from 31 published papers and six unpublished theses on the broom fauna at Silwood Park. If not directly from Waloff (1968), the data are from publications cited in this paper.

Scotch broom, henceforth called broom, is a widely distributed shrub in the British Isles and is found especially on disturbed soils. It grows to a height of 1.8–2.4 m and has a life span of 10–15 years (Waloff 1968). Broom supports a large fauna of phytophagous insects, many of which are confined to the species, together with their complex of parasitoids and predators. At Silwood Park there were nine Lepidoptera, five Diptera, one Hymenoptera, seven Coleoptera and 13 Hemiptera species feeding regularly on broom during the study period.

During the research programme, parasitoid–host data were gathered by rearing out parasitoids from their hosts, predator–prey data were collected using immunological techniques to analyse predator gut contents and pathogen–host data were gathered from herbivore rearings. Many thousands of insects were collected during the project to collect parasitoids. In his work on predation on the broom fauna, Dempster (1960, 1963, 1964, 1966) carried out over 40 000 precipitin tests (Waloff 1968). These tests identified the prey of three species of *Anthocoris*, the prey of the five species of broom Miridae and the arthropod predators of the Mirids. These data were supplemented by 2000 tests by Watmough (1963), identifying the psyllid predators and 1500 tests by Danthanarayana (1965) identifying the predators of the weevil, *Sitona regenstienensis* Hbst. A precipitin test is based on the reaction between the prey material from the gut of a predator and the blood serum of domesticated rabbits. The rabbits have been vaccinated with an extract of potential prey species and consequently their blood contains antibodies to the prey. Data from precipitin tests were supplemented by data from laboratory and field observations of predator prey interactions. Using these methods, the most important predators on broom and in the broom litter were identified. These predator data are summarized in Waloff (1968).

Three pairs of insects species could not be distinguished from each other using the precipitin tests, the two species of psyllid, the two species of aphid and the two species of *Orthotylus*. For the purposes of analysis, it was assumed that each pair shared the same predators. The data on the broom fauna was used to construct Appendix I, a list of species found on broom and their prey. A figure of the food web has not been presented, as the density of links is too great to permit the tracing of individual links (Cohen *et al.* 1993a).

The herbivores and omnivores were put into the six classes used by Hawkins (1988): (a) external feeders (13 species); (b) semi-concealed feeders (0 species); (c) leaf miners (3 species); (d) gall formers, in this study including inquiline species (2 species); (e) concealed feeders (5 species) and (f) root feeders (1 species). The broom miners were actually stem miners rather than leaf miners. However, they are extremely visually apparent to the extent that they suffer extensive predation by birds (Waloff 1968). Consequently, these stem miners were classified as leaf miners rather than placed in the concealed herbivore category as done by Hawkins & Lawton (1987).

In addition to data on consumer–resource relationships, Waloff (1968) also provided data on the percent mortality attributable to predators and parasitoids for 12 of the herbivorous species. If mortality data were available for more than 1 year, average values were calculated.

FOOD WEB STATISTICS

A measure of trophic complexity called directed connectance (the number of trophic links divided by the square of species richness (Martinez 1992) was calculated for the entire 154-species web, the 76-species parasitoid sub-web, the 84-species predator sub-web and the 23-species pathogen web. Each of these webs contains the consumers, the herbivores and the plant. The subdivision of the web was carried out to evaluate the effect, on food web structure, of ignoring the predators (usually done in parasitoid sub-webs), ignoring the parasitoids (usually done in predator sub-webs) or ignoring the pathogens (usually done in both parasitoid and predator sub-webs). Geographically defined terrestrial communities (Fauth *et al.* 1996) typically comprise parasitoids, predators and pathogens, but the three groups rarely appear simultaneously in published food webs.

Food-web statistics have frequently been based on ‘trophic species’ which are functional groups of all organisms in a web that appear to share the same set of consumer and resource species (Briand & Cohen 1984). The properties of trophic-species webs are calculated after all taxa that share the same consumers and resources are aggregated into the same trophic species. Directed connectance in particular has been shown to be robust to trophic aggregation (Martinez 1991; 1993b) and variations in species richness (Martinez 1993a) and sampling effort (Martinez *et al.* 1999). Food webs based on trophic species ameliorate taxonomic disparities (Cohen 1989a) and exhibit statistically consistent patterns (Martinez 1993b, 1994). Thus, connectance was also calculated for trophic-species versions of the entire species web, the parasitoid sub-web, the predator sub-web and the pathogen sub-web. There were 84

trophic species in the entire web, 48 trophic species in the parasitoid and predator sub-webs and 22 in the pathogen sub-web.

The body lengths of 52 species from the 154 species web were collected from field guides or from direct measurement of the species. Body length data could not be located for the remaining 102 species. There were 97 links between consumer species and resource species among these 52 species. These data were used for two purposes. First, by using the data to investigate the relationship between body size and feeding relationships in a natural community, we evaluated generalizations about predators, parasitoids and pathogens. These generalizations concerned their size and the size of their prey. Secondly, the data were used to test an interpretation of the cascade model. In the cascade model, the species are arranged a priori into a hierarchy. If this hierarchy is interpreted as body size, and if predator and prey species are arranged in order of increasing body size along the rows and down the columns of a food web matrix, the non-zero elements are predicted to lie predominantly above the leading diagonal. Such a matrix is termed ‘upper triangular’. Parasitoids and pathogens usually attack species larger than themselves and so create food web matrices that are ‘lower triangular’ and the assumptions of the cascade model are still met (see Cohen & Newman 1985 for further details). For the broom web, the body lengths of the 52 species were arranged into hierarchical order for the whole web, the predator sub-web, and the parasitoid/pathogen sub-web. Food web matrices were drawn for each of the three data sets. Rather than drawing the conventional array of 0 (no interaction) and 1 (consumption), the matrices were plotted as graphs. Thus, a data point on the graph shows consumption between the species numbered on the *x* and *y* co-ordinates. This method makes the triangularity of the matrices simpler to interpret.

Results

HOST RANGE OF PARASITIDS, PREDATORS AND PATHOGENS

Predator generality, as measured by the species richness of resource species, is significantly larger than parasitoid generality, as measured by the species richness of host species. Predators consumed a median of two species (range = 1–9) while parasitoids consumed a median of one species (range = 1–4), Wilcoxon two-sample test, $W = 3146.5$, $P < 0.001$: Fig. 1a,b). Pathogen generality was not statistically analysed because only three pathogen species were present in the web. However, pathogen generality is very small (Fig. 1c). The five main groups of predators were examined separately; for each group the sample size, plus the mean number of species con-

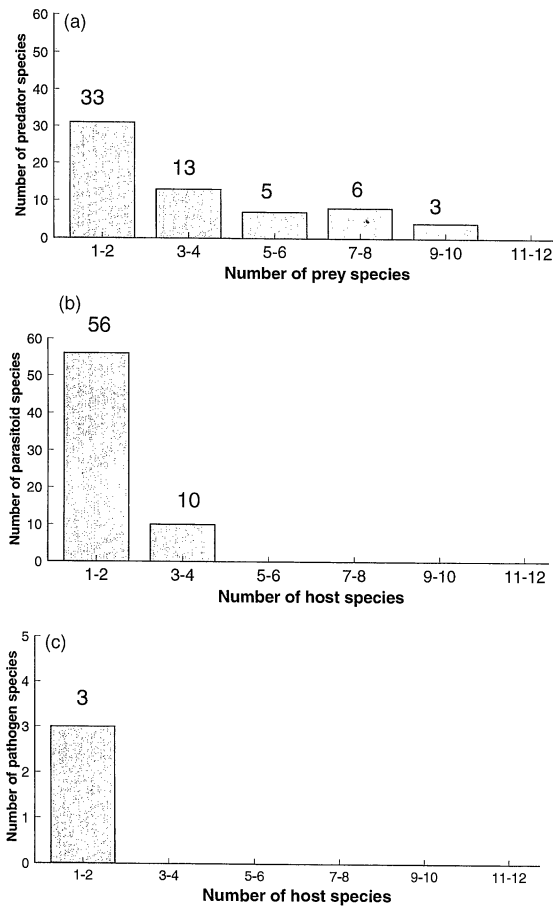


Fig. 1. Trophic generality of consumer species in the broom web among: (a) predators, (b) parasitoids and (c) pathogens. The numbers above each bar show the exact number of consumer species in that category.

sumed, are as follows: birds ($n = 5$, median = 4), spiders ($n = 11$, median = 5), Coleoptera ($n = 21$, median = 1), Diptera ($n = 6$, median = 2) and Hemiptera ($n = 14$, median = 7). There was a significant difference between the generality of these five predator groups: Kruskal–Wallis test, $H = 18.08$, $P < 0.001$ (Fig. 2). The spiders and the Hemiptera were the most generalized. The Coleoptera and the Diptera were the most specialized.

EFFECTS OF FEEDING STYLE ON VULNERABILITY TO PREDATION, PARASITISM AND HYPERPARASITISM

Herbivore feeding style had a significant effect upon overall vulnerability in terms of the richness of consumer species ($F = 9.16$, $P < 0.005$, Fig. 3a), upon vulnerability to predator species ($F = 5.14$, $P < 0.005$, Fig. 3b) and to parasitoid species ($F = 3.25$, $P < 0.05$, Fig. 3c). Herbivore feeding style

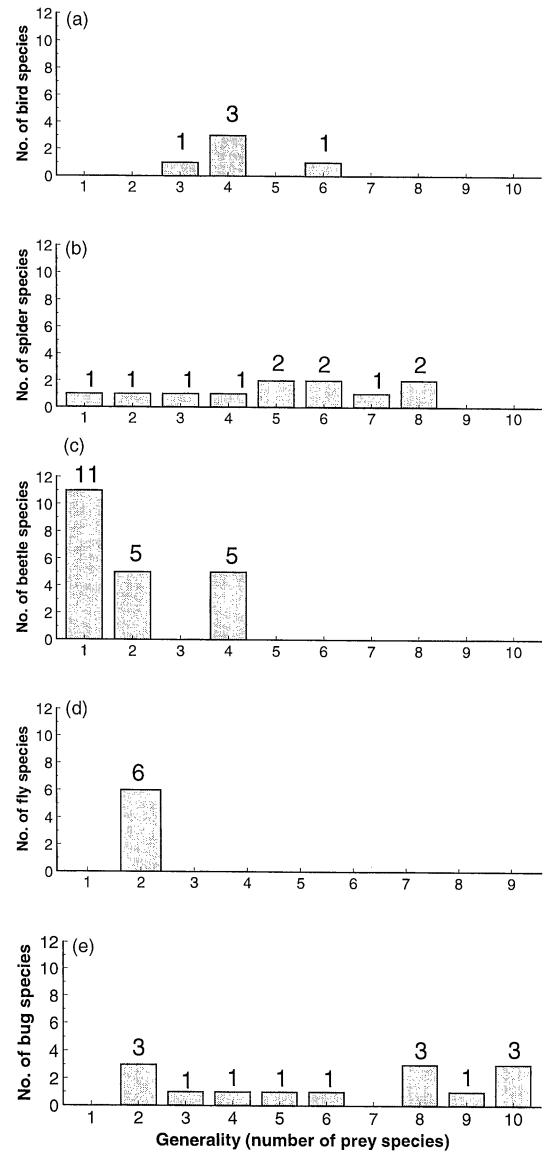


Fig. 2. Trophic generality among the five main types of predators in the broom web: (a) birds, (b) spiders, (c) beetles, (d) flies and (e) bugs.

did not have a significant effect on primary parasitoid vulnerability to hyperparasitoid attack ($F = 2.34$, $P > 0.05$, Fig. 3d). In these statistical tests, the data were log-transformed to meet the assumptions of normality and the data from the single root feeding species were excluded from the analysis. Externally feeding herbivores were most vulnerable to predators, mining herbivores were most vulnerable to parasitoids and primary parasitoids feeding on the gall inhabitants and concealed herbivores were most vulnerable to hyperparasitoids (Fig. 3a–d). The pathogens consumed an externally feeding herbivore, a miner and the root feeder (Fig. 3e).

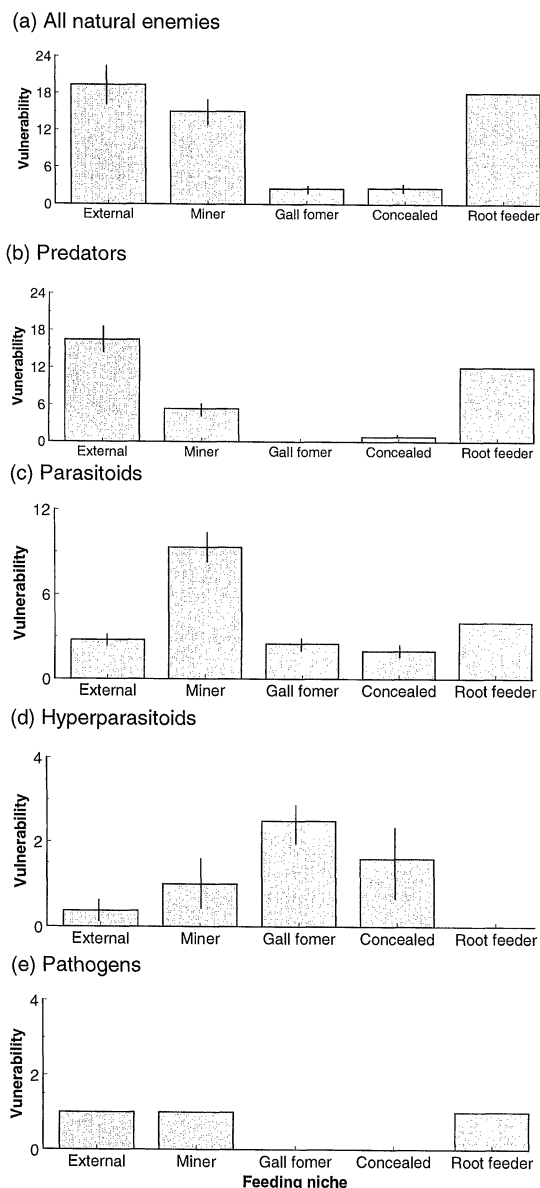


Fig. 3. Effect of feeding style on herbivore vulnerability (number of consumer species per herbivore species) for: (a) all consumers, (b) predators, (c) primary parasitoids, (d) hyperparasitoids and (e) pathogens. Error bars represent standard errors.

DISTRIBUTION OF VULNERABILITY AMONG HERBIVORES

The distribution of the species richness of consumers (predators, parasitoids and pathogens) among herbivore species is shown in Fig. 4a. All species of herbivores had at least one consumer species. The range in vulnerability is large, going from one to 31 consumer species and is skewed to the left with a median value of 13 consumers. The distribution of the number of predator species per herbivore species shows a rather bimodal distribution: seven species of herbivores have more than 16 predators, and seven spe-

cies have no predators (Fig. 4b). The herbivores with no predators are found mostly living inside the broom seed pod. The distribution of the number of parasitoid species per herbivore species is skewed to the right with most hosts having 3–4 parasitoids (Fig. 4c). The primary parasitoids on most herbivores are invulnerable to hyper-parasitoids, but a few species are consumed by 3–4 species (Fig. 4d). The average herbivore's vulnerability to predators is higher than its vulnerability to parasitoids with median values of 5.5 consumers and three consumers, respectively; however, this effect is not significant (Wilcoxon two-sample test, $W = 645.5$, $P > 0.05$, Fig. 4b,c). Very few herbivores were diseased: only three species were consumed by pathogens (Fig. 4e).

THE RELATIONSHIP BETWEEN VULNERABILITY TO PREDATORS AND VULNERABILITY TO PARASITIDS

For the herbivore community on broom, there was a positive but not statistically significant relationship between species richness of predators and species richness of parasitoids: $r = 0.37$, $P > 0.05$. However, there is a negative correlation ($r = -0.79$, $P < 0.001$) between the percentage mortality induced by predators and the percentage mortality induced by parasitoids among the 13 species for which we have data (Fig. 5). Thus, a reduction in the mortality attributable to predators appears to be offset by an increase in the mortality attributable to parasitoids and vice versa.

THE FOOD WEB

The web describes the interactions between nine insect orders, which comprise both predators and prey species, plus five other types of consumers: spiders, harvestmen, birds, mites, fungi and bacteria. Cannibalism was rare in this food web; in the whole web, two predator species and two parasitoid species were cannibals.

Using taxonomic species (not trophic species or higher-level taxa) food web statistics were calculated for the whole web, the parasitoid sub-web, the predator sub-web and the pathogen sub-web. The number of species is obviously greatest in the whole web (154), approximately equal in the parasitoid (76) and predator (85) sub-webs and smallest in the pathogen sub-web (23). Connectance for the predator sub-web (0.036) is higher than that for the whole web (0.016) or the parasitoid sub-web (0.018) (Fig. 6a) and reflects the wider host range of the predators. Food web statistics were also calculated for these webs after their taxa were aggregated into trophic species (Fig. 6b). This treatment increased connectance as well as slightly changing the ranking of connectance among webs. Compared

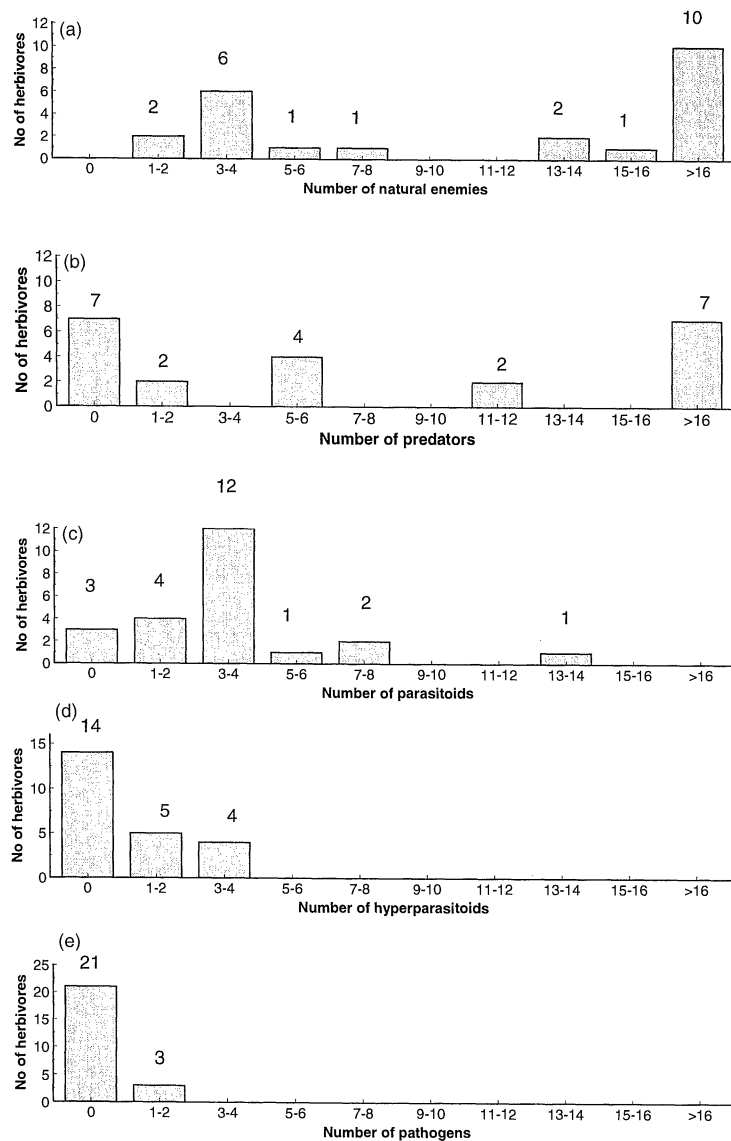


Fig. 4. Distribution of vulnerability (species richness of consumers) among herbivore species for: (a) all natural enemies, (b) predators, (c) parasitoids, (d) hyperparasitoids and (e) pathogens.

to the whole web and the parasitoid sub-web, the predator sub-web with 48 trophic species still had the highest connectance (0.072). However, the connectance of the whole web with 85 trophic species (0.032) became 19% higher than that of the parasitoid sub-web with 48 trophic species (0.027). The connectance of the 22 trophic-species pathogen web is 0.045.

A larger predator consumes a smaller prey in 93% of the 80 predator-prey interactions for which body sizes are known. A smaller parasitoid attacks a larger host in 79% of the 14 parasitoid-host interactions. Not surprisingly, all pathogens were smaller than their hosts. Parasitoids were smaller than predators (Wilcoxon two-sample test, $W = 123$, $P < 0.001$, Fig. 7). There was a greater range in predator body size compared to parasitoid body size: a

145-fold difference in size between the smallest and the largest predator compared to a six-fold difference in size between the smallest and the largest parasitoid.

Figure 8 depicts the food web matrices for the whole web, the predator sub-web and the parasitoid sub-web. The predator sub-web is predominantly upper triangular, the parasitoid sub-web is predominantly lower triangular and the whole web neither upper nor lower triangular. A simple measure of upper triangularity in a matrix is the number of non-zero elements above the leading diagonal minus the number below, divided by the total number of off-diagonal non-zero elements (Warren & Lawton 1987). This gives an index, U , from -1 to $+1$. The more positive the value the more upper triangular the matrix; for the predator sub-web $U = 0.85$ and

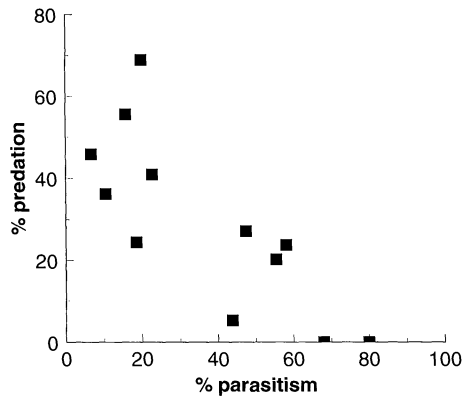


Fig. 5. Relationship between the percentage mortality attributable to predators and the percentage mortality attributable to parasitoids for 13 herbivorous species in the broom web.

for the parasitoid sub-web, $U = -0.57$. U was not calculated for the whole web as body length data were biased towards predators. This would result in a biased measure of triangularity.

Discussion

This study reports the first description and analysis of a large food web describing the trophic interactions among insect herbivores, their predators, para-

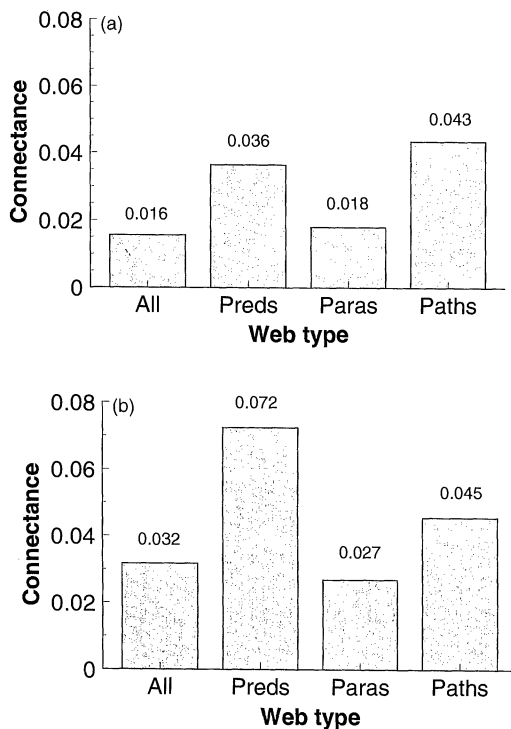


Fig. 6. Connectance of the whole web, the predator sub-web, the parasitoid sub-web and the pathogen sub-web for (a) taxonomic species and (b) trophic species.

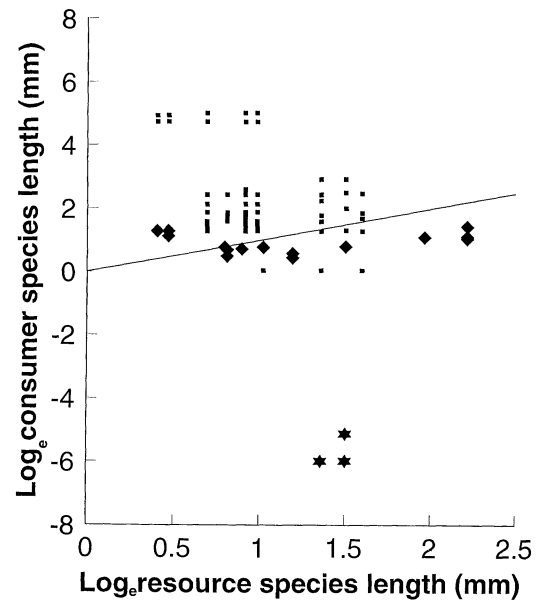


Fig. 7. The relationship between \log_e consumer size and \log_e resource size for: parasitoids (\blacklozenge), pathogens (\blackstar), and predators (\blacksquare). The line shows the expected relationship if consumer and resource species are of equal size. Above this line the consumer species is larger than the resource species, below the line the consumer species is smaller than the resource species.

sitoids and pathogens. Food chains comprising green plants, insect herbivores and parasitoids include over half of all known species of metazoa (Strong, Lawton & Southwood 1984). Thus the web may be characteristic of a substantial fraction of biodiversity.

First, we outline potential sources of bias in the broom food web. Then we discuss predator and parasitoid trophic generality and the effect of herbivore feeding style upon herbivore mortality. We next look at the relationship between body size and the feeding relations of the organisms in this community. We end by discussing the advantages of studying complete communities of natural enemies rather than working on subsets of communities.

BIASES IN THE WEB

Three broad categories of web can be found in the literature: sink, source and community webs (Cohen 1978). The broom web is a source web; it was constructed by tracing trophic links upward from a species, in this case upward from broom, to broom herbivores and to herbivore natural enemies. However, broom does usually form dense monocultures, with other vegetation being shaded out by the broom (J. Memmott, personal observation). Thus, in the middle of a broom patch there would be few, if any other plants or herbivores present other than

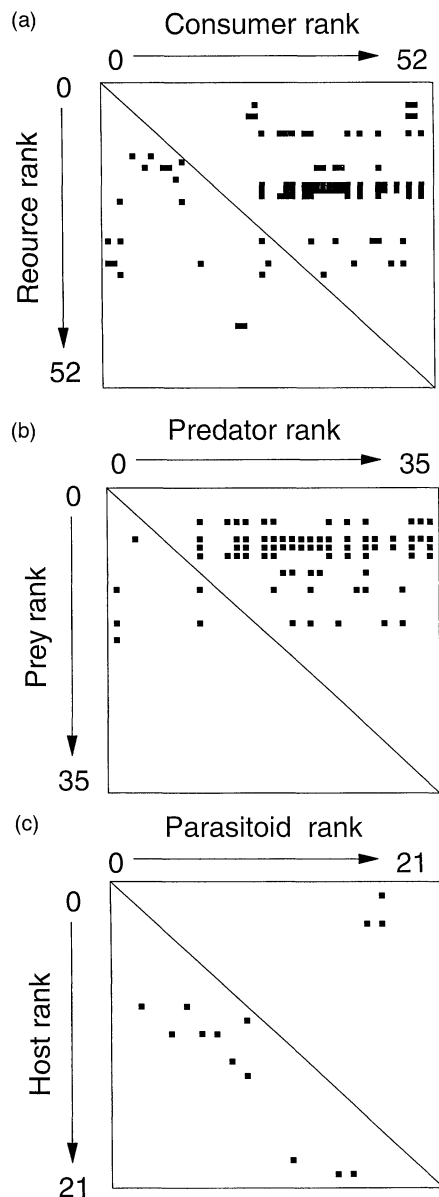


Fig. 8. Graphical illustrations of the food web matrices for (a) the entire web, (b) the predator sub-web and (c) the parasitoid sub-web. The species are arranged in increasing body length along the rows and columns; ■ denotes a consumer species feeding on a resource species.

those associated with broom. The use of source webs is a widespread practice in food-web biology. For example, all 12 of the plant-herbivore webs described in Schoenly, Beaver & Heumiers' (1991) study of insect food webs are source webs. Source webs, as subgraphs of their respective communities, overestimate or underestimate prey-to-predator ratios (Schoenly *et al.* 1991). Furthermore, the fractions of basal, intermediate and top species are sensitive to the number of source species in the web and linkage densities (Hawkins *et al.* 1997). We did not calculate predator:prey ratios or the fractions of basal, intermediate and top species for these reasons.

Most insect food webs qualify as 'regional' food webs (Kitching 1987) as they are based on the summed data from a number of field seasons and field sites. The broom web has similar traits. Most of the studies lasted for 3 years and took place in more than one of the six broom patches at Silwood Park. Food web structure will vary both spatially and temporally and the data presented here are inappropriate for analysing spatiotemporal variability (Schoenly & Cohen 1991). This shortcoming is shown by most published food webs.

Sample size can be a confounding effect in determining both the number of consumer species per resource species and the host range of the consumer species. For example, the number of parasitoid species reared from leaf miner species was significantly affected by the leaf miner sample size (Memmott *et al.* 1994). In the broom predator data, it is quite likely that common predators were tested more frequently than rare predators. This would lead to common predators having a greater host range than rare predators.

The study of the broom community by Waloff and colleagues, while extensive, is not conclusive. Not all species that trophically interact with the 154 taxa at the Silwood site were sampled. Thus, some species will probably be missing from the web. For example, predators were not screened for pathogens, parasitoids or predators of their own, and some of the rarer herbivores found on broom were not studied at all.

DISTRIBUTION OF TROPHIC GENERALITY

The ecological and evolutionary conditions selecting for trophic specialization are not well understood (Futuyma & Moreno 1988). However, the processes leading to specialization by parasitoids and predators are likely to be different. For predators, the size of prey often determines whether or not it can be handled (e.g. Sih 1987), whereas for parasitoids the physiological characteristics of the host are important (e.g. Lawrence & Lanzrein 1993; Strand & Pech 1995). Foraging strategy can also affect host range. For example, predators exhibiting an ambush-type foraging strategy typically exhibit broad host ranges, capturing and consuming a wide array of species (Strand & Obrycki 1996). In the broom web, the largest host ranges are found in the spiders and the bugs, many of which exhibit an ambush style strategy.

Schoenly *et al.* (1991) reported that predaceous insects are less trophically general than most other insectivores and that most insect species have no more than three local consumers. Sixty-six per cent of consumed species in the broom web have more than three local consumers and 37% of species had more than 16 local consumers (Fig. 4a), assuming

that all six sites in Silwood Park qualify as a single locality. The predator generality data presented here were determined by gut analysis, a method that does not rely on field observation. We suspect that the high specialization reported by Schoenly *et al.* (1991) might be a simple consequence missing predator-prey interactions in the field. For example, nocturnally feeding carabid beetles were found in the broom web and their resources included weevil eggs, a dietary item that would almost certainly have been missed if observational methods were used to determine trophic interactions.

The effect of feeding style upon parasitoid species richness agrees with that observed by Hawkins & Lawton (1987). One difference between the broom data and the data of Hawkins & Lawton was the high vulnerability of root feeders. While data from only a single root feeder were available, it does illustrate the fact that stages other than the concealed larval stage may be vulnerable to attack. Thus, the eggs of the root feeder were consumed by 12 species of predator and the adults were consumed by parasitoids.

Hawkins *et al.* (1997) looked at the life tables of 78 holometabolous insect species and found that, on average, parasitoids killed a greater proportion of each species than did either predators or pathogens. It is not possible to generalize about which class of consumers in the broom web is the main source of mortality due to the negative relationship between mortality caused by predators and mortality caused by parasitoids. Thus, it appears that if a herbivore has a low level of mortality from predators, it suffers from a high level of mortality from parasitism and vice versa. A problem remains with the data in that parasitized insects could be consumed by predators before the parasitoid has emerged which would conceal the parasitoid attack. Alternatively, parasitism or disease may render the herbivore more likely to succumb to predation. Unfortunately, correcting for hidden interactions among mortality sources requires information that is generally unobtainable in the field (Hawkins *et al.* 1997). Consequently, the data in Fig. 5 are only suggestive.

THE FOOD WEB

If the patterns observed in the broom web are general, it appears that insect food webs which exclude predators do not bias estimates of community connectance as much as excluding parasitoids. Webs that exclude parasitoids overestimated the value of connectance in our whole web by more than a factor of two. Given that much food-web theory centres on the idea of connectance (Lawton 1995) and given the reluctance of many food web biologists to include parasitoids or pathogens among the consumers in their communities (but see Huxham,

Raffaelli & Pike 1995 and Huxham, Beaney & Raffaelli 1996, for exceptions), this bias is a cause for concern. The connectance of terrestrial webs (e.g. Goldwasser & Roughgarden 1993) and aquatic webs (e.g. Martinez 1991; 1993a) that ignore parasitoids and other highly specialized species, such as parasites and pathogens, may substantially overestimate the connectance of more complete communities in those habitats.

Connectance of trophic-species webs has been shown to be particularly robust to variable aggregation (Martinez 1991; 1993b) and sampling effort (Martinez *et al.*, 1999). The connectance of our trophic-species webs appears comparable to other webs in the literature. Many predator-dominated webs have connectance approximately equal to 0.1 or from about 0.06–0.14 (e.g. Huxham *et al.* 1996; Martinez 1992; 1993a, 1995; Goldwasser & Roughgarden 1993) while another intensely observed parasitoid sub-web (Martinez *et al.* 1999) has a connectance of 0.02. Our predator and parasitoid sub-webs fall within similar ranges. It is reasonable that the combined web would have an intermediate level of connectance between these extremes. Further analyses of trophic webs may generalize our result that the connectances of whole webs are intermediate between those of predator sub-webs and those of parasitoid sub-webs.

Huxham *et al.* (1996) studied the effect of web completeness upon food web statistics using data from an estuarine web in the Ythan estuary, England. In this study, webs of four different levels of resolution were constructed. Two of these webs (version 1 and version 2) use data based on observed, as opposed to hypothesized, links and consequently are comparable to the broom web. Version 1 was predominantly a predator web, while version 2 included substantial numbers of parasites. The connectance of these two webs were 0.098 and 0.058 respectively. While these data are different from the comparable values from the broom web (0.036 and 0.016) the effect of excluding parasites is the same – connectance is overestimated.

In the broom web, parasitoids constitute half the consumer species of broom herbivores and 81% of the parasitoids measured attacked prey larger than themselves. Parasitoids and parasites that attack only species larger than themselves create food web matrices that are lower triangular. In this case, the cascade model still holds because species are still ordered in hierarchy. In the broom food web, the predator sub-web is nearly completely upper triangular and the parasitoid/pathogen web is nearly completely lower triangular. That is, the whole web is not triangular and therefore inconsistent with the cascade model if body size is the basis of the feeding hierarchy. Still, the trophic cascade model based on body size may be applicable to subsets of food webs

such as those based on predators or on parasitoids/pathogens as long as none of these species is cannibalistic.

THE USES OF MORE COMPLETE FOOD WEBS

A number of critiques of food web research have lamented the flaws in published webs and listed the ways in which they can be improved (e.g. Paine 1988; Lawton 1989; Cohen *et al.* 1993b). Attempts have been made to remedy some of their ills. Thus, the effects of spatial and temporal variation have been addressed (e.g. Warren 1989; Schoenly & Cohen 1991; Tavares-Cromar & Williams 1996), interaction strength has been quantified (Paine 1992; Hall & Raffaelli 1993; Muller *et al.* 1999) and webs have been experimentally manipulated (e.g. Paine 1992; Memmott, Godfray & Bolton 1993). However, there remains a decided paucity of webs, such as ours, that include multiple classes of consumers.

Ideally, such community webs should be fully quantitative, with the densities of all consumers and resource species expressed in common units. Quantitative webs are superior to connectance webs for addressing intra-system population dynamics because they provide quantitative insight into the relative influence of shared consumers and the degree to which one or a few species might affect population dynamics within the system (Memmott *et al.* 1994). The study of host–parasitoid and predator–prey interactions has proved a fruitful and active area of population dynamics over the last 20 years. However, attention has focused almost exclusively on interactions between pairs of species or, at the most, assemblages of a few species. Aside from the simplest agricultural systems, the vast majority of terrestrial trophic interactions are embedded in a complex food web including predator, parasitoid and pathogen interactions. Although there may be a complex web of interactions linking many consumer species with their resource species, a few interactions may dominate the system numerically (Paine 1988, 1992). The idea that communities may be dominated by a few keystone species has a long history in ecology (Mills, Soule & Doak 1993) (but see McCann, Hastings & Huxel (1998) and Berlow (1999) for an alternative viewpoint). The presence of keystone species within comprehensive food webs will increase the likelihood that we can extend our understanding of simple consumer–resource interactions to the study of more complex communities.

As already stated, there are many data on parasitoid trophic habits but few data on predator, parasite or pathogen trophic habits. The predator data presented here were collected using a method developed by Leone in 1947 (Dempster 1960). More

modern techniques (e.g. molecular probes) may be adapted to identify predator gut contents. Such methods exist and are widely used in applied studies; for example, Symonson *et al.* (1996) used enzyme-linked immunosorbent assay (ELISA) to determine the concentration and quantity of slug haemolymph in the crops of carabid beetles. To date, such methods have not been applied to food web research. Pathogen data in webs are lacking probably because the field of pathogen community ecology is in its infancy, particularly in comparison to the study of the impact of pathogens on host population dynamics. This problem may be addressed by involving pathologists in food web studies.

We have shown that including more classes of consumers in the same web identified new patterns, such as the low connectance in parasitoid sub-webs, and suggested that predator-dominated food webs may overestimate connectance, at least in source food webs. Systematic inclusion of pathogens in food webs may lead to further advances as well as provide a more realistic description of the trophic structure of natural communities.

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Appendix 1

A list of the species found associated with broom at Silwood Park. For each species, the following information is listed: code number, name, order, feeding style, feeding location and resource species. Feeding location is coded for the herbivores and omnivores. E: external feeder; M: miner; P: inside seed pod; PG: Inside gall on pod; R: root feeder.

- 1 *Cytisus scoparius* PLANT PLANT 0 0 0 0 0 0 0 0 0 0
- 2 *Bruchidius ater* (Marsham) COLEOPTERA POD/SEED-FEEDER P 1 0 0 0 0 0 0 0 0 0
- 3 *Apion fuscirostre* Fabrocus COLEOPTERA POD/SEED-FEEDER P 1 0 0 0 0 0 0 0 0 0
- 4 *Contarinia pulchripes* (Kieffer) DIPTERA POD/SEED-FEEDER P 1 0 0 0 0 0 0 0 0 0
- 5 *Clinodiplosis sarothamni* Kieffer DIPTERA POD/SEED-FEEDER P 1 0 0 0 0 0 0 0 0 0
- 6 *Asphondylia sarothamni* H. Loew DIPTERA POD/SEED-FEEDER PG 1 0 0 0 0 0 0 0 0 0
- 7 *Phytodecta olivacea* (Forster) COLEOPTERA FOLIVORE E 1 0 0 0 0 0 0 0 0 0
- 8 *Sitona regensteiniensis* Hbst COLEOPTERA ROOT-FEEDER R 1 0 0 0 0 0 0 0 0 0
- 9 *Chesias legatella* (Schieffermueller) LEPIDOPTERA FOLIVORE E 1 0 0 0 0 0 0 0 0 0
- 10 *Chesias rufata* (Fabricius) LEPIDOPTERA FOLIVORE E 1 0 0 0 0 0 0 0 0 0
- 11 *Acyrtosiphon spartii* (Koch) HOMOPTERA SAP-FEEDER E 1 0 0 0 0 0 0 0 0 0
- 12 *Aphis sarothamni* Fransen HOMOPTERA SAP-FEEDER E 1 0 0 0 0 0 0 0 0 0
- 13 *Arytaina spartii* Guerin-Memeville HOMOPTERA SAP-FEEDER E 1 0 0 0 0 0 0 0 0 0
- 14 *Arytaina genistae* Latreille HOMOPTERA SAP-FEEDER E 1 0 0 0 0 0 0 0 0 0
- 15 *Ptezodoratus lituratus* Fabricius HEMIPTERA SAP-FEEDER E 1 0 0 0 0 0 0 0 0 0
- 16 *Apion immune* Kirby COLEOPTERA MINER M 1 0 0 0 0 0 0 0 0 0
- 17 *Leucoptera spartifoliella* Hubner LEPIDOPTERA MINER M 1 0 0 0 0 0 0 0 0 0
- 18 *Phocephthorus rhododactylus* (Marsh.) COLEOPTERA MINER M 1 0 0 0 0 0 0 0 0 0
- 19 *Halystinus obscurus* (Marsh.) COLEOPTERA MINER M 1 0 0 0 0 0 0 0 0 0
- 20 *Orthotylus adenocarpi* (Perris) HEMIPTERA OMNIVORE E 1 7 11 12 13 14 20 21 22 0 0
- 21 *Orthotylus virescens* (Douglas and Scott) HEMIPTERA OMNIVORE E 1 7 11 12 13 14 22 0 0 0
- 22 *Orthotylus concolor* (Kirschbaum) HEMIPTERA OMNIVORE E 1 7 11 12 13 14 0 0 0 0
- 23 *Heterocordylus tibialis* (Hahn) HEMIPTERA OMNIVORE E 1 7 11 12 13 14 20 21 22 24 0
- 24 *Asciodema obseletum* (Fieber) HEMIPTERA OMNIVORE E 1 7 11 12 13 14 20 21 22 0 0
- 25 *Anaphes autumnalis* Forster HYMENOPTERA PARASITOID 21 0 0 0 0 0 0 0 0 0
- 26 *Aphidius* sp.1 HYMENOPTERA PARASITOID 11 0 0 0 0 0 0 0 0 0
- 27 *Aphidius* sp.2 HYMENOPTERA PARASITOID 11 0 0 0 0 0 0 0 0 0
- 28 *Aphanoginus venustus* (Parr) HYMENOPTERA PARASITOID 95 0 0 0 0 0 0 0 0 0
- 29 *Apanteles fulvipes* Halliday HYMENOPTERA PARASITOID 9 0 0 0 0 0 0 0 0 0
- 30 *Apanteles vitripennis* Curtis HYMENOPTERA PARASITOID 9 10 0 0 0 0 0 0 0 0
- 31 *Asolcus* sp.1 HYMENOPTERA PARASITOID 15 0 0 0 0 0 0 0 0 0
- 32 *Asolcus* sp.2 HYMENOPTERA PARASITOID 15 0 0 0 0 0 0 0 0 0
- 33 *Bacillus* sp. nr lentus FUNGI DISEASE 17 0 0 0 0 0 0 0 0 0
- 34 *Beauveria* sp. FUNGI DISEASE 7 8 0 0 0 0 0 0 0 0
- 35 *Centistes excrucians* Haliday HYMENOPTERA PARASITOID 8 0 0 0 0 0 0 0 0 0
- 36 *Cheiopachys colon* (L.) HYMENOPTERA PARASITOID 18 0 0 0 0 0 0 0 0 0

37	<i>Chrysocharis gemma</i> (Walker)	HYMENOPTERA PARASITOID	17 0 0 0 0 0 0 0 0 0 0
38	<i>Diasparsis</i> sp.	HYMENOPTERA PARASITOID	94 0 0 0 0 0 0 0 0 0 0
39	<i>Dinotiscus bidentulus</i> Thoms.	HYMENOPTERA PARASITOID	18 19 0 0 0 0 0 0 0 0 0
40	<i>Diospilus ephippium</i> (Nees)	HYMENOPTERA PARASITOID	94 0 0 0 0 0 0 0 0 0 0
41	<i>Entodon</i> sp. nr <i>cyanellus</i> Zett.	HYMENOPTERA PARASITOID	18 19 0 0 0 0 0 0 0 0 0
42	<i>Ephedrus</i> sp.	HYMENOPTERA PARASITOID	11 0 0 0 0 0 0 0 0 0 0
43	<i>Erythmelus goochi</i> Enoch	HYMENOPTERA PARASITOID	24 0 0 0 0 0 0 0 0 0 0
44	<i>Eupelmella vesicularis</i> (Retz)	HYMENOPTERA PARASITOID	18 19 0 0 0 0 0 0 0 0 0
45	<i>Eurytoma</i> sp. nr <i>morio</i> Boh.	HYMENOPTERA PARASITOID	18 0 0 0 0 0 0 0 0 0 0
46	<i>Habrocytus sequester</i> (Walker)	HYMENOPTERA PARASITOID	2 3 0 0 0 0 0 0 0 0 0
47	<i>Inostemma lycon</i> Walker	HYMENOPTERA PARASITOID	4 0 0 0 0 0 0 0 0 0 0
48	<i>Leiophron heterocordyli</i> Richards	HYMENOPTERA PARASITOID	20 23 24 0 0 0 0 0 0 0 0
49	<i>Leiophron orthotyli</i> Richards	HYMENOPTERA PARASITOID	20 21 22 24 0 0 0 0 0 0 0
50	<i>Leiophron apicalis</i> Curtis	HYMENOPTERA PARASITOID	20 21 22 24 0 0 0 0 0 0 0
51	<i>Macquartia brevicornis</i> (Panzer)	DIPTERA PARASITOID	7 0 0 0 0 0 0 0 0 0 0
52	<i>Meigenia mutabilis</i> (Fallen)	DIPTERA PARASITOID	7 0 0 0 0 0 0 0 0 0 0
53	<i>Microctonus aethiops</i> (Nees)- <i>secalis</i> Hal. complex	HYMENOPTERA PARASITOID	16 0 0 0 0 0 0 0 0 0 0
54	<i>Microlitis fordi</i> Nixon	HYMENOPTERA PARASITOID	9 10 0 0 0 0 0 0 0 0 0
55	<i>Necremnus metalarus</i> Walk.	HYMENOPTERA PARASITOID	17 0 0 0 0 0 0 0 0 0 0
56	<i>Necremnus</i> sp.	HYMENOPTERA PARASITOID	17 0 0 0 0 0 0 0 0 0 0
57	<i>Nepiesta</i> sp.	HYMENOPTERA PARASITOID	7 0 0 0 0 0 0 0 0 0 0
58	<i>Paecilomyces</i> sp.	FUNGI DISEASE	8 0 0 0 0 0 0 0 0 0 0
59	<i>Patasson diana</i> (Girault)	HYMENOPTERA PARASITOID	8 0 0 0 0 0 0 0 0 0 0
60	<i>Patasson brachygaster</i> (Debauche)	HYMENOPTERA PARASITOID	22 0 0 0 0 0 0 0 0 0 0
61	<i>Perilitus dubius</i> (Wesmael)	HYMENOPTERA PARASITOID	7 0 0 0 0 0 0 0 0 0 0
62	Phoridae sp.	DIPTERA PARASITOID	9 10 0 0 0 0 0 0 0 0 0
63	<i>Platygaster</i> sp.	HYMENOPTERA PARASITOID	5 0 0 0 0 0 0 0 0 0 0
64	<i>Platygerrhus dolosus</i> (Walk.)	HYMENOPTERA PARASITOID	94 0 0 0 0 0 0 0 0 0 0
65	<i>Praon</i> sp.	HYMENOPTERA PARASITOID	11 0 0 0 0 0 0 0 0 0 0
66	<i>Pringalio soemias</i> Walk.	HYMENOPTERA PARASITOID	17 0 0 0 0 0 0 0 0 0 0
67	<i>Prionomitus mitratus</i> Dalm.	HYMENOPTERA PARASITOID	14 0 0 0 0 0 0 0 0 0 0
68	<i>Pseudocatolaccus thoracicus</i> (Walker)	HYMENOPTERA PARASITOID	6 0 0 0 0 0 0 0 0 0 0
69	<i>Raphitelus maculatus</i> Walk.	HYMENOPTERA PARASITOID	18 0 0 0 0 0 0 0 0 0 0
70	<i>Spathius rubidus</i> (Rossi)	HYMENOPTERA PARASITOID	18 19 0 0 0 0 0 0 0 0 0
71	<i>Systasis encyrtoides</i> (Walker)	HYMENOPTERA PARASITOID	4 0 0 0 0 0 0 0 0 0 0
72	<i>Telenomus truncatus</i> Mayr	HYMENOPTERA PARASITOID	15 0 0 0 0 0 0 0 0 0 0
73	<i>Telenomus sokolovi</i> Mayr	HYMENOPTERA PARASITOID	15 0 0 0 0 0 0 0 0 0 0
74	<i>Tetrastichus</i> nr <i>flavovarius</i> (Nees)	HYMENOPTERA PARASITOID	18 69 0 0 0 0 0 0 0 0 0
75	<i>Tetrastichus</i> nr. <i>galactopus</i> (Ratz)	HYMENOPTERA PARASITOID	17 0 0 0 0 0 0 0 0 0 0
76	<i>Tetrastichus</i> sp.	HYMENOPTERA PARASITOID	7 0 0 0 0 0 0 0 0 0 0
77	<i>Triaspis</i> sp. nr <i>obscurellus</i> (Nees)	HYMENOPTERA PARASITOID	2 0 0 0 0 0 0 0 0 0 0
78	<i>Trichogramma</i> sp.1	HYMENOPTERA PARASITOID	2 0 0 0 0 0 0 0 0 0 0
79	<i>Trichogramma</i> sp.2	HYMENOPTERA PARASITOID	7 0 0 0 0 0 0 0 0 0 0
80	<i>Ablaxis</i> sp.	HYMENOPTERA PARASITOID	18 0 0 0 0 0 0 0 0 0 0
81	<i>Aprostocetus</i> sp. nr <i>aethiops</i> (Zetterstedt)	HYMENOPTERA PARASITOID	4 81 0 0 0 0 0 0 0 0 0
82	<i>Aprostocetus brevicornis</i> Panzer	HYMENOPTERA PARASITOID	6 82 154 0 0 0 0 0 0 0 0
83	<i>Eupelmus urozonus</i> Dalman	HYMENOPTERA PARASITOID	46 18 19 0 0 0 0 0 0 0 0
84	<i>Eurytoma dentata</i> Mayr	HYMENOPTERA PARASITOID	82 6 0 0 0 0 0 0 0 0 0
85	<i>Tetrastichus</i> nr <i>attalus</i> (Walk.)	HYMENOPTERA PARASITOID	18 19 69 0 0 0 0 0 0 0 0
86	<i>Torymus</i> nr <i>microstigma</i> (Walker)	HYMENOPTERA PARASITOID	46 82 154 0 0 0 0 0 0 0 0
87	<i>Aprostocetus tibialis</i> (Kurdjumov)	HYMENOPTERA PARASITOID	46 0 0 0 0 0 0 0 0 0 0
88	<i>Asaphes</i> sp.	HYMENOPTERA PARASITOID	26 27 42 65 0 0 0 0 0 0 0
89	<i>Charips</i> sp.	HYMENOPTERA PARASITOID	26 27 42 65 0 0 0 0 0 0 0
90	<i>Lygocerus</i> sp.	HYMENOPTERA PARASITOID	26 27 42 65 0 0 0 0 0 0 0
91	<i>Mesochorus</i> sp.	HYMENOPTERA PARASITOID	54 0 0 0 0 0 0 0 0 0 0
92	<i>Mesopolobus mediterraneus</i> (Mayr)	HYMENOPTERA PARASITOID	46 77 0 0 0 0 0 0 0 0 0
93	<i>Torymus</i> sp. nr <i>micropterus</i> (Walker)	HYMENOPTERA PARASITOID	46 0 0 0 0 0 0 0 0 0 0
94	<i>Laemophloeus ater</i> (Ol.)	COLEOPTERA PREDATOR	M 18 19 0 0 0 0 0 0 0 0 0
95	<i>Lestodiplosis</i> sp.	DIPTERA PREDATOR	P 5 95 0 0 0 0 0 0 0 0 0

96	<i>Abax parallelopedus</i> (Pill and Mitt.)	COLEOPTERA PREDATOR	7 8 0 0 0 0 0 0 0 0
97	<i>Adalia bipunctata</i> (L.)	COLEOPTERA PREDATOR	11 12 13 14 0 0 0 0 0 0
98	<i>Adalia decempunctata</i> L.	COLEOPTERA PREDATOR	11 12 13 14 0 0 0 0 0 0
99	<i>Anatis ocellata</i> (L.)	COLEOPTERA PREDATOR	11 12 13 14 0 0 0 0 0 0
100	<i>Anthocoris nemoralis</i> (Fab.)	HEMIPTERA PREDATOR	7 11 12 13 14 20 21 22 23 24 0
101	<i>Anthocoris nemorum</i> (L.)	HEMIPTERA PREDATOR	7 11 12 13 14 20 21 22 23 24 0
102	<i>Anthocoris sarothamni</i> (Douglas and Scott)	HEMIPTERA PREDATOR	7 11 12 13 14 20 21 22 23 24 0
103	<i>Anystis baccarum</i> L.	ACARINA PREDATOR	2 7 20 21 22 23 24 0 0 0 0
104	<i>Araneus diadematus</i> Clerck	ARANEAE PREDATOR	13 14 20 21 22 24 0 0 0 0 0
105	<i>Araneus</i> sp.	ARANEAE PREDATOR	17 0 0 0 0 0 0 0 0 0 0
106	<i>Chrysopa carnea</i> Stephens	NEUROPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
107	<i>Coccinella septempunctata</i> L.	COLEOPTERA PREDATOR	11 12 13 14 0 0 0 0 0 0 0
108	<i>Deraeocoris ruber</i> (L.)	HEMIPTERA PREDATOR	13 14 0 0 0 0 0 0 0 0 0
109	<i>Ectobius laponicus</i> (Oliver)	DICTYOPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
110	<i>Evarcha arcuata</i> Clerck	ARANEAE PREDATOR	13 14 20 21 22 0 0 0 0 0 0
111	<i>Exochomus quadripustulatus</i> L.	COLEOPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
112	<i>Feronia madidus</i> (Fab.)	COLEOPTERA PREDATOR	7 8 0 0 0 0 0 0 0 0 0
113	<i>Feronia nigra</i> (Schall)	COLEOPTERA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
114	<i>Forficula auricularia</i> (L.)	DERMAPTERA PREDATOR	7 11 12 13 14 17 0 0 0 0 0
115	<i>Fringilla coelebs</i> (Kleinschmidt)	BIRD PREDATOR	11 12 13 14 0 0 0 0 0 0 0
116	<i>Halysia sexdecimguttata</i> L.	HEMIPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
117	<i>Harpulus rubripes</i> (Duft)	COLEOPTERA PREDATOR	7 0 0 0 0 0 0 0 0 0 0
118	<i>Hemerobius</i> sp.	NEUROPTERA PREDATOR	13 14 0 0 0 0 0 0 0 0 0
119	<i>Himacerus apterus</i> (Fab.)	HEMIPTERA PREDATOR	7 13 14 0 0 0 0 0 0 0 0
120	<i>Heterotoma merioptera</i> (Scopoli).	HEMIPTERA PREDATOR	7 11 12 13 14 20 21 22 0 0 0
121	<i>Ilyobates nigricollis</i> (Paykull)	COLEOPTERA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
122	Immature spiders	ARANEAE PREDATOR	103 0 0 0 0 0 0 0 0 0 0
123	<i>Leistus</i> spp.	COLEOPTERA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
124	<i>Lyniphia triangularis</i> Clerck	ARANEAE PREDATOR	13 14 17 20 21 22 23 24 0 0 0
125	<i>Meta segmentata</i> Clerck	ARANEAE PREDATOR	13 14 17 20 21 22 24 0 0 0 0
126	<i>Nabis flavomarginatus</i> (Scholtz)	HEMIPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
127	<i>Ocypus compressus</i> (Marsh)	COLEOPTERA PREDATOR	7 0 0 0 0 0 0 0 0 0 0
128	<i>Oxyptoda longiuscula</i> (Gravenhorst)	COLEOPTERA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
129	<i>Parus caeruleus</i> (Prazak)	BIRD PREDATOR	11 12 13 14 94 18 19 0 0 0 0
130	<i>Parus major</i> L.	BIRD PREDATOR	94 18 19 0 0 0 0 0 0 0 0
131	<i>Pergamasus crassipes</i> L.	ACARINA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
132	<i>Phaenobremia</i> sp.	DIPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
133	<i>Philodromus aureolus caespiticolis</i> Walck.	ARANEAE PREDATOR	13 14 17 20 21 22 0 0 0 0 0
134	<i>Philonthus politus</i> (L.)	COLEOPTERA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
135	<i>Pisaura mirabilis</i> Clerck	ARANEAE PREDATOR	13 14 20 21 22 0 0 0 0 0 0
136	<i>Plagiognathus arbustorum</i> (Fab.)	HEMIPTERA PREDATOR	11 12 13 14 0 0 0 0 0 0 0
137	<i>Platybunus triangularis</i> Herbst.	OPILIONES PREDATOR	7 0 0 0 0 0 0 0 0 0 0
138	<i>Platycheirus scutatus</i> (Meigen)	DIPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
139	<i>Propylea quatuordecimpunctata</i> (L.)	COLEOPTERA PREDATOR	11 12 13 14 0 0 0 0 0 0 0
140	<i>Prunella modularis occidentalis</i> (Hart.)	BIRD PREDATOR	11 12 13 14 0 0 0 0 0 0 0
141	<i>Rhagonycha elongata</i> (Fall.)	COLEOPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
142	<i>Staphylinus</i> sp.	COLEOPTERA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
143	<i>Stenus</i> sp.	COLEOPTERA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
144	<i>Sylvia curruca curruca</i> (L.)	BIRD PREDATOR	11 12 13 14 0 0 0 0 0 0 0
145	<i>Syrphus luniger</i> Meigen	DIPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
146	<i>Syrphus vitripennis</i> Meigen	DIPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
147	<i>Syrphus calteatus</i> Degeer	DIPTERA PREDATOR	11 12 0 0 0 0 0 0 0 0 0
148	<i>Tachynus rufipes</i> (Degeer)	COLEOPTERA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
149	<i>Theridion ovatum</i> Clerck	ARANEAE PREDATOR	20 21 22 0 0 0 0 0 0 0 0
150	<i>Theridion redimitum</i>	ARANEAE PREDATOR	13 14 0 0 0 0 0 0 0 0 0
151	<i>Xantholinus linearis</i> (Olivier)	COLEOPTERA PREDATOR	8 0 0 0 0 0 0 0 0 0 0
152	<i>Xysticus audax</i> Schrank	ARANEAE PREDATOR	20 21 22 24 0 0 0 0 0 0 0
153	<i>Xysticus cristatus</i> Clerck	ARANEAE PREDATOR	7 13 14 17 20 21 22 24 0 0 0
154	<i>Trotteria sarothamni</i>	DIPTERA POD/SEED-FEEDER	PG 1 0 0 0 0 0 0 0 0 0 0