

Chapter 6

Size, Phylogeny and Life-History in the Evolution of Feeding Specialization in Insect Predators

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6.1 Introduction

The existence of a vast array of animals that are feeding specialists presents evolutionary theory with a problem. How are we to explain their existence? Either we accept that there are adaptive reasons why many animals, particularly insects, should specialize (and then we must understand the selective forces operating to promote specialization in some circumstances, and generalization in others: Scriber 1983; Rausher 1983; Futuyma and Moreno 1988), or we must explain specialists as “dead ends” in evolution (Simpson 1944; Moran 1988).

Feeding specialization is a major ecological feature of animals, with many ramifications. The vast bulk of the literature is concerned with understanding the feeding strategies of herbivorous insects on their host plants, and understanding the ecology of host preference (for a review, see Scriber 1983; Rausher 1983; Futuyma and Peterson 1985; Thompson 1988a). Much of our understanding of the evolution of feeding patterns among herbivorous insects involves a consideration of plant chemistry. Recently, Tauber and Tauber (1987) pointed out that virtually nothing is known about the evolution of feeding specialization in carnivorous insects, particularly species that are not parasitoids. This lack of attention is all the more surprising in view of the fact that predators and parasitoids are responsible for nearly all biocontrol programmes, and make up the majority of insect species. Bristowe (1988) remarked that the “conventional wisdom” about predators is that they tend to be generalists precisely because animal tissues are supposed to be much more nutritious, providing a balanced diet and not differing greatly from species to species. Despite this, all entomologists and ecologists are well aware of the high degree of specificity shown by many if not most carnivorous insects, especially parasitoids but also many predators. The field of predator specialization is thus largely unexplored.

In this chapter I consider some predictions about specialization, garnered largely from the literature concerned with the relationships between herbivorous

insects and their host plants. I test these predictions using data from predatory and non-predatory species from an insect group particularly suitable for this purpose, namely the hoverflies (Diptera, Syrphidae). Adult feeding ecology is reasonably uniform in this family, since the adult flies all visit flowers for pollen and nectar (Gilbert 1981, 1985a, 1986), whilst the larval feeding biology varies widely, and includes predators and non-predators.

In testing these predictions, I categorize the degree of specialization as a species characteristic: I am aware that the concept of a generalist species is a difficult one to maintain, since populations can be local specialists and regional generalists (Fox and Morrow 1981), and even within populations some individuals are more specialized than others (Via 1986; Rossiter 1987; Ng 1988). Here, hoverfly species are assigned to categories of specialization based upon within-habitat sampling of food types. Arguments could be made against all of my predictions; I am, however, attempting to test them against the data.

6.2 Predictions

I make three predictions about the evolution of specialization in the diet range of larval insects. Specialization is defined here as the narrowing of diet range, and often involves a narrowing of the range of habitats used by the larvae, e.g. in saprophagous species. The three predictions are concerned with the trade-off between egg size and egg number, the direction of evolution of diet range, and the reasons why selection might favour a decreased range of food types.

The Trade-off Between Egg Size and Egg Number

The basic postulate is that females of insect specialists on average encounter suitable oviposition sites at a lower rate than generalists, and hence on average ("ceteris paribus") lay fewer eggs in their lifetime. This allows them to increase the allocation of nutrients to each egg.

Prediction 1: *Specialists will lay fewer, larger eggs than generalists.*

A trade-off in nutrient allocation to various activities including reproduction has been a constant feature of theories of life-histories for many years. A recent review (Reznick 1985) concluded that, while some phenotypic studies have failed to detect any trade-offs, genetic studies have nearly always shown negative genetic correlations between fitness components (but see Rollo (1986) for counter arguments). However, some more recent genetic studies have shown positive, not negative, genetic correlations between stocks (e.g. in *Drosophila*; Giesel 1986). van Noordwijk and de Jong (1986) suggested that studies of interspecific differences often show trade-offs between fitness components, whereas studies of individual or population variation often do not: J. Stevens and P. Calow (personal communication) and van Noordwijk and de Jong (1986) independently suggested that a likely cause of this apparent paradox lies in individual differences in resource gathering abilities. Some individuals merely

have more resources to allocate, generating positive genetic correlations. In this study, I assume that the principle of allocation is valid for syrphids in interspecific comparisons, giving data that support this contention.

The prediction that specialists will tend to lay fewer, larger eggs seems very simplistic. However, there is a good deal of direct and indirect support for it, and I cite three examples, below.

Lack of oviposition opportunities may play an important role in determining the size of butterfly eggs. Wiklund et al. (1987) suggest that sun-loving satyrid and pierid butterflies have plenty of time available for oviposition, since they spend much of their time in the sun; instead they are limited in fecundity by egg size, and therefore have reduced egg sizes to a physiological minimum. In shade-loving species of the same groups, there is nothing to be gained by decreasing egg size, since this will not lead to larger numbers of eggs being laid: lack of ovipositional opportunities limits reproductive success in these species. Egg size is related to body size in shade-loving species, but is a constant independent of body size in sun-loving species. Thus, where opportunities for oviposition are limited, eggs are larger in size.

Tauber and Tauber's (1987) study of two *Chrysopa* predators is also consistent with the prediction. The egg volume of the specialist *C. slossonae* is 42% larger than that of the generalist *C. quadripunctata*.

Finally, I have used data from the Drosophilidae (from Kambysellis and Heed 1971; Atkinson 1979) to produce Fig. 6.1, similar to, but not the same as, the

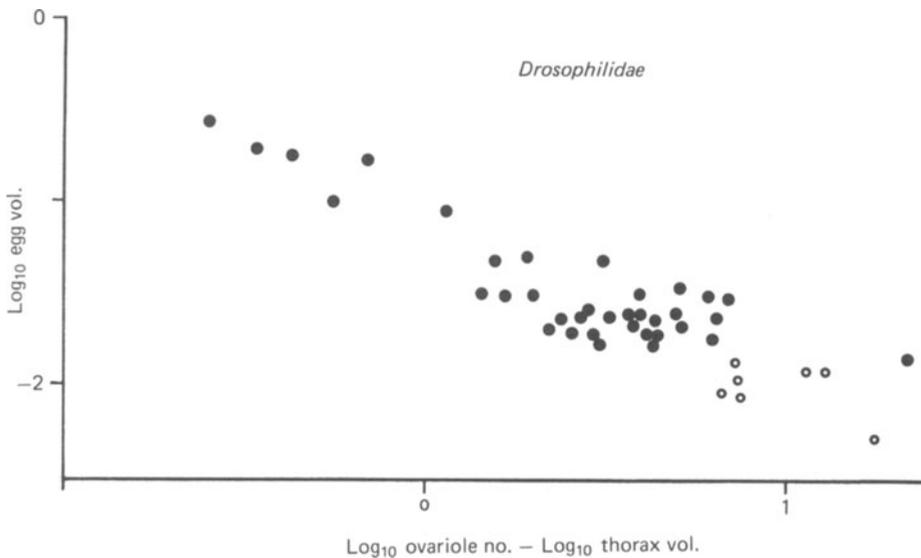


Fig. 6.1. Trade-off between egg size and egg number for the Drosophilidae. Egg numbers are represented by the number of ovarioles in the ovaries, and are adjusted for body size (= thorax length³) as indicated. Data are taken from Kambysellis and Heed (1971: solid circles) and Atkinson (1979: open circles).

representation of the same data by Montague et al. (1981). The graph shows egg size plotted against the number of eggs per unit of body size, and clearly illustrates the trade-off between egg size and egg number in this group. The generalists such as *D. melanogaster* are at the low end of this spectrum, i.e. having many small eggs, whilst the specialized flower-breeding species are at the opposite end, with a few, very large eggs.

However, note that Courtney (1986) challenges the assumption that fecundity is a function of host encounter rate. Some insects fail to lay on many potential host plants even when encountered. This phenomenon is also encountered in parasitoids, and constitutes in part the evidence for "spreading of risk" theories of population regulation (see Hengeveld 1989)

The Direction of the Evolution of Prey Range

Do specialized species always develop from more generalized ancestors, or vice versa; or is there no general direction of the evolution of prey range?

Prediction 2a: *Specialization is a derived or apomorphic trait.*

Prediction 2b: *Specialists tend to be larger in size than generalists.*

Evidence from studies of the host range of phytophagous insects is unclear on whether prediction 2a is reasonable. "It is commonly presumed that specialists evolve from generalists, and this is surely true in many instances. . . . Many, perhaps most, specialists arise from other specialists" (Futuyma and Moreno 1988).

Strong et al. (1984 p 176) suggested that monophagy is neither primitive nor derived, because the evidence shows that diet breadth can expand or contract within a taxon, according to the prevailing selective pressures. The two references that they cited in support of this statement were Benson's (1950) work on British sawflies and Holloway and Hebert's (1979) study of trends in host selection within the Macrolepidoptera. Neither of these studies used a phylogeny, or provided quantitative evidence for their viewpoints: presumably these viewpoints are beliefs derived from their extensive experience with these groups. While such feelings should be taken seriously, they clearly need to be tested.

Courtney (1986 p 97) considered five theories of diet width in some detail in the context of the evolution of diet breadth in pierid butterflies. Three of these theories predict the conditions under which polyphagy is favoured or selected against; the other two make specific predictions, one that specialization is a derived trait (Courtney 1982), and the other that, while high host densities favour monophagy, monophagous species generally evolve from other monophagous species (Futuyma 1983).

An alternative and venerable view is seen in the recent paper by Moran (1988) on host-plant use in aphids. By comparing morphs with identical genotypes, Moran found support for Simpson's (1944) opinion that specialization was an evolutionary dead end, and that it limited further evolutionary opportunities. This viewpoint is clearly consistent with specialization as a derived characteristic. In contrast, however, Thompson (1988b) recently looked for, and found, genetic variation in host choice in a monophagous swallowtail butterfly (*Papilio oregonius*), implying that the local monophagy of this species masks genetic variation for host choice that could allow host shifts if opportunities became available.

Tauber and Tauber (1987) suggested that in the predatory Chrysopidae the evidence indicates that prey specificity is a derived trait. I follow Futuyma and Moreno (1988) and take as an initial working hypothesis the prediction that specialization is a derived or apomorphic trait.

An additional prediction concerns the average size of specialists as against generalists. Most phyletic sequences have involved size increases rather than decreases (Hayami 1978). Also, older life-history theories such as *r*- and *K*-selection predict that larger species are more likely to be specialized (e.g. Horn 1978). I do not regard this prediction as a particularly strong one, but it is supported by data from the Drosophilidae used in Fig. 6.1: in this case, specialists are decidedly larger than generalists.

Selective Forces Involved in Specialization

Prediction 3a: *The selective pressure for specialization involves at least in part an escape from competitive forces.*

Prediction 3b: *Populations of specialists should be less stable.*

We know very little about the selective forces that promote specialization. In the theory of host-plant selection, efforts have concentrated upon differences in the suitability of hosts, in part because of our knowledge of plant toxins. Berenbaum et al. (1986) provided clear evidence for a selective effect of herbivores on wild parsnips *Pastinaca sativa* (see Chap. 5); in the absence of herbivory, the heritable traits for resistance via toxin production are disadvantageous. Insect oviposition preferences can also be adapted to the suitability of the host as a larval food source (Via 1986; Thompson 1988a). This agrees with the idea that coevolution has occurred in insect-plant relationships.

However, in other instances adult oviposition preferences appear to be unrelated to larval performance (e.g. Courtney 1981; Wiklund 1975). In the *Dacus* fruit flies studied by Fitt (1986), larvae could develop successfully on most of the fruits offered as food, which included hosts not normally used in the wild. Diet breadth of these species in the wild, which ranged from a broadly generalized diet to monophagy, was a product of adult oviposition preferences and not larval physiological specialization.

In this paper I am concerned with diet breadth in predators and saprophagous species, where arguments about diet suitability may have less force. It has always been argued that the populations of generalists should be more stable than those of specialists because of the buffering effects of alternatives to fluctuating prey abundances (see Owen and Gilbert 1989). The populations of specialists are tied to fluctuations in the abundance of their food resources. If this is true, then generalists should be much more likely to compete with one another than with specialists, whilst specialists should rarely compete with each other. Part of the evolutionary pressure for specialization (if specialization is to be regarded as a derived trait) can then be seen as an escape from competition with generalists. Competition is not seen as an important general force in communities of phytophagous insects (Lawton and Strong 1981; Shorrocks et al. 1984), but here I am predicting that among predators and saprophages competition may be important only to part of the community, perhaps only a very small part.

Predators and parasitoids can also have a major impact on the evolution of host

characteristics, and the concept of “predator-free space” (Jeffries and Lawton 1984) is likely to be important in the evolution of insect life-cycles (see e.g. Zwölfer 1975). Although not considered here, parasitoid-induced selective pressures are likely to have been important in the evolution of predatory syrphids (G. E. Rotheray & F. S. Gilbert, unpublished results).

6.3 The Hoverflies (Diptera, Syrphidae)

The hoverflies are a particularly suitable group for testing these predictions because of the wide variety of larval feeding habits found among substantial sections of the family. Most dipteran families have one very common larval feeding habit, usually with a few small groups of mavericks (e.g. amongst the Drosophilidae; Ashburner 1981). In contrast, larvae from large proportions of the 5378 recognized syrphid species (data on numbers of species are taken from Thompson (1989)) belong to the different major feeding groups of predators (40%), phytophages (16%), and a diverse array of saprophages (44%); the saprophage group contains species with a wide variety of feeding mechanisms, from dung-feeders to aquatic filter feeders (see Gilbert 1986). Larval habitats in the saprophage group can be divided roughly into generalized aquatic species (45% of saprophage species), species associated with trees and tree-holes (34%), or terrestrial rotting organic matter (19%) or inquilines in the nests of Aculeata (2%). Larvae belonging to each major group can be specialized or generalized: for example, in the predators some species are monophagous while others take a wide range of different aphids (Rotheray and Gilbert 1989); aquatic species can be specialized to relatively rare habitats (e.g. elm sap flows).

There are three subfamilies: the Syrphinae (all with predatory larvae), the Eristalinae (=Milesiinae) (with phytophagous or saprophagous larvae), and the Microdontinae (whose larvae are traditionally regarded as saprophages (Donisthorpe 1927) but are probably predators (Garnett et al. 1985) in the nests of ants). Microdons are relatively rare, and there are not enough data on them for any conclusions to be drawn: nearly all analysis and discussion will therefore be restricted to species of the other two subfamilies.

6.3.1 Species Considered

Predators. I consider here only data from the Syrphinae, whose 1644 recognized members are all predatory, as far as is known. I include in the Syrphinae the tribe Pipizini, a predatory group previously placed in the Eristalinae. The predatory habit of feeding on aphids has almost certainly evolved only once, and the Syrphinae probably form a monophyletic group (Rotheray and Gilbert 1989). There is a range of specialization in larval habitat, and also in prey range (these are of course not independent classifications). Prey range was scored on the basis of the experience of G. E. Rotheray's systematic sampling of aphid colonies for syrphid predators (see Owen and Gilbert 1989). Species from North America were assigned to categories where known (some are Holarctic, and I assume that

feeding habits are the same across the entire range). Larval habitats were scored as follows: occurring in leaf litter; widely on herbs, shrubs and trees; only on herbs; only on trees; and occurring only in specialized enclosed habitats (in galls or underground). This order is assumed to represent increasing specialization of habitat, since it undoubtedly represents diminishing proportions of the available prey.

Saprophages. I use data from saprophages of any type, from the generalized aquatic filter feeders such as *Eristalis tenax* to the specialized scavengers in wasp and bee nests such as *Volucella*. In this case specialization of feeding habits is equivalent to a narrowing of larval habitat, and this is the basis upon which decisions were made about positions on the spectrum of specialization. Categories were as follows, in order of increasing specialization: generalized aquatic or semi-aquatic detritivores, tree-hole species, and inquilines.

Phytophages. All *Cheilisia* species were assumed to belong to this group, even though the larvae of some species feed in rotting fungi, presumably as saprophages. Not enough is known to be able to differentiate them without specific rearings, but the vast majority of the 386 species are almost certainly phytophagous (cf. Rotheray 1988). Species of *Merodon* and *Eumerus* from the Eumerini were also assumed to be phytophagous, although experiments with *Eumerus* have shown that fungal decay of plants is necessary before larvae can develop successfully (Creager and Spruijt 1935). Nothing adequate is known about specialization in phytophagous syrphids, and therefore the group is not subdivided further.

6.3.2 Data Used

The data are of three types: phenotypic characteristics, population densities, and a cladogram of generic evolution.

Size, and the Trade-off Between Egg Size and Number

As part of a larger study on ecomorphological relationships within communities (Gilbert 1985a,b), I have measured a standard set of 25 variables on more than 250 species of hoverfly from Cambridge (UK), Maine, Florida, Arizona and Oregon (USA). Only three of these measures are used here to assess body size and reproductive strategy; complete data are available for 184 species. These data will shortly be published in full, so the raw values are not presented here. Of the 184 species, 67 are predators, for many of which the degree of larval specificity can be assessed.

Thorax volume is used as an index of body size. Three variables were actually measured on each fly: thorax width between the wing bases, thorax length from the extreme front edge of the prothorax (anteprepronotum) to the tip of the scutellum, and thorax height from the lowermost tip of the katapisternum (sternopleuron) (see Speight 1987). The three measures are multiplied together

to give an index of thorax volume, and averaged over individuals to give a mean value for each species.

Egg sizes were measured on mature eggs dissected from gravid females; egg maturity is recognized by complete chorionic development. Maximum lengths (L) and widths (W) of ten eggs were measured for each female where possible, and egg volumes calculated from the equation for an ellipsoid:

$$\text{vol} = (4/3) \pi (L/2) (W/2)^2$$

The number of eggs laid during the lifetime of an individual female is difficult and time-consuming to measure on a large number of species. In parasitoids, there is a good correlation between lifetime fecundity and the number of ovarioles in the ovaries (Price 1975), and ovariole number is widely recognized as an index of potential fecundity. I therefore decided to use the numbers of ovarioles in females as an index of egg number.

In saprophagous species that often lay their eggs in a large batch, the number of ovarioles sets a maximum on batch size, since no mature eggs are retained in the oviducts. Predatory Syrphinae usually lay only a single egg at a time, and it is not known whether they lay all their mature eggs during a single day. Unlike the synchronous development of ovarioles in saprophagous species, ovarioles of syrphines develop asynchronously and only a few eggs are mature at any one time (F. S. Gilbert, unpublished results).

There is a clear allometry of reproductive effort, here taken to be the maximum clutch volume (ovariole number \times egg volume). Fig. 6.2 shows the relationship

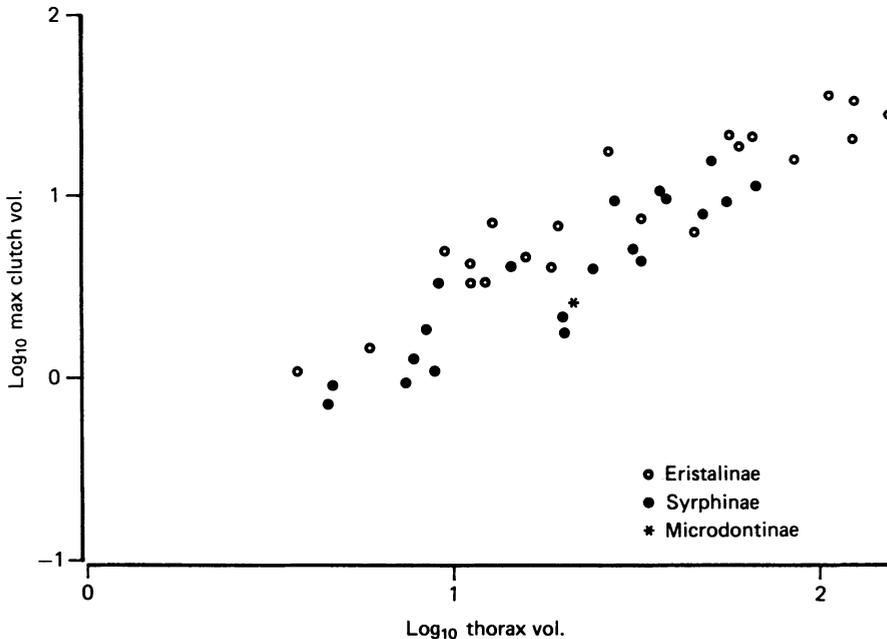


Fig. 6.2. Relationship between the maximum volume of eggs that could be produced at one time (= number of ovarioles \times egg volume) and body size. There is no significant difference between the slopes of the regression lines of the Syrphinae and Eristalinae, but the elevations are significantly different (see the text).

between clutch volume and body size for data from one site (Maine), and it is clear that size exerts a strong influence. There is no difference between the slopes of the regression lines of the Eristalinae and the Syrphinae ($F_{1,123} = 1.0$, n.s.), but the elevations are significantly different ($F_{1,124} = 17.1$, $P < < 0.001$). The adjusted mean clutch volumes differ by 0.16, and since this is a logarithmic scale, this implies that the mean clutch volume of the Syrphinae is only 69% of that of the Eristalinae. This is interesting, since it implies little difference in reproductive allocation between the synchronous batch layers (Eristalinae) and those that lay only a single egg at a time, maturing eggs asynchronously (Syrphinae); I conclude from this that both subfamilies have a similar basic allocation to reproduction, which is to mature one batch of eggs synchronously, even though many do not. Why should this be? It is probably because adults do not live long in the wild, and I have only rarely found evidence for more than one egg being laid from each ovariole (F. S. Gilbert, unpublished results).

The trade-off between egg size and number is most clearly seen by plotting data from syrphids in the same way as for the Drosophilidae. Fig. 6.3 shows the number of ovarioles per unit thorax volume plotted against egg volume (in a log-log plot). Clearly larger eggs imply smaller numbers of ovarioles for a given body size. The extremes of this line run from the huge (2.5 mm long) eggs of *Volucella* species to the numerous and tiny eggs (0.6 mm) of the Xylotini (e.g. *Xylota*, *Criorhina*). The predatory Syrphinae encompass a narrower range of size-adjusted egg numbers and egg sizes. Once again there is no difference between the slopes of the regression lines for the Eristalinae and the Syrphinae ($F_{1,123} = 2.65$, n.s.), but the elevations are significantly different ($F_{1,124} = 16.5$, $P < < 0.001$): the different elevations imply that the Eristalinae lay eggs that are

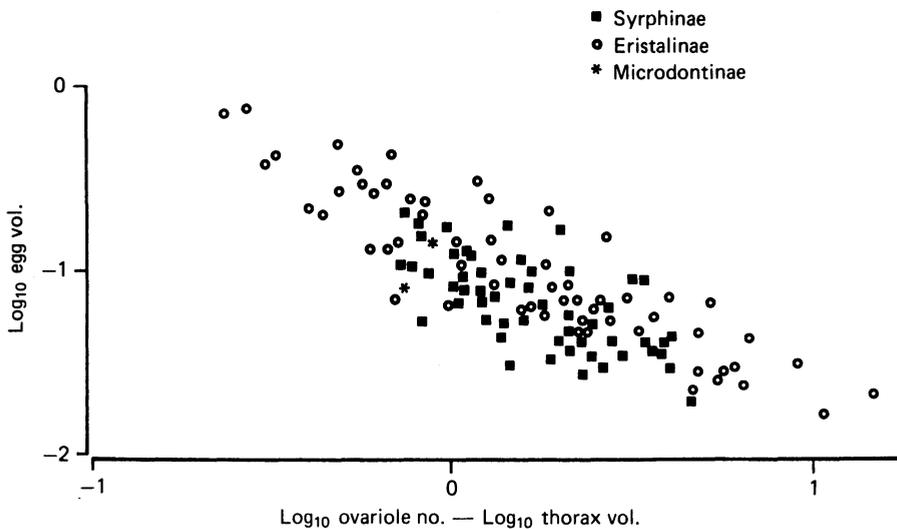


Fig. 6.3. Trade-off between egg size and egg number for adult Syrphidae. Egg numbers are denoted by the number of ovarioles in the ovaries, adjusted for body size in the way indicated. Regression lines for the Syrphinae and Eristalinae do not differ in slopes, but differ significantly in elevation (see the text).

41% larger for a standardized fecundity. These regression lines are very similar to that of the Drosophilidae (Fig. 6.1), with an identical slope ($F_{2,164} = 1.86$, n.s.), but different intercept ($F_{2,166} = 30.1$, $P < < 0.001$). Thus the trade-off between fecundity and egg size is very similar in these different dipteran families.

With these data, body size and the trade-off between egg size and number are confounded. It is not adequate merely to divide one variable by body size to remove the effects of body size. Using multiple regression one can look at the relationship between the two predictor variables with relatively low intraspecific variance (body size and egg size) and ovariole number, which varies much more between individuals of one species (F. S. Gilbert, unpublished results). This is very successful ($R = 0.82$, $F_{2,127} = 131.6$, $P < < 0.001$), and the relationship is:

$$\log_{10}(\text{ovariole number}) = 0.83 \log_{10}(\text{size}) - 0.70 \log_{10}(\text{egg size}) - 0.34$$

However, principal components analysis (PCA) is a much better way of separating the two influences of body size and the egg size–egg number trade-off. PCA is a method of taking intercorrelated, and producing uncorrelated, variables. Table 6.1 shows the results of a PCA of the three log-transformed variables. The first axis explains 60% of the variation in the data, and has high positive loadings on egg volume and number, and very high with thorax volume: it is clearly a body size axis. The second axis explains a further 36% of the variation, and has a very low loading on thorax volume, but loads positively with egg volume, and negatively with ovariole number. Thus, from three intercorrelated variables, PCA produces two uncorrelated ones that explain 96% of the original variance: scores along the first axis are a measure of body size, whereas scores along the second axis measure the trade-off between egg size and number, independent of body size. I therefore use these PCA scores to test predictions about the effects of specialization, and I label scores along axis 1 (PCA 1) as measuring “size”, and scores along axis 2 (PCA 2) as measuring the “reproductive strategy”, the position of the species along the egg size–number trade-off. To test for differences between groups, I use a one-way analysis of variance using program P7D of the BMDP package of programs (Dixon 1983): this uses Levene’s test to check whether variances are homogeneous, and if not, calculates Welch’s F -ratio in place of the usual F -ratio.

Table 6.1. Results of a principal components analysis of size and reproductive variables

Original variables	Factor loadings	
	Axis 1	Axis 2
Thorax volume	0.97	0.00 ^a
Egg volume	0.65	0.74
Number of ovarioles	0.65	-0.74
Order	Eigenvalues	% variance
1	1.7888	60
2	1.1044	36
3	0.1067	4

^a <0.25, and set to 0.0 by the BMDP program.

Fig. 6.4 uses these PCA scores to look for differences in size and reproductive strategy between species in the three major larval feeding categories. There are

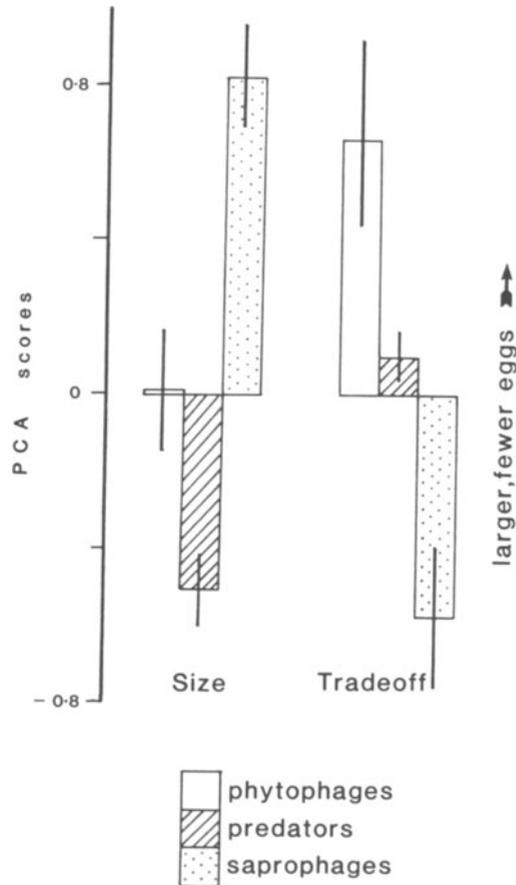


Fig. 6.4. Mean values for “size” (scores along PCA1) and “reproductive strategy” (scores along PCA2) for the major feeding groups of larval Syrphidae. For details, see the text.

very clear and significant differences between the categories in both size ($F_{2,124} = 32.1$, $P < 0.001$) and reproductive strategy (Welch $F_{2,42} = 8.6$, $P < 0.001$). Phytophagous species are of average size, but have relatively few, large eggs; predators are small with an average number of average-sized eggs; saprophagous species are large, with a large number of small eggs.

Phylogeny of the Syrphidae

To test quantitatively whether specialization is a derived trait, a well-differentiated phylogeny is needed, ideally at the species level. This is not available for any syrphid group, and therefore we cannot make a quantitative test of the prediction at the species level. However, my colleague Graham Rotheray and I have developed a generic-level phylogeny for the predatory Syrphinae (Rotheray and Gilbert 1989), which does allow a certain amount of analysis to be done.

The phylogeny is based upon larval morphological characters, such as details of the posterior respiratory process, that are constant across genera. We used a numerical cladistic technique (parsimony) implemented by the computer package PAUP (Swofford 1985) to generate the most likely cladogram from the

characters that were scored. Fig. 6.5 shows the resulting cladogram, which incidentally confirms in many details opinions about the phylogeny of those who have worked on adult or larval Syrphinae.

I regard Fig. 6.5 as a reasonably accurate phylogeny, for two reasons. Firstly, the constancy of characters within genera also confirms nearly all the generic boundaries that taxonomists working with adults have spent decades reorganizing, refining and finally agreeing. This engenders confidence in the use of larval characters to indicate relationships. Secondly, I believe that larval characters clearly contain a great deal more phylogenetic information than do adult characters (Rotheray and Gilbert 1989). We are currently working on generic-level phylogeny of the whole family from larval characters (G. E. Rotheray, F. S. Gilbert, C. T. Maier, F. C. Thompson and J. C. Hartley, unpublished results).

I identify the quantitative influence of phylogeny on size and reproductive traits using the technique of Cheverud et al. (1985). There has been a good deal of interest in exploring techniques for assessing the role of phylogeny (Stearns 1983; Harvey and Clutton-Brock 1985; Felsenstein 1985; Derrickson and Ricklefs 1988; Bell 1989), but the method of Cheverud et al. (1985) is the only one with an explicit quantitative model. It uses network autocorrelations and an attempt to describe the genetics of ancestor–descendant relationships in the same way as Mendel's laws describe the genetics of parent–offspring relationships.

The method requires a species \times species matrix of the degree of relatedness. With a reasonably well-differentiated phylogeny, one can estimate this relatedness matrix by counting the number of hypothetical ancestors (“nodes”) between pairs of species. This is the approach adopted here. The technique is only valid if the evolution of taxa occurs at a constant rate.

I am indebted to J. M. Cheverud for sending me the program for calculating the relevant parameters for the model, but note that I have been unable to reproduce accurately the standard errors (SE) of phylogenetic autocorrelations using his sample data, and no such SE values are reported here.

Population density and stability

A third type of data used in testing the predictions concerns population fluctuations and competition between species. Manipulative experiments to test for the occurrence of competitive forces among adults are very difficult if not impossible to do with a highly mobile group such as the hoverflies. The large number of species involved make it impractical to do manipulations of larval densities, even if we knew where they all were in the habitat. An indirect method is required that analyses long-term population data to look for reciprocal fluctuations in density between competitors. As a by-product of such data, we can assess the stability of populations and thereby test another of the predictions (i.e. that generalists will have more stable populations).

Jennifer Owen has trapped insects in her suburban garden in Leicester (UK) with a Malaise trap every week for the past 17 years, and the Syrphidae are one of the groups that she has already identified to species level. This constitutes one of the finest and most detailed sets of long-term population data for an insect community.

The analysis of stability of these populations involves using an index of

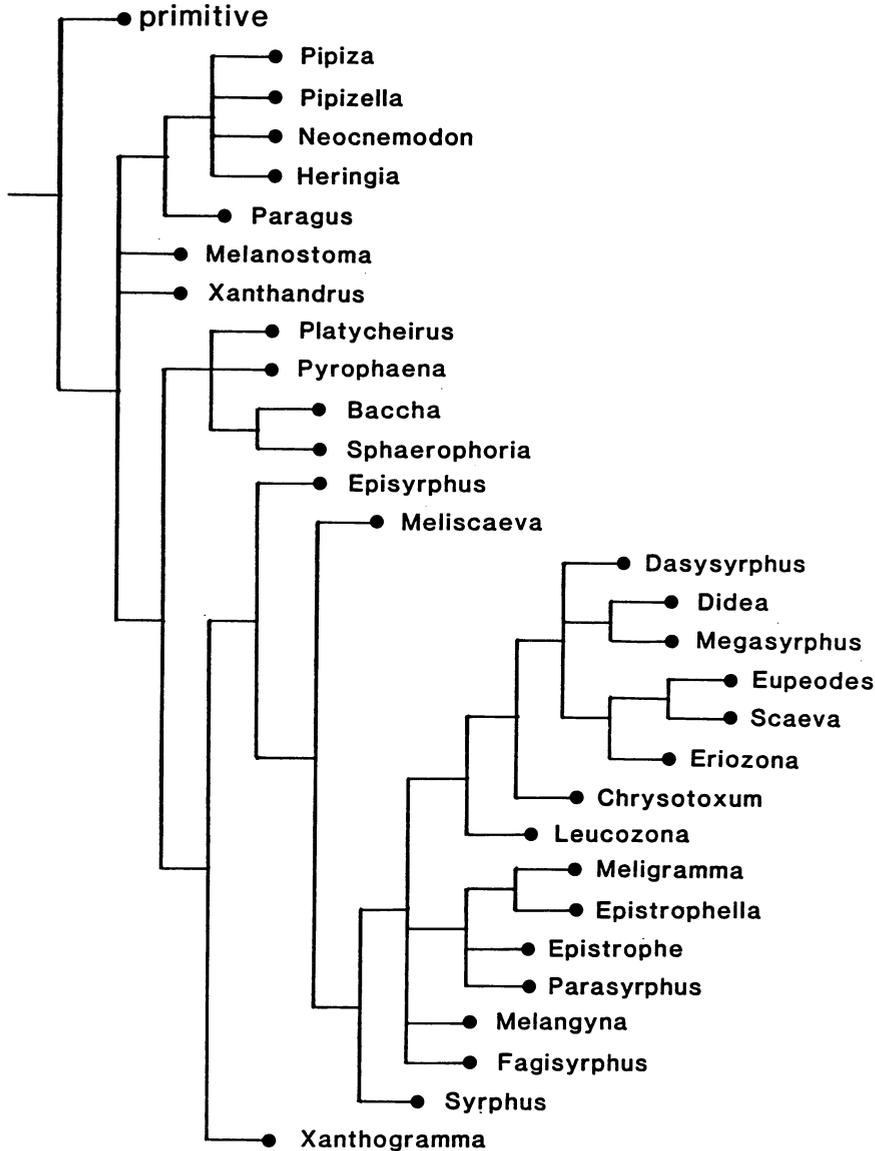


Fig. 6.5. Cladogram of the genera of the Syrphinae (redrawn from Rotheray and Gilbert 1989). The cladogram results from a consensus tree of the multiple equally parsimonious trees from the PAUP package (for details, see Rotheray and Gilbert 1989).

stability, the standard deviation of log-transformed annual totals; the detailed analysis has recently been published (Owen and Gilbert 1989). Here I test whether groups of differing specificity have different population stabilities, using a one-way analysis of variance (ANOVA).

I test for competition using the similarity measure from correspondence analysis, χ^2 similarity. Correspondence analysis is a multivariate technique for

analysing contingency-table data, and is ideal for this purpose since it compares the profiles of annual abundances between pairs of species using what is very similar to a calculation of χ^2 . It thus automatically allows for differences in the relative abundances of species, and in the overall suitability of different years for syrphids. The test assumes that no time delays are involved in the competition. A large χ^2 similarity between two species implies reciprocal deviations from the expected abundances generated from the marginal totals of years and species.

To test for an unusually large χ^2 similarity, the mean of χ^2 similarities between all pairs of species of a subgroup of the data (e.g. generalists) is compared to 100 means of the same subgroup generated from a random model, one that randomizes the differences of the observed numbers from the "expected" numbers generated from the marginal totals. This randomization of residuals will disrupt any putative reciprocal fluctuations in density. If the observed mean is in the top five of the random means, I take it as being a significantly large mean value for χ^2 , and therefore as an indicator of the reciprocal fluctuations in density that would indicate the action of competitive forces. Full details of this approach are given by Gilbert and Owen (1990). It remains possible that groups consistently respond differently to environmental variables, such that resulting covariation has nothing to do with competitive effects. The fact that these are very closely related species taxonomically should minimize this confounding effect.

6.4 Testing the Predictions

Prediction 1: *Specialists should lay fewer, larger eggs.*

Prediction 2b: *Specialists should tend to be larger.*

I test these predictions separately on saprophages and predators. Species in both groups were assigned to different categories according to larval habitat (saprophages) or prey range (predators).

Saprophages

Species were assigned to three groups: generalized detritivores, tree-hole detritivores, and inquilines in the nests of social Hymenoptera. Undoubtedly among the "generalized detritivore" group, there are species with narrower niches than others. Because of the lack of detailed data for the majority of species, I am unable to divide into a finer classification. I ordered these groups a priori into a sequence of increasing specialization, from generalized detritivores to inquilines.

Fig. 6.6 compares the sizes and reproductive strategies of each group, and for comparison also gives data for the phytophages (where no division into specialists and generalists is possible). All the saprophages tend to be larger than the average for all syrphids, and hence their scores are all positive, denoting relatively large sizes. The more specialized groups living in tree-holes or in nests of social Hymenoptera are probably larger than those of generalized detritivores

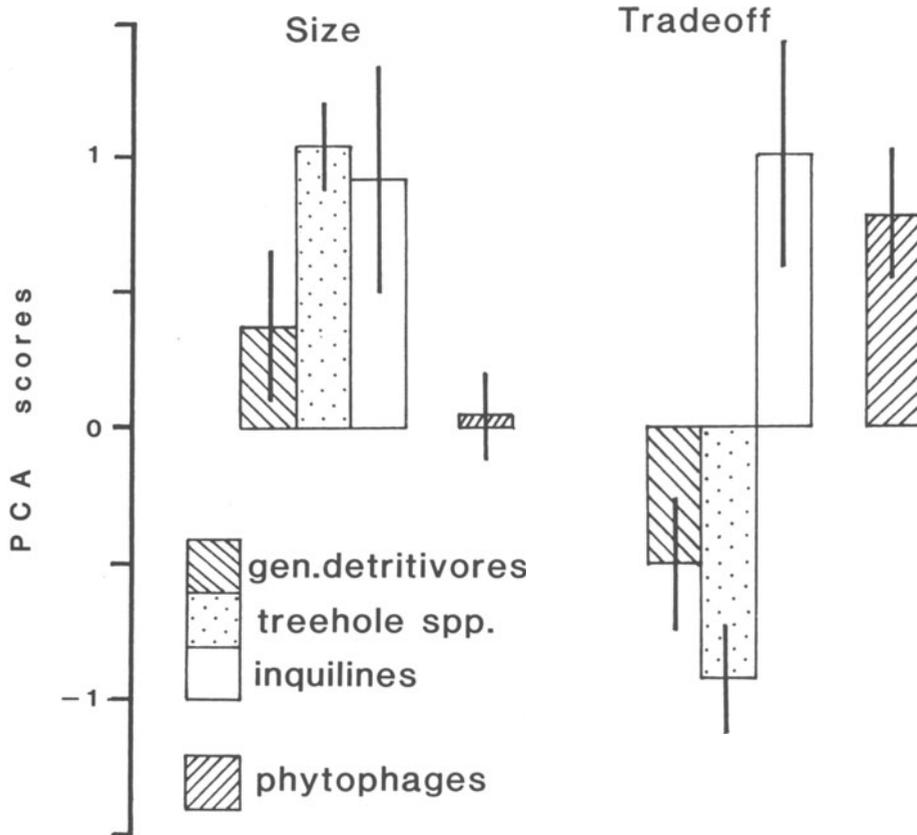


Fig. 6.6. Mean values (\pm SE) for “size” and “reproductive strategy” (see the text) for adult syrphids with phytophagous and saprophagous larvae. The saprophagous group has been split into three types according to the degree of specialization of larval habitat. gen., generalized.

($F_{2,39} = 2.58$, $P = 0.09$), conforming to the predicted pattern. Also the most specialized group, the inquilines, have very large eggs, while the other two groups are not different from one another ($F_{2,39} = 7.04$, $P < 0.003$). Again this tends to support the prediction that specialized species should lay fewer, larger eggs.

Predators

Predators are divided into five categories according to their larval habitat, and this is also a prey-range classification:

1. Leaf litter species probably feed on many different kinds of arthropod in the leaf litter, but appear to prefer aphids (e.g. *Melanostoma*)
2. Some species are generalized aphid predators, to be found feeding on many types of aphids on trees, shrubs and herbs (e.g. *Syrphus ribesii*)
3. Some occur only on herbs, again feeding only on aphids but still of many types (e.g. *Sphaerophoria*)

4. Other species are more restricted, being found only in tree-aphid colonies (e.g. *Dasysyrphus*)
5. Some species feed only on aphids in specialized enclosed habitats such as galls or underground (e.g. *Heringia*)

This order is assumed to be an order of increasing specialization in habitat, on the basis of field experience. It is an a priori order, but one that I am aware is open to dispute. Data are needed to quantify the relationship between habitat type and numbers and types of aphid colonies: I am unaware of the existence of any data of this kind.

Fig. 6.7 shows the average sizes and reproductive strategies of these groups. Although there are strong differences between the groups in size (Welch $F_{4,20} = 29.6$, $P < < 0.001$), there is no obvious pattern conforming to the prediction. There are no differences in reproductive strategy ($F_{4,61} = 1.25$, n.s.). Therefore there is no support for the prediction that more specialized predators will be larger, and will lay fewer, larger eggs.

Among the species where we are certain that aphids are the only acceptable

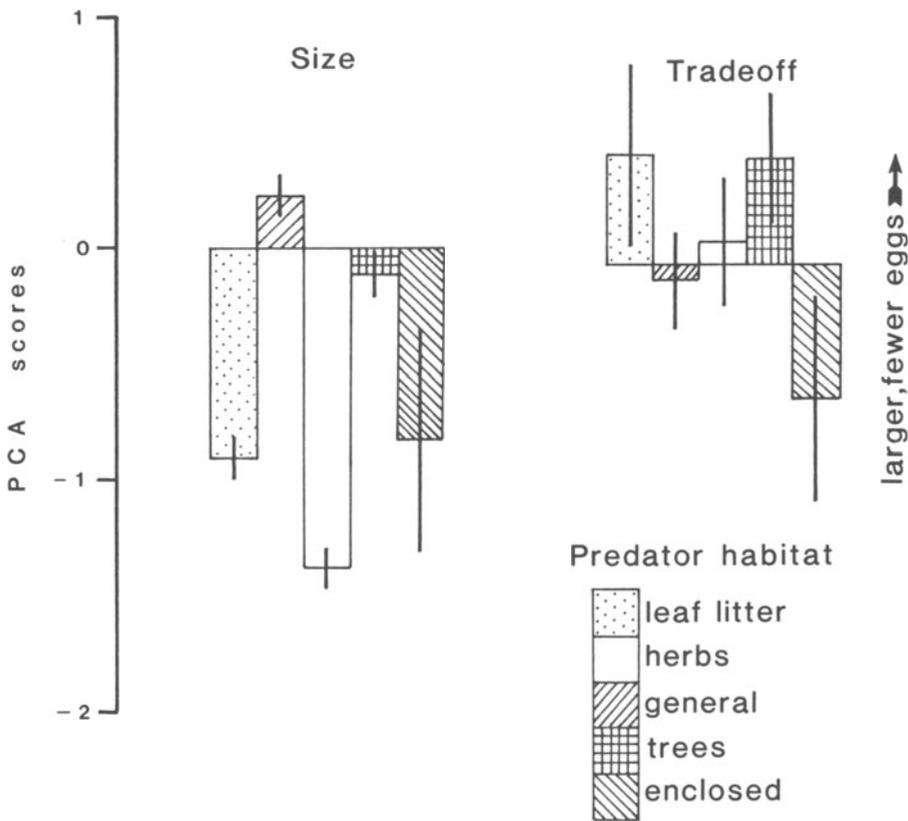


Fig. 6.7. Mean values (\pm SE) for “size” and “reproductive strategy” (see the text) for adult syrphids with predatory larvae. The data are split into groups according to larval habitat, and are displayed in order of increasing specialization of larval habitat.

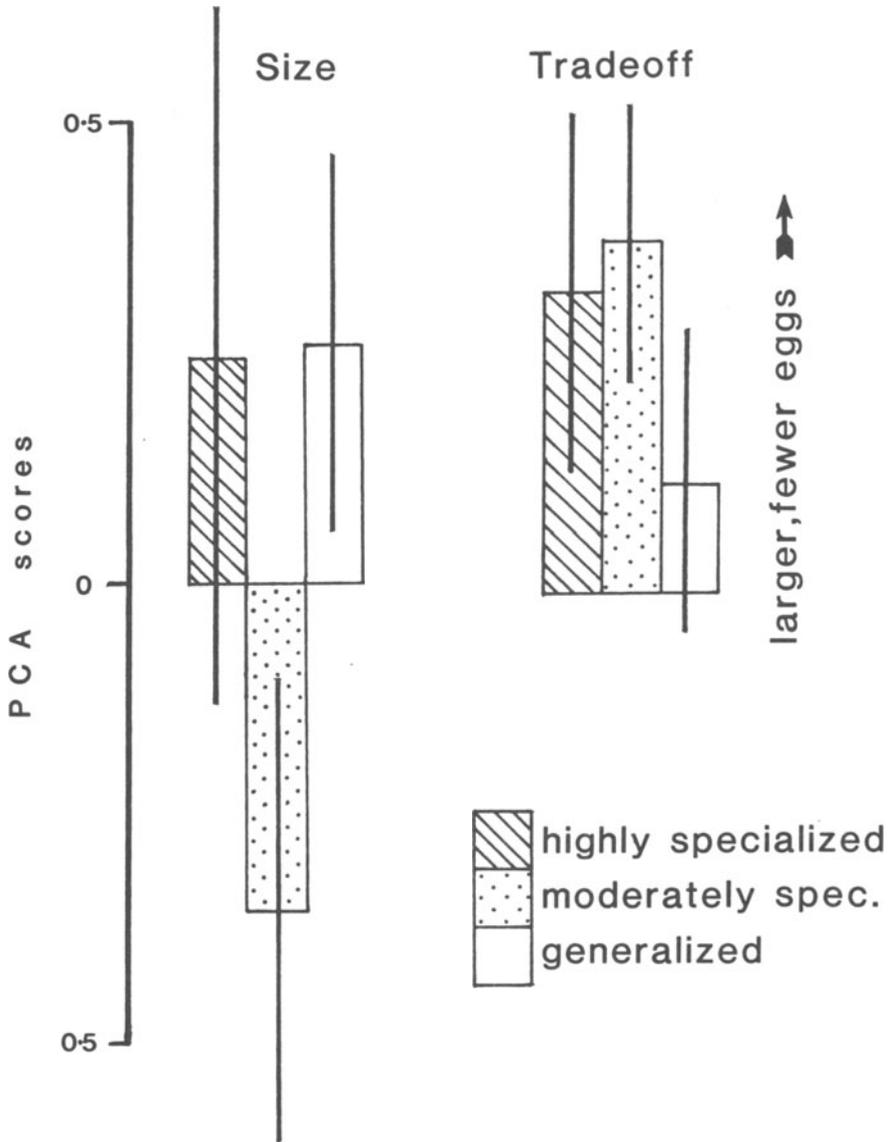


Fig. 6.8. Mean values (\pm SE) for “size” and “reproductive strategy” (see the text) for adult syrphids with predatory larvae whose range of prey within habitats can be assessed (see the text). The data are split into three groups differing in their degree of specialization, and are displayed in order of decreasing specialization. spec., specialist.

food, systematic sampling allows an accurate assessment of the prey range, from extreme specialists (monophages), to moderate specialists (oligophages), to generalists (polyphages). Details of the way in which these assessments were done, and the species in each group, are given by Owen and Gilbert (1989). Fig. 6.8 gives the mean sizes and reproductive strategies for the species of each

category: there are no significant differences between groups in size (Welch $F_{2,6} = 1.81$, n.s.) or reproductive strategy (Welch $F_{2,6} = 0.64$, n.s.). Trends in the data do support the main prediction that specialists should lay fewer, larger eggs, but the variance is high, probably because of the low number of species that can definitely be assigned to the categories.

In conclusion, the prediction that more specialized species will lay fewer, larger eggs is supported by data from non-predators, but not from predators, although some of the data suggest that, given larger sample sizes, support might be forthcoming. The subsidiary prediction that specialists will also be large is also supported by evidence from non-predators, but not that from predators.

Prediction 2a: *Specialization is a derived trait.*

I have only a generic phylogeny of predators. One cannot characterize the degree of specialization of a genus when knowledge is patchy, and so I am unable to test this prediction quantitatively. Work is currently in progress on a species-level phylogeny of the genus *Platycheirus*, and, when complete, a more rigorous quantitative test can be carried out.

In spite of this, it is obvious that the whole trend of evolution has been one of increasing specialization (Rotheray and Gilbert 1989). All the plesiomorphic basal species are generalists (e.g. *Melanostoma*), probably living in the leaf litter as general zoophages, although taking aphids by choice. As one comes up the phylogenetic tree on the main "branch", so the species become grassland generalists (e.g. *Sphaerophoria*, *Platycheirus*), then generalist aphidophages on herbs, shrubs and trees (e.g. *Episyrphus*), and finally increasingly restricted to arboreal aphids (e.g. *Dasysyrphus*). As always, the pattern is not completely regular (e.g. the apparently highly specialized *Xanthandrus* (feeding on gregarious Lepidoptera) and *Xanthogramma* (feeding on aphids associated with ants?)). On the secondary branch of the evolutionary tree a parallel specialization has occurred: *Paragus* species appear to be herb-layer generalists, whilst members of the Pipizini are arboreal or subterranean specialists, often highly specialized to feed within the galls produced by aphids.

Thus, the history of the evolution of the predatory syrphids appears to be one of increasing specialization, from feeding generally on invertebrates to aphidophagy, from ground-layer aphids to tree aphids, from generalists to specialists.

I am able to use generic-level data to assess the role of phylogeny in influencing size and reproductive strategy, since 23 generic mean values for the Syrphinae can be calculated and used in Cheverud et al.'s (1985) model. The calculated value of the phylogenetic autocorrelation coefficient measures the degree to which the phylogenetic relatedness matrix accounts for variation in the trait being considered.

For size (scores on PCA1), the phylogenetic autocorrelation is 0.62, a very high value. This implies that more closely related species are more alike in size. From the pattern of mean sizes, phylogeny is clearly correlated with a general increase in body size, as predicted. The genera with the largest mean sizes are all towards the top of the tree (e.g. *Scaeva*, *Didea*, *Eriozona*, *Chrysotoxum*), whilst the smallest ones are basal (*Melanostoma*, *Platycheirus*, *Paragus* and all the Pipizini).

For scores on PCA2, i.e. position on the trade-off between egg size and number, there is an equally high phylogenetic autocorrelation coefficient, but it is negative (-0.62). Cheverud and Dow (1985) measured similar correlations in morphology for social groups of rhesus monkeys produced by fission, and also

discovered negative values. They suggest that negative values should be rare, because this means that phylogenetic connections between genera produce dissimilarity, i.e. more closely related genera are more dissimilar. This has obvious implications for the process of fission itself, which must be one that divides a genus according to the most dissimilar elements. Ecological factors could be invoked here, e.g. character displacement, but this is mere speculation. Until more such analyses are carried out, we cannot know the full implications of negative phylogenetic autocorrelations.

Prediction 3a: *Generalists should compete, but specialists should not.*

Prediction 3b: *Generalists should have more stable populations.*

A test of the second part of this prediction is relatively straightforward. Fig. 6.9 shows the average stabilities of generalists, moderate specialists, and extreme specialists. Generalists do not have more stable populations, but are just as variable as extreme specialists. Populations of moderate specialists are more stable than either of the other two categories (Owen and Gilbert 1989).

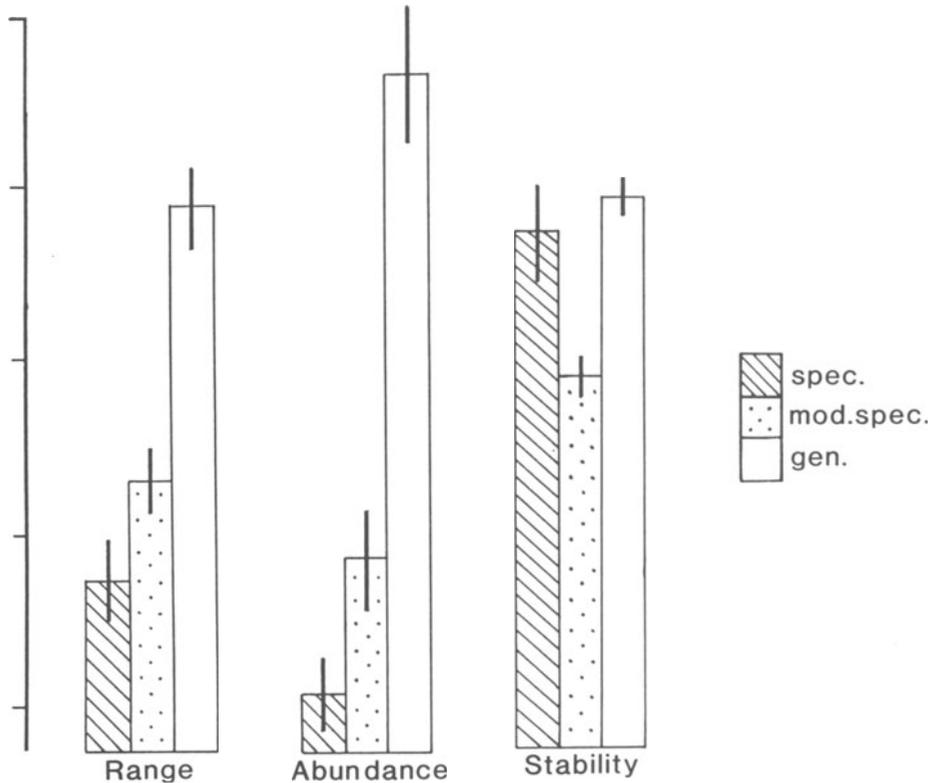


Fig. 6.9. Mean values (\pm SE) of the range (distribution of 10 km \times 10 km squares: see Owen and Gilbert 1989), abundance (log annual numbers), and stability (s.d. of log census numbers) for populations of adult syrphids with predatory larvae whose range of prey can be assessed. Three groups are shown in order of decreasing degree of specialization. spec., specialist; mod., moderately; gen., generalist.

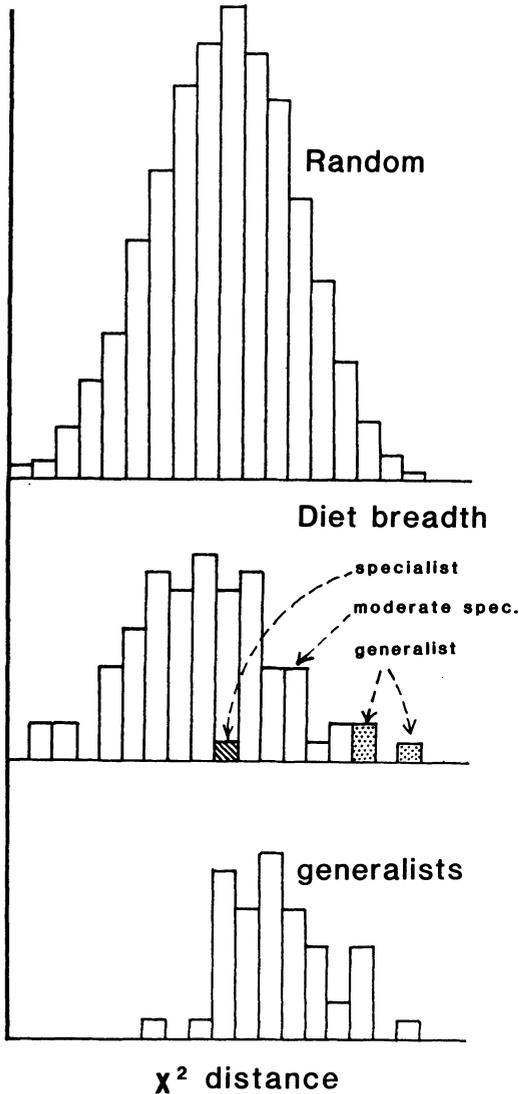


Fig. 6.10. Distribution of χ^2 similarities in abundance between species in different categories of predatory larval specialization, and for randomly reshuffled residual abundances (see the text). *Upper distribution*, randomly reshuffled residuals for all species together; *middle distribution*, distribution of similarities *within* groups (e.g. between generalist and generalist); *lower distribution*, distribution of similarities between generalists and all other predators. spec., specialist.

Why should this be? The argument advanced in Owen and Gilbert (1989) mirrors other similar explanations (see Owen and Gilbert 1989) in suggesting that it is possible that the populations of extreme specialists are tied to fluctuations in their food supply, whilst populations of generalists take advantage of outbreaks of the commonest aphid species, which may fluctuate greatly from year to year (Taylor 1984). It is the moderately specialized predators that regularly switch to

the common prey type of the range that they accept, and thus even out yearly fluctuations in food availability.

Testing for competition involves comparing the observed mean χ^2 similarity of the group of species (e.g. generalists) against 100 random mean values generated as described above (see also Gilbert and Owen 1990). We expect the mean χ^2 similarity to be unusually high between generalists, but not between either moderate or extreme specialists. This is exactly the pattern found. Fig. 6.10 shows the distribution of similarities. Only two of the 100 random mean similarities were larger than the observed mean similarity between the generalists. Mean similarities were not unusually large between moderate specialists, or between extreme specialists, or even between generalists and either type of specialist. This pattern is interpreted as implying that generalists compete with one another, but not with other predators. This is consistent with the prediction that part of the impetus towards specialization is avoidance of competition with generalists (although this implies no causality). Because generalists are "primitive" in a phylogenetic sense, this may be part of the reason why the history of the evolution of the predatory Syrphinae seems to have been one of increasing specialization.

6.5 Discussion

Futuyma and Moreno's (1988) recent review called for more phylogenetic information in the search for a general explanation for specialization. I concur strongly: a phylogeny imposes a pattern and an order to ecological features, narrowing the focus of hypothesis testing to particular sister groups.

The results of this comparative study of species of the Syrphidae show that there are clear patterns of specialization within predators that require explanation. Most of the predictions about size and reproductive strategy hold for non-predators, but fewer are supported by data from predators. In more detail:

1. Specialization of habitat in saprophagous species involves an increase in size, and a reproductive strategy of fewer, larger eggs, just as predicted. In predatory species, however, these predictions are not supported when one compares across different larval habitats (and assuming that these represent different degrees of specialization). For those predators where prey range is known with some confidence, there is also no support for the predictions, although specialized species do tend to have fewer, larger eggs.

2. I predicted that specialization should be an apomorphic character: the phylogenetic history of predatory syrphids is indeed one of increasing specialization. Plesiomorphic genera are leaf-litter or herb-layer generalists, and the more apomorphic the genus, the more its constituent species are confined in their prey range to a much narrower range of arboreal aphids.

Generic average size is strongly associated with this pattern of specialization as measured by Cheverud et al.'s (1985) method. Size increases in more apomorphic genera.

The average reproductive strategy of genera is also strongly associated with the pattern of phylogenetic relationships in that more closely related genera have more divergent reproductive strategies. This implies that the founding of new

genera involves a splitting of the old genus into components with highly divergent reproductive patterns.

3. The prediction was made that generalists should compete with one another, but specialists should not. The suggestion from this, if supported, is that at least part of the selective pressure for greater specialization (cf. point 2, above) involves an escape from competition. This asymmetry was evident in long-term population data from an urban site in the UK: there was evidence that generalists do compete, resulting in reciprocal fluctuations in density, but there was no evidence that specialists compete either between themselves or with generalists.

Generalists are predicted to have more stable population densities because they can switch to the commonest prey types of any one year. This hypothesis is rejected: generalists and extreme specialists have equally unstable populations, while moderate specialists have relatively stable population densities.

This study demonstrates the utility of using a taxon such as the Syrphidae that contains examples of all types of life-cycle strategy. Detailed work on specialization of predatory syrphids is under way and, in the light of further refinement of the phylogenetic relationships between species, should bear fruit in the understanding of the basis of their specialization.

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