ECOMORPHOLOGY OF SYRPHIDAE

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Introduction

There are two influences upon the evolutionary ecology of organisms that I believe have been underrated, namely the effect of morphology, i.e. body size and shape, upon a whole suite of ecological variables, and the constraining influence of phylogeny upon the range and magnitude of possible changes in these variables (see Stearns 1983). Here I want to describe some of these influences as they express themselves in the ecology of hoverflies. This work will be published in full elsewhere.

Morphological aspects

For about ten of each sex of 34 species, 14 variables were measured, including five associated with the size and shape of the proboscis, two wing- and three abdomen-associated variables. One species, Syrphus ribesii L., had much larger sample sizes. Multivariate morphometric techniques were used, as indicated.
Intraspecific variation (Principal Components Analysis)

Overwhelmingly the main difference between individuals of the same species was size, with few shape differences. Apart from size, the most important difference was usually weight contrasted with size: since reproductive condition and crop contents vary independently of body size, this was not entirely unexpected. Further differences were normally associated with shape differences between the sexes.

Sexual dimorphism (Discriminant Function Analysis)

Females were usually larger than males, but in addition there were significant shape differences. Males had shorter, relatively broader wings, a bigger thorax, and a narrower abdomen. In all species except Xylota, males had a relatively longer proboscis.

Interspecific differences (Canonical Variates Analysis)

The main trend was that species differ primarily in proboscis length relative to their body size, i.e. in shape. The main axis separated species such as Rhingia, with a tremendously long proboscis for its size, from others such as Baccha and Xylota, with very short tongues for their size. A secondary feature was body size differences independent of the covariance between proboscis length and body size.

Foraging behaviour

Summing data from standard census walks gave a crude estimate of overall time budgets for the various activities, which were divided into feeding, flying, and resting. The feeding category was further subdivided into feeding on pollen, feeding on nectar, or feeding from leaves (see Gilbert 1981).

Species took nectar and pollen in varying proportions, with some nearly always taking pollen (e.g. Episyrsophus balteatus, Syrphus ribesii), and others taking much more nectar (e.g. Metasyrsophus corollae, Volucella bombylans). Two species of
Xylota were virtually never seen at flowers, but instead collected food from the surfaces of leaves. Dissection revealed alimentary tracts packed with pollen.

Males spent more time feeding on nectar than females. Proboscis length is linearly related to the average depth of corolla from which nectar is obtained (Gilbert 1981). It is consistent with the hypothesis of morphological adaptation that males, spending more time feeding on nectar and requiring more energy, have relatively longer tongues. Deeper corollae contain more energy (Prys-Jones 1982).

Activity in relation to morphology ( Canonical Correlation Analysis)

Canonical correlation relates a set of predictor variables (here morphology) to a set of response variables (here the time budgets). The main feature of the two data sets lies in the correlation between relative proboscis length and the proportion of time devoted to feeding on nectar or on pollen. Thus the main difference in morphology between species, proboscis length relative to body size, is also the factor directly related to feeding behaviour. The second feature of the two data sets documents a decrease in the proportion of time spent flying as body size increases. Covarying with this is a tendency to spend more time feeding, particularly on nectar. This suggests that energy may be in limited supply.

Reproduction

Borisova (1983) has recently published extensive data on 'potential fecundity' in hoverflies, i.e. the number of ovarioles in the ovaries. She found a poor correlation between body size (femur length) and ovariole number.

Having dissected some 250 species of hoverfly, I can confirm Borisova's (1983) observations on the degree of synchronicity in maturing eggs, and the number of oocytes per ovariole.
Aphidophagous species generally have asynchronous development, with a relatively high number of oocytes per ovariole.

\[ \text{Log}_{10} \text{[Number of ovarioles per ovary/thorax volume]} \]

Fig. 1 Size-specific potential maximum clutch size against egg size

There is clear evidence in my data for a 'trade-off' between egg size and ovariole number (Fig 1). The greater the number of eggs laid relative to body size, the smaller the volume of each egg. This 'trade-off' is directly proportional, because the slope of the regression of maximum clutch volume (egg volume x number of ovarioles) against body size is not significantly different from 1.0; thus in syrhids there is a constant proportion of materials available for building eggs, irrespective of body size.

The other notable feature of these data is the difference between the subfamilies. Currently there are two main subfamilies, the Eristalinae and the Syrphinae. Some features of adult anatomy support this division, e.g. the position of the
spermathecae. The slope of the two lines in Fig. 1 is not significantly different, but the elevations are. Aphidophagous species lay smaller eggs and have a significantly smaller maximum clutch volume than Eristalinae species. Also they have a much narrower range of egg sizes and relative ovariole numbers. Clearly the Syrphinae is a much more homogeneous subfamily, and perhaps a return to the recognition of more subfamilies within the 'Eristalinae' is warranted.

Further work will consider quantitative features of the male reproductive tract.

Conclusion

As in Stearns' (1983) study, the work here highlights the fact that one should remove the influences of size and phylogeny before considering whether a particular morphology or behaviour is adaptive or not. The study also shows that measuring body size and shape allows reasonably accurate predictions to be made regarding the feeding behaviour and reproductive characteristics of hoverflies. These predictions have been tested (unpubl data). These results also lay the groundwork for morphological treatment of communities, using the analysis of size ratios and models of species composition (unpubl data).

References

Stearns SC 1983 The influence of size and phylogeny on
patterns of covariation among life-history traits in the mammals. Oikos 41: 173-187