Adult feeding by holometabolous insects: pollen and nectar as complementary nutrient sources for *Rhingia campestris* (Diptera: Syrphidae)

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Summary. Examination of the gut contents of adult *Rhingia campestris* reveals that there are considerable differences in the relative amounts of pollen and nectar ingested by individual insects. Pollen, a rich protein source, is required most by females, particularly during those stages of ovarial development when yolk deposition occurs. Nectar, which is mainly carbohydrate, is required in large amounts by males, and is also required by females before and after oogenesis. These results are discussed in relation to the likely nutritional needs of the flies, and it is suggested that similar feeding patterns may be found in a variety of other flower visiting insects. Finally, reference is made to the problems of making ecological assumptions about feeding behaviour on the basis of the morphological attributes of the mouthparts.

Key words: *Rhingia campestris* – Holometabolous insects – Nectar – Pollen – Nutritional requirements

The specialisation of the larvae of holometabolous insects for feeding and growth and of the adults for reproduction and dispersal has been postulated as an advantage consequent on the evolution of 'complete metamorphosis', with the pupal stage (Hinton 1948, 1977). However, it now appears that so far as feeding is concerned, this generalisation is at most only partly true.

Blood-feeding and social insects aside, it has long been known that adult females of some holometabolous insect species require protein to achieve or to enhance reproductive success (eg. Harlow 1956; Schneider 1958). Recently, a number of studies of flower visiting insects have directed attention to the relevance of such 'essential' adult feeding to their life history strategies. Nectar provides a rich source of easily accessible carbohydrate (Percival 1961) with trace amounts of protein (Baker and Baker 1973). Pollen contains substantial amounts of carbohydrate, protein and lipid, as well as traces of many minerals and other compounds (Stanley and Linskins 1974). However, much of the carbohydrate component of pollen is bound up in the grain wall which is not digested by most insects.

Boggs (1981) has shown that pollen feeding by some

adult heliconiine butterflies is part of a strategy in which there is a balance between larval and adult nutrient contributions to reproductive tissues. The exact position of the balance is dependent upon sex and species. Murphy et al. (1983) have demonstrated that nectar ingestion by adult females of the nymphalid butterfly *Euphydryas editha* can enhance longevity and fecundity, and thus help the population to survive years when weather conditions are unfavourable.

Differences in the apparent importance of pollen and nectar as nutrient sources for different species has led to the suggestion by Boggs (1986) that the Lepidoptera may be placed along a continuum of the potential importance of adult nutrients to egg production. The spectrum would range from species which do not feed at all as adults, through nectar feeders (said to have only a relatively poor source of nutrients), to pollen feeders (said to have a relatively rich source of nutrients). This may be an accurate interpretation for certain insects, but it places perhaps rather too little emphasis on the possibility that many species may feed on *both* types of resource. Pollen and nectar are often available together, so that foraging for one of these foods need not preclude swapping over to feed on the other as well. In the present paper I will show that adults of the syrphid fly *Rhingia campestris*, a species often labelled a 'nectar specialist' because of its obviously elongated mouthparts, feed on both pollen and nectar in amounts determined by the immediate needs of the individual animals.

Methods

Field sampling

Samples of *Rhingia campestris* were collected from Broad Oak Ride in Wytham Wood near Oxford, England on 5 and 19 May, 3 and 18 June and on 16 September 1980 using a hand held net. All flies were captured on warm, sunny days between 10.00 and 13.00 BST. This sampling programme covered the full flight season of the species and ensured that all individuals had opportunity to forage at flowers before capture. A description of the field site and the main plant species present is given in Haslett (1989). After capture, the insects were transferred from the net to individual glass tubes, anaesthetised with CO_2 and stored under ice for transport back to the laboratory. Here they

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were kept in a deep freeze ($-18°$ C) until required for analysis.

Laboratory procedure

The total volume of pollen within each fly gut was estimated as an intermediate step in the calculation of pollen proportions undertaken as part of another study. All grains were assumed to be spheres, and were identified and counted across transects of a microscope slide (see Haslett 1989).

The liquid component of the gut content was measured by using the crop as a 'natural' sampling unit (justification for this in Haslett 1982). The proportion of liquid, hereafter referred to as nectar, as this is usually the main constituent, relative to pollen within the crop was estimated by eye through its thin wall, and expressed as a percentage. Such estimates could be made with reasonable accuracy, as the wall of the crop is so transparent that individual pollen grains may be distinguished inside. The stage of oogenesis of female flies was determined by undertaking a dissection of the ovaries to allow examination of the terminal follicle. The follicle could then assigned to one of ten developmental classes as defined by the following system modified from Adams (1974).

Stage 1. The germarium.
Stage 2. The newly formed follicle, spherical in shape. The oocyte within is not visible.
Stage 3. The oocyte is distinct from the nurse cells within the slightly ovate follicle, but forms less than 10% of the total follicular volume.

Stage 4. The oocyte occupies between 10% and 20% of the follicle, which is now distinctly oval in shape. This stage represents the onset of yolk deposition.
Stage 5. The oocyte (with yolk) occupies 20%–30% of the follicle.
Stage 6. The oocyte occupies 30%–50% of the follicle.
Stage 7. The oocyte occupies 50%–75% of the follicle.
Stage 8. The oocyte occupies up to 90% of the follicle. Yolk deposition is near completion.
Stage 9. The mature egg, occupying nearly the entire follicle. The egg is more opaque than at earlier stages and is longer and thinner.
Stage 10. The eggs have been discharged and the ovaries have shrunk and appear rather degenerate.

Results

Examination of the gut contents of a total of 30 ♂ and 49 ♀ flies revealed that there is considerable variation between individuals (0–100%) in the relative amounts of pollen and nectar ingested. Mann-Whitney 'U' tests performed on the raw data show that the male flies had ingested a significantly larger proportion of nectar than the females, ($P < 0.05$). Conversely, the volume of pollen ingested was significantly greater in the females ($P < 0.05$).

The relationship between diet and the degree of ovarial development in female *Rhingia* is shown in Fig. 1. It is immediately apparent that the graphs of nectar and pollen intake are rather neat inverses of each other. They indicate a switch from nectar feeding to pollen feeding and then back to nectar feeding again as the flies' ovaries mature and the eggs are laid.

Discussion

The results of the present study add to a small but significant body of evidence which suggests that an adult contribution of nutrients and energy to the reproductive reserves of holometabolous insects is more important and more widespread than previously thought. Much of this evidence has come from laboratory studies of flower visiting insects (references in Introduction), in which physiological aspects of nutrient utilization have been the main consideration. It is now possible to supplement this information with a more behavioural interpretation of adult feeding, relating differential food intake to the likely requirements of the individual insects under field conditions.

Male flies were found to ingest significantly more nectar and significantly less pollen than females. This result is accountable by the observation that the males invest little in reproductive tissues and are at the same time the more active sex, spending much of their time hovering. Conversely, the females are generally more lethargic in their habits, and they apparently need to invest considerable reserves for producing eggs. It may be noted that the period of most pollen ingestion by females is the same as the time of yolk deposition in the eggs. Females do feed on nectar as well, but as the results have shown, only at the beginning and the end of ovarial development. It would seem logical to suppose that the first peak of nectar feeding is associated with finding a mate, while the second is most likely related to oviposition behaviour. Both activities have substantial energy costs.
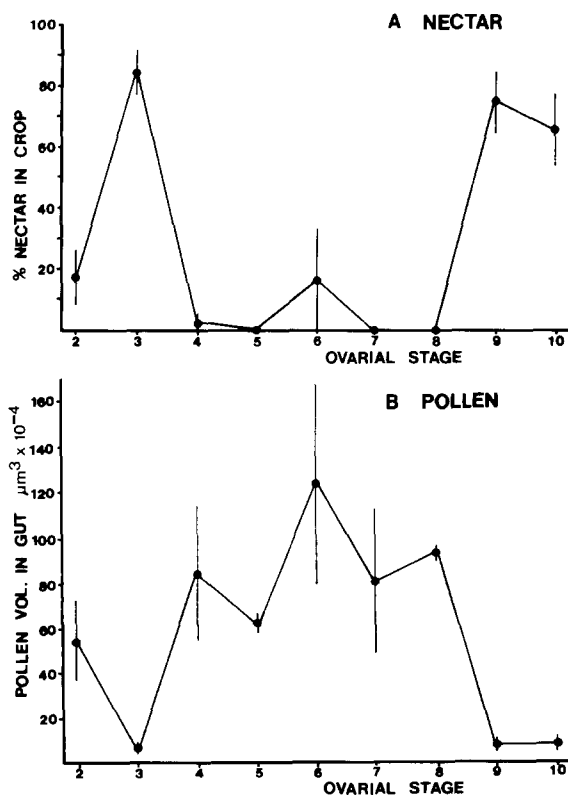

Fig. 1A, B. Relationship between ovarial development and diet of adult female *Rhingia campestris*. Points are means from a minimum of 4 flies. Vertical lines represent one standard error either side of the means

Although the present study has made reference to only one species of hoverfly, there is partial evidence (from gut analyses where samples were small) that similar patterns may be found in some other syrphids, including *Episyrphus balteatus*, *Eristalis pertinax*, *E. tenax* and *Volucella pellucens* (Haslett, unpublished data). Further, Boggs et al. (1981) have reported comparable sexual dimorphism in pollen feeding by *Heliconius* butterflies, and indeed their observation that older individuals tend to collect more pollen than younger individuals, particularly among females, would seem likely to be at least partly a manifestation of the correlate with ovarial development described here. Whether these patterns of nutrient intake are indeed as widespread within the guild of flower visiting insects as they appear remains to be seen.

Quite apart from the life-history aspect, the present study clearly illustrates the weaknesses of using mouthpart morphology to make ecological inferences about feeding and foraging behaviour. I have previously drawn attention to this problem in relation to pollen and nectar feeding in syrphids (Haslett 1989), and there are also clear indications that among members of another family of Diptera, the Bombyliidae, a 'nectar only' label is just as questionable (N Evenhuis, pers comm). This lack of confidence in ecomorphological interpretations of feeding is being echoed in a variety of fields, from studies of birds (Wiens and Rotenberry 1980) and bees (Harder 1985) to work on eastern Pacific blennioid fish (Kotrschal 1989). However, the debate still seems far from settled (see Fryer 1988). It may only be hoped that in the future, ecological assumptions made on the basis of morphological attributes will be examined very carefully before being incorporated into models designed to address other ecological problems, from foraging strategies to competitive interactions.

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