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Evolution of prey specialization in aphidophagous syrphids of the genera *Melanostoma* and *Platycheirus* (Diptera: Syrphidae)

1. Body size, development and prey traits

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Abstract. Interactions between syrphid predators and their prey are poorly known. The adaptations of syrphids to aphid defences and the consequences for the evolution of life history traits in these predators especially are mostly unstudied. This is the first of two papers investigating the evolution of prey specialization in aphidophagous hoverflies. The study focuses on two questions: (1) Are differences in the body size of syrphid predators reflected in differences in the size of their prey? (2) Are differences in body size, body mass and development time of the syrphid predators correlated with the defence strategies of their aphid prey (e.g. mobility, toxicity)? *Platycheirus clypeatus* (Meigen, 1822), *Platycheirus fulviventris* (Macquart, 1829), *Melanostoma mellinum* (Linnaeus, 1758), and *Melanostoma scalare* (Fabricius, 1794), which differ considerably in their prey specialization, but are closely related, were chosen as model species. Life history data for these syrphids came from a laboratory study, and that for the aphids from a literature survey. These syrphid species can be arranged on a gradient of increasing prey specialization, from 32 prey species for the generalist *M. mellinum* and only 3 for the specialist *P. fulviventris*. Differences in prey specialization were even more evident when the defence ability of the various species of aphid prey was considered. For instance, the specialization on ant-attended aphids in *M. scalare*. Larvae exhibited a one or two weeks diapause which made the determination of developmental time imprecise. Body size of the predators was not reflected in that of their aphid prey. The postulated relationship between body size of the predator and the defence strategies of their prey was not supported by our data. A comparison of a wider range of syrphid species from different taxonomic groupings together with a phylogenetic correction procedure might reveal clearer trends. The second part of this paper (Dziock, in prep.) will investigate the correlation between prey specialization and reproductive strategies (i.e. clutch size, egg size and number) and will put the results into a broader framework.

INTRODUCTION

Predatory hoverflies (subfamilies Syrphinae and Microdontinae) are good models for investigating the relationships between prey specialization and life history strategies. The percentage of specialists among them has been assumed to be low, but there is increasing evidence that this is not so (Gilbert, 1990; Gilbert et al., 1994; Branquart, 1999; Sadeghi & Gilbert, 2000a). This is supported by field observations (e.g. Mizuno et al., 1997) as well as by numerous experimental studies (Yakhontov, 1966; Lyon, 1968; Schmutterer, 1972; Láska, 1978; Rotheray, 1988; overview in Sadeghi & Gilbert, 2000b). One possible explanation, the selective attention hypothesis states that there are costs for generalists of making decisions among potential prey that are avoided by specialists concentrating on just one cue (Bernays, 1998; Sadeghi & Gilbert, 2000a). Another cause may be the wide range of aphid defences against enemies. These include waxy secretions, toxins, hiding in galls, active defence, and recruitment of ants that are effective deterrents (Heie, 1982–1995; Malcolm, 1992; Stern & Foster, 1996; Dixon, 1998; Branquart, 1999; Elmes et al., 1999; Agarwala & Yasuda, 2001).

These aphid defence strategies have lead to numerous adaptations in syrphid predators and their specialization on particular prey species. Some syrphid species produce a hardened egg chorion to protect them from penetration by the horns of their aggressive prey aphids (Mizuno et al., 1997). *Eupeodes confrater* changes its oviposition strategy depending on the activity of the soldiers of its prey aphid species. In autumn and winter, when the soldiers are active, the eggs are laid on deserted spider webs in the vicinity of the aphid colonies, in spring and summer the eggs are laid directly into the aphid colonies (Ohara, 1985; Shibao, 1998). Predators of gall-inducing aphids (*Heringia* spp., *Pipiza* spp.) have small and mobile larvae, that are adapted to penetrate into these aphid-induced galls (Dušek & Křístek, 1959, 1967; Kurir, 1963; Rojo & Marcos-García, 1997). Wax-secreting aphids are the preferred prey of *Heringia* (*Neocnemodon*)-species. Their mouthparts are highly modified, presumably to be able to cope with their wax-secreting prey (Delucchi et al., 1957; Dušek & Křístek, 1967). Some *Parasyrphus*-species specialize on chrysomelid beetles and are unaffected by the sequestered chemical defence of the beetle larvae, which is obtained from the salicin in their host plants (willows) (Rank & Smiley, 1994; Rotheray, 1997). *Eupeodes*-species, some of which specialize on lachnid aphids on coniferous trees, use a special grasping organ and lateral movements to achieve high searching rates on conifer needles (Rotheray 1987, 1993). *Microdon* species are obligate social parasites feeding on ant colonies. They seem to be extreme specialists which employ chemical and behavioural adaptations to penetrate their host's defences (Schönrogge et al., 2002). The results of Elmes et al. (1999) indicate local adaptation by *M. mutabilis* not simply to one species of host, but to an individual host population. These examples show the diverse modes of specialization in predatory hoverflies. Adaptations of syrphids to prey defences, and particularly the presence of ants, are a mostly unstudied component of syrphid evolution (Sadeghi & Gilbert, 2000b).

Prey defence strategies are only one important selection factor leading to specialization in predatory hoverflies. Body size, for example, is one of the key characteristics of animals (Hutchinson, 1959; Pagel et al., 1991; Roff, 1992; Stearns, 1992; Blackburn & Gaston, 1994; Nylin & Gotthard, 1998). The selective factors that determine the size of an organism are very complex and still largely unknown (Dixon, 2000; Dixon & Hemptinne, 2001). Body size is correlated with a large number of other species attributes, for example longevity, reproductive rate, or resource use (Harvey & Pagel, 1991; Blackburn & Gaston, 1994).

Two different models have been proposed to explain body size in invertebrates. The energetic concept proposed by Brown and colleagues defines the fitness of an animal in terms of its rate of conversion of energy from its environment into offspring (Brown et al., 1993). It is assumed that the rate of acquisition of energy (e.g. respiration rate) scales with body mass to the power of +0.75 (Blackburn & Gaston, 1994; Purvis & Harvey, 1997; West et al., 2000).

Some authors have challenged these physiological models and propose ecological explanations (Pagel et al., 1991; Witting, 1998; Kindlmann et al., 1999; Bokma, 2001). In predatory coccinellids for instance, assimilation and respiratory rates do not seem to be correlated with body size (Dixon, 2000). On the contrary it is often the body size and other characteristics of the prey that are associated with the body size of the predator (Hutchinson, 1959; Tauber et al., 1995; Dixon, 2000; Dixon & Hemptinne, 2001). The defence strategies of aphids (the regular prey of predatory hoverflies) could affect the body size of their hoverfly predators.

In this study two questions will be investigated: (a) Are differences in body size/body mass of syrphid predators reflected in the differences in body size of their prey? (b) Are differences in body size, body mass, and development time of the syrphid predator correlated with the defence strategies of their aphid prey (e.g. mobility, toxicity)?

This is the first of two papers dealing with the evolution of prey specialization in the Syrphinae. This first part deals with the influences of body size, body mass, development time and prey traits on prey specialization. The second part will focus on reproductive strategies and their relation to prey specialization and present general conclusions.

MATERIALS AND METHODS

Choice of species

Comparative analyses of predator-prey associations in closely related species offer an array of attractive opportunities for basic and applied studies (Tauber et al., 1993). The selection of species for comparative studies should – whenever possible – be guided by the closeness of their phylogenetic affinity (Huey & Bennett, 1986). The four species chosen are from two closely related genera (*Melanostoma*, *Platycheirus*). One species from each genus is a specialist [*Melanostoma scalare* (Fabricius, 1794), *Platycheirus fulviventris* (Macquart, 1829)], the other one a generalist [*Melanostoma mellinum* (Linnaeus, 1758), *Platycheirus clypeatus* (Meigen, 1822)]. The genera *Platycheirus* and *Melanostoma* do not only differ considerably in their prey specialization, but are also very closely related. This ensures a "phylogenetic control" that would otherwise only have been achieved by labour- and data-intensive (especially data on the species phylogeny, which is not well known) statistical methods (Huey & Bennett, 1986; Garland et al., 1999; Desdevides et al., 2003).

Gilbert et al. (1994) argue in favour of specialized feeding being evolutionary advanced in these two genera. This allows comparisons between these four species to be used to infer how specialization arose and simultaneously avoid confounding phylogenetic effects (Tauber et al., 1993; Sloggett & Majerus, 2000). Table 1 shows some biological characteristics of the species studied.

Laboratory experiments

Laboratory cultures of the four species were established from gravid females captured in the field (vicinity of Steckby northwest Dessau, Elbe floodplain, Saxony-Anhalt, central Germany, 9 July, 20 July, 6 August, 24 August, 10 September 1999). They were put individually into plastic boxes (12 cm diameter) with water soaked cotton pads on the day they were collected. In total 97 gravid females were caught, 93 of which oviposited in the laboratory. Their total offspring consisted of 128 pupae, from which 100 adults emerged. Sample sizes of the different parameters measured are given in the results section.

Unlike other Syrphidae, *Melanostoma* and *Platycheirus* adults mainly feed on the pollen of anemophilous plants (Leereveld, 1982). Thus, every two days they were offered inflorescences of

TABLE 1. Biological characteristics of the species studied (taken from Dziock, 2002).

	generalist		→	specialist
	Melanostoma mellinum	*Platycheirus clypeatus*	*Melanostoma scalare*	*Platycheirus fulviventris*
habitat	open ground	open ground	woodland (and open ground)	wetlands
distribution	holarctic	holarctic	palaearctic	palaearctic
no. of generations per year	≥ 3	≥ 3	≥ 3	2–3
migratory status	seasonal migrant	wind-dependent seasonal migrant	low migratory power	no migration
no. of prey species	32	12	10	3

grasses (Poaceae and Cyperaceae), *Plantago media* and *P. lanceolata* collected from the field. The boxes were kept in a constant environment of 22 ± 2°C and a 16-h day length. The boxes were checked for eggs every two days. The number of eggs and clutch size were noted (results on reproduction will be presented in a forthcoming paper, Dziock, in prep).

When the gravid females started ovipositing, bean leaves (*Vicia faba*) infested with *Aphis fabae* were placed in the boxes. After the larvae hatched from the eggs, fresh food was supplied every two days. Date of pupariation was noted for each larva and pupae were weighed and then kept individually in tubes with water soaked cotton wool. These were checked daily for adults. The adult and remains of the puparium were weighed immediately after adult emergence. A micro balance with an accuracy of 0.01 mg (Mettler Toledo MT 5) was used. Morphometric measurements (Table 2) were made using a stereomicroscope Leica Wild M3C at a 10- to 40-fold magnification.

Detailed morphological studies have shown that head width is a good indicator of total body size in syrphids (Kikuchi, 1965; Gilbert, 1985a,b). Consequently head width was used as a surrogate for body size in this study. Table 2 gives the parameters used in the present analysis.

Prey spectrum

Aphid prey species lists for the four syrphid species investigated can be found in Rojo et al. (2003) and a few additional papers. The original citations and prey species lists are given in Dziock (2002). It is difficult to evaluate specialization in predators based only on the number of known prey species (Strand & Obrycki, 1996). Therefore the defence strategies of the aphids were also taken into consideration. Biological traits of the prey species (only aphids) were taken from the literature. Traits chosen were average body size, secretion of wax, formation of closed galls, chemical defences, escape behaviour and ant attendance. Information was gathered from Heie (1980, 1982, 1986, 1992, 1995), Blackman & Eastop (1984, 1994), Branquart (1999) and Stary & Láska (1999). Body size was measured in mm, the other traits were coded on an ordinal scale (fuzzy coding). A "0" means no affinity to a given feature (e.g. no ant attendance), "1" means medium affinity (e.g. facultative ant attendance) and "2" means strong affinity (e.g. obligate ant attendance). A table with the original data can be found on the web (www.ufz.de/index.php?de=1897).

The average body size of all aphid prey was calculated for each syrphid species on the basis of the original data. Multiple citings of the same species of aphid prey in different publications were all included in the calculation. Additionally we calculated an index of defence for each syrphid species. This is a measure of the average defence ability of the prey of a given syrphid species. The index of defence of the prey species was calculated as the sum of the ordinal scaled traits divided by the number of relevant citations in the literature.

$$\text{Index of defence} = \frac{\sum(\text{ant attendance} + \text{wax} + \text{galls} + \text{toxins} + \text{escape behaviour})}{\text{number of citings of the prey species}}$$

The higher the index, the higher the average defence ability of the aphid prey of a particular species of syrphid.

Statistics

For the comparison of mean values, one way-ANOVA was used. Normal distribution of residuals was tested graphically, because test statistics for normal distribution are insensitive when applied to small data sets (Bärlocher, 1999). Homogeneity of variance was tested using the Levene-procedure. For multiple comparisons of mean values, post-hoc-tests were used (Spjotvoll & Stoline, 1973). These are generalizations of Tukeys HSD (honest significance difference)-test for the case of unequal sample sizes. This test is one of the most conservative tests for the comparison of multiple mean values (Statsoft, 2000). All tests were carried out using Statistica 5.5 (Statsoft, 2000). The following p-values were defined as "significant" ($p < 0.05$) and "highly significant" ($p < 0.01$).

RESULTS

Prey defence strategies

The four syrphid species under investigation can be grouped along a gradient of increasing prey specialization based on the number of prey species recorded in the lit-

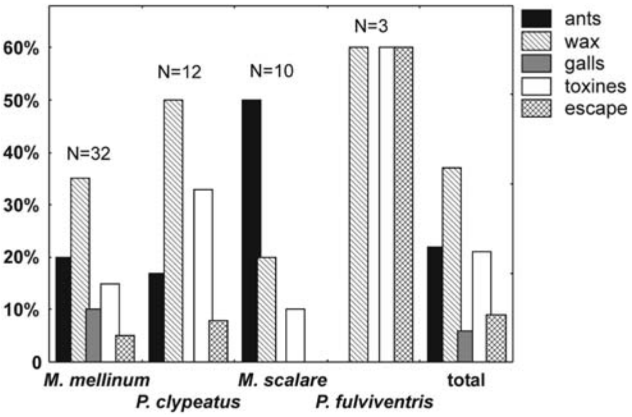

Fig. 1. Defence strategies of the prey of the four species of syrphid studied. Given is the percentage of the five defence strategies shown by the prey of each of the syrphid species. Total refers to the prey spectrum of all four species of syrphid. Defence strategies: ants – ant attendance, wax – secretion of wax, galls – formation of closed galls, toxins – chemical defences, escape – escape behaviour/high mobility, N – number of prey species.

TABLE 2. Parameters recorded in the laboratory studies.

Development time to adult	Time from first oviposition of the mother to eclosion of adult
Development time to pupation	Time from first oviposition of the mother to pupariation
Length of the pupal stage	Time from pupariation to eclosion of adult
Head width	Maximum width of the head, frontal view
Wing length	Shortest length between the junction of the costal vein (C) with the humeral crossvein (h) and the junction of R4+5 with the medial vein (M)
Adult biomass	Biomass of an adult fly immediately after emergence, but with its wings inflated and hardened
Pupal biomass	Biomass of a pupa at pupariation

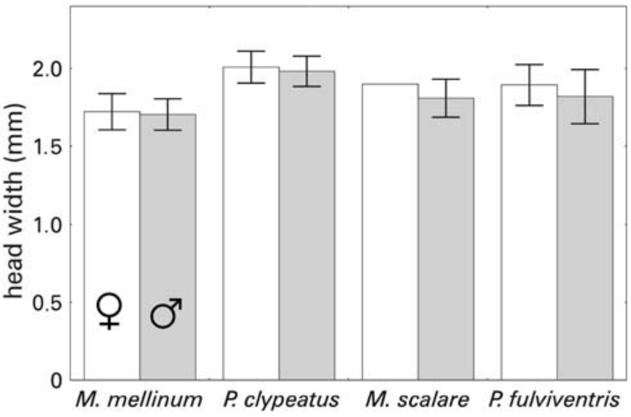

Fig. 2. Head widths of the four species. Means ± SD. ♀ of *M. scalare* lack an SD, because the sample size was one.

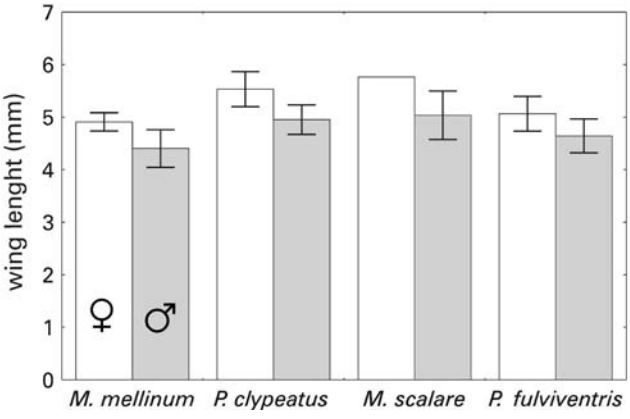

Fig. 3. Wing lengths of the four species. Means ± SD. ♀ of *M. scalare* lack an SD, because sample size was one.

erature. This ranges from 32 prey species for *Melanostoma mellinum* to three for *Platycheirus fulviventris*. Fig. 1 gives an overview of the defence strategies of the prey of the four syrphid species. For comparison, the total spectrum of defence strategies of the aphid prey of all four species of syrphid are figured together.

P. fulviventris shows the highest specialization. It feeds on three species, with *Hyalopterus pruni* the most common (Waitzbauer, 1976; Imhof, 1979; Rotheray & Dobson, 1987; Maibach & Goeldlin de Tiefenau, 1991). This aphid secretes wax, synthesizes toxins and shows escape behaviour (Branquart, 1999). Thus the calculated defence index of the prey of *P. fulviventris* is comparatively high (3.2).

The number of species of prey recorded for *M. scalare* is ten. Apparently this species prefers prey with little defence which results in the low defence index of 1.6. However, of the four species studied, *M. scalare* has the highest percentage of prey attended by ants.

P. clypeatus has been observed feeding on twelve different species of aphid. Although this is only two more than *M. scalare*, this species is definitely less specialised than the former. This can be concluded from a comparison of the prey spectrum of these two species with that for all four species. *P. clypeatus*' spectrum is more similar to the total spectrum than that of *M. scalare*, suggesting that *M. scalare* is much more specialised than *P. clypeatus*.

M. mellinum is a prey generalist and has been found in association with 32 aphid species. This generalist character is also evident when its prey spectrum is compared with the total spectrum, which are virtually identical (Fig. 1).

Body size of predators

Head width

M. mellinum had the smallest head width (♂ 1.7 mm, ♀ 1.7 mm) of the four species, *P. clypeatus* the largest (♂ 2.0 mm, ♀ 2.0 mm) (Fig. 2). The difference between these two species is highly significant (one way-ANOVA, $F_{7,85} = 17.2$, $p < 10^{-5}$, Tukeys posthoc test). There were no significant intraspecific differences in head width between the sexes.

Wing length

Females have longer wings than males in all species (Fig. 3). This difference is significant in *M. mellinum* and *P. clypeatus* (one way-ANOVA, $F_{7,77} = 17.89$, $p < 10^{-5}$, Tukeys posthoc-test). *M. mellinum* has the shortest wings, *M. scalare* the longest. *P. clypeatus* has significantly longer wings than *M. mellinum* (Tukeys posthoc-test).

Body size of aphids

Table 3 gives an overview of the size of the four syrphid species studied and the mean size, number and defence ability of their prey. Average prey size is 2.6 mm for three species, and 2.29 mm for the specialist *P. fulviventris*. Table 3 shows that average prey size is only weakly correlated with the body size of the predator.

Development time

Development time did not differ significantly between the species and the sexes (one way-ANOVA, $F_{7,89} = 0.283$, $p < 0.959$). Development from the time of oviposition to eclosion of the adult from the pupa took 37.2–39.6 days depending on the species (Fig. 4).

The pupal stage lasted for 8.0 to 9.3 days (Fig. 5). There were no significant differences between the species

TABLE 3. Size and defence ability of the aphid prey of predatory syrphids of the genera *Platycheirus* and *Melanostoma*. For defence index calculation, see Materials and Methods.

	mean size (mm)	mean size prey (mm)	defence index	no. of prey species
M. mellinum	1.71	2.60	2.05	32
P. clypeatus	2.00	2.61	2.50	12
M. scalare	1.85	2.61	1.60	10
P. fulviventris	1.87	2.29	3.20	3

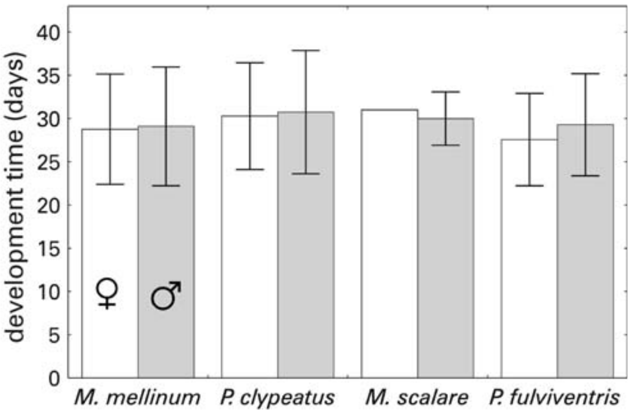

Fig. 4. Development time from oviposition to eclosion of adult. Means ± SD.

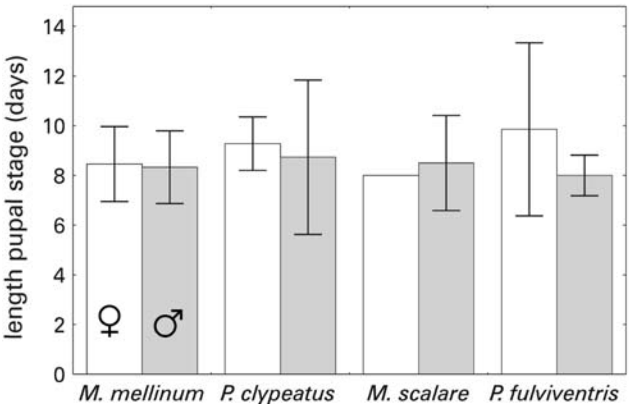

Fig. 5. Duration of the pupal stage. Means ± SD.

and the sexes (one way-ANOVA, $F_{7,\ 89} = 0.6988$, $p < 0.673$).

Biomass

Adults of *M. mellinum* were the lightest of the four species weighing on average 3.71 mg (♂) or 3.98 mg (♀). *P. clypeatus* were heaviest (Fig. 6). The difference between these two species is significant (one way-ANOVA, $F_{7,82} = 3.34$, $p < 0.0035$, Tukeys posthoc test). The same applies for the pupae of the four species (Fig. 7), where the difference between pupal biomass of *M. mellinum* (♂: 7.85 mg, ♀: 7.91 mg) and that of *P. clypeatus* (♂: 11.76 mg, ♀: 12.23 mg) is highly significant (one way-ANOVA, $F_{7,\ 82} = 16.17$, $p < 10^{-6}$, Tukeys posthoc test).

DISCUSSION

Body size and development time

A comparison with the head widths measured in other studies shows some differences (Table 4). The head widths recorded in this study were consistently smaller than those given by Gilbert (1985a) and Branquart & Hemptinne (2000).

The nutritional quality and quantity of food available during larval development has a large effect on body size of the resulting adults (Dixon, 2000). It is therefore possible that there are seasonal differences in body size that result from feeding on different qualities and quantities of prey. Unfortunately, Gilbert (1985a) and Branquart & Hemptinne (2000) did not explicitly state when they made their studies.

It is possible that the aphid (*Aphis fabae*) fed to the syrphids was less suitable for the specialists than for the generalists. This is indicated by the fact that the difference in head width recorded in this study compared to that in other studies was higher for the specialists than for the generalists. Nonetheless the relative differences in head width between the four species are similar in the different studies. *M. mellinum* is the smallest of the four species, and *P. clypeatus* and *P. fulviventris* are the largest. In general, the species are quite similar in head width, with the difference between the smallest and the largest being ca. 17%. The body masses accord well with the head widths. The differences between the species in body mass, however, are even larger.

In all species, females have longer wings than males. Maybe this is because of the important role females play in migration processes. If longer wings indicate a better flight ability, then selection favouring flight ability could result in longer wings. Longer wings in females may be a consequence of the important role of inseminated females in the migration processes (Aubert et al., 1976; Gatter & Schmid, 1990).

Development time has previously been recorded for only two of the four species (*M. mellinum*, *P. clypeatus*). Larval development in a related species, *Melanostoma orientale* (Wiedemann, 1824), takes 9.1 days and pupal development another 9.1 days (Kumar & Varma, 1996). Larval development in *M. mellinum* takes 10 days according to Bankowska et al. (1978) and 11 to 17 days and 24 to 31 days according to Polak (1980) and Metcalf (1916). Egg plus larval development of *M. mellinum* took 28 days (mode) in this study. Egg development takes 2 to 4 and 5 to 7 days according to Metcalf (1916) and Polak (1980), respectively. Thus larval development in our study took between 21 to 26 days.

Accounting for the discrepancies in the duration of the larval stage in the different studies (ranging from 10 to 31 days!) is difficult. Laboratory conditions could play a role. Temperature has a significant influence on development time (e.g. Bombosch, 1963). Unfortunately there is no information on the rearing temperatures used in the above studies. Aphid quantity and quality is also a major

TABLE 4. Head widths of the four species recorded in the literature and this study. Values in mm.

	M. mellinum	*P. clypeatus*	*M. scalare*	*P. fulviventris*
Gilbert, 1985a	2.05	2.30	2.21	—
Branquart & Hemptinne, 2000	1.80	2.00	2.00	2.20
This study	1.71	2.00	1.85	1.87

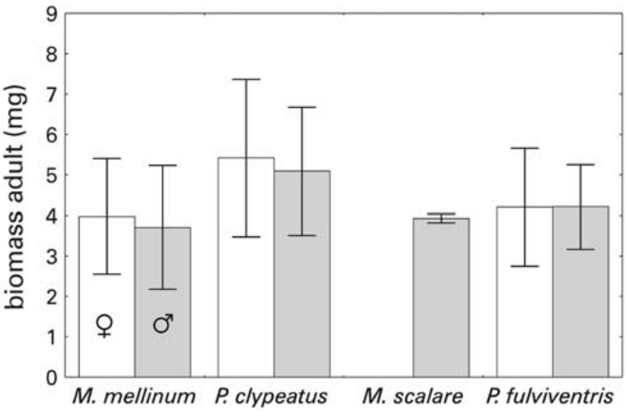

Fig. 6. Biomass (fresh) of the adults. Means ± SD. No data for female *M. scalare*, because no pupa produced an adult.

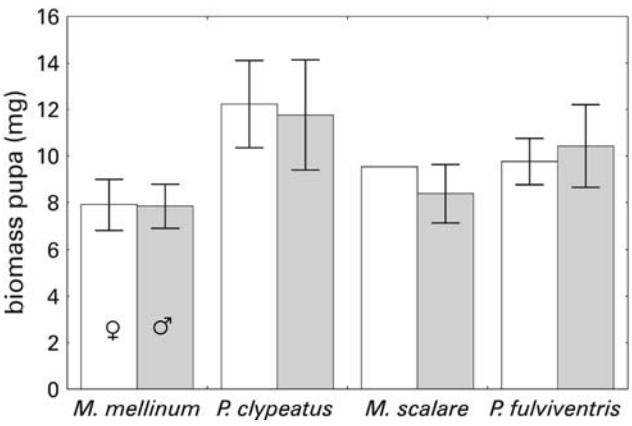

Fig. 7. Biomass (fresh) of the pupae. Means ± SD. ♀ of *M. scalare* lack an SD, because the sample size was one.

factor. Polak's experiments show that larval development takes 17 days on a daily ration of 10 aphids and 11 days when supplied with 60 aphids a day (Polak, 1980). Larvae could not finish their development when supplied with less than 10 aphids a day. In our study aphids were offered ad libitum. Thus, the observed developmental time of 21 to 26 days can not be due to starvation, as even extremely hungry larvae (10 aphids a day) took only 17 days to complete their larval development in Polak's experiments.

A similar phenomenon occurs in *P. clypeatus*. Larval development took 9 and 15 days respectively, in the experiments of Bankowska et al. (1978) and Bolet & Dahl Jensen (1980). In this study egg plus larval development took an average of 30.5 days. For the same reasons as stated above this cannot be due only to differences in laboratory conditions. It is more likely the larvae entered a short diapause which prolonged their development. Larvae of numerous species of predatory syrphids show facultative diapause (Schneider, 1948; Dušek & Láska, 1986). Dunn (1949) observed a one week diapause in *Platycheirus manicatus* (Meigen, 1822). The same species entered a diapause of one to two months in the studies of Goeldlin de Tiefenau (1974) and Bolet & Dahl Jensen (1980). *Platycheirus europaeus* Goeldlin de Tiefenau, Maibach & Speight, 1990, and *Platycheirus peltatus* (Meigen, 1822) are also known to have a facultative diapause of one to two months (Goeldlin de Tiefenau, 1974). That is, it is very probable that the species entered a one or two week diapause in our study. The reason for this is unknown, as they were reared under constant conditions.

There were no significant differences in development times of the species, neither for the time from oviposition to adult eclosion, nor for the length of the pupal stage. As indicated above, a facultative diapause could account for this. Possibly, this diapause was of unequal length in the four species, and this resulted in their developmental times being similar. Maybe the differences in development time are too small to be revealed when development is recorded at one to two day intervals, as in this study. It is remarkable, that even the species with the largest eggs, *M. scalare* (Dziock, in prep), did not have a shorter development time. This should be the case, because due to their large initial size the larvae have to ingest less food to achieve their final size.

Prey traits and body size

In predatory insects, body size of the predator is often reflected in the size of their prey. In the four species studied, this is not evident. Average prey size is 2.6 mm for three of the species, and 2.29 mm for the specialist *P. fulviventris*. Table 3 shows that average prey size is only weakly correlated with the body size of the predator. This is inconsistent with the hypothesis that the most specialised species (*P. fulviventris*) ingests the largest prey. The opposite is the case; average prey size is comparatively low. Although only four species were studied, it is possible that prey size is relatively independent of body size in these predators. This could be due to the fact that the four species, as predators of aphids, have quite similar prey. The correlation between size of predatory coccinellids and their prey postulated by Dixon & Hemptinne (2001) considers prey as different in size as mites, aphids, coccids and larvae of chrysomelids and Lepidoptera. Thus if a wider range of syrphids and their prey had been compared, they might have shown a similar trend. This is because predatory syrphids also use a wide range of prey such as aphids, coccids, larvae of Lepidoptera and the early stages of ants and wasps etc. (Thompson & Rotheray, 1998). Thus predator size is more a function of the membership of a taxonomic group, i.e. the degree of specialisation of respective syrphid species, rather than of the size of their prey.

There is often a close connection between prey defence and the body size and other life history traits of the predator. There was not an unambiguous relationship between the defence index of the prey spectrum and predator body size in this study. Consequently, body size of the four species studied seems to be relatively independent of the defence ability of their prey. The highly specialised species, *P. fulviventris* (highest defence index), is medium-sized like the species with the lowest defence index (*M. scalare*). However, *M. scalare* seems to have specialised on ant-attended aphids, which is indicated by the high proportion of ant-attended aphids among its prey (Fig. 1). At the species level, aphids have developed an array of associations with ants from unattended to obligate myrmecophiles (Stadler & Dixon, 1999; Stadler et al., 2003). There are also considerable intraspecific differences in performance depending on the degree of ant attendance of a specific aphid colony (Banks & Nixon, 1958; Stadler & Dixon, 1999). Thus the study of the effect of ant attendance on prey specificity of aphidophagous syrphids is very complex and deserves more attention.

In summary, the postulated relationship between body size of a syrphid and the defence strategies of its prey was not supported by the data. A comparison of a wider range of syrphid species, from different taxonomic groupings, together with a phylogenetic correction procedure seems to be more promising. However, Branquart (1999) was not able to find a phylogenetic trend towards higher specialization. There are highly specialized species at the base of the hypothetical phylogenetic tree (e.g. *Pipizella* spp., *Platycheirus* spp.). On the other hand, highly evolved species like *Eupeodes corollae* (Fabricius, 1794) or *Scaeva pyrastri* (Linnaeus, 1758) which have a wide range of prey species, may show that generalization evolved secondarily. That is, there is no clear trend towards an increasing specialization within the Syrphinae and therefore clear trends with body size should be even more difficult to identify.

The recently published world review of predatory hoverflies and their prey (Rojo et al., 2003), provides a useful source of information for exploring the relationships between the traits of predatory hoverflies and defence strategies of their prey. This should be accompanied by statistical techniques that account for the phylogenetic relatedness of the syrphid species. As the hypothesized phylogeny of the Syrphidae has proceeded significantly in the last years (Rotheray & Gilbert, 1999; Ståhls & Nyblom, 2000; Barkalov, 2002; Ståhls et al., 2003, 2004), there is now a sounder basis for such an approach.

In the second part of this study, the relationship between prey specialization and reproductive strategies in *Melanostoma* and *Platycheirus* species will be presented (Dziock, in prep). These results we presented in a broader framework and discussed in the context of the habitat templet concept of Southwood (1977).

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