

Behavioural mimicry of honeybees (*Apis mellifera*) by droneflies (Diptera: Syrphidae: *Eristalis* spp.)

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Droneflies (Syrphidae: *Eristalis* spp.) resemble honeybees (*Apis mellifera*) in appearance and have often been considered to be Batesian mimics. This study used a focal watch technique in order to compare the foraging behaviour of droneflies (*Eristalis tenax*, *Eristalis pertinax*, *Eristalis arbustorum* and *Eristalis nemorum*) whilst they were feeding on patches of flowers with the behaviour of honeybees and other hymenopterans and dipterans. It was found that, on a range of plant species, the time droneflies spent on individual flowers and the time spent flying between them was more similar to that of honeybees than to the times of other hymenopterans and dipterans. These results suggest that dronefly behaviour has evolved to become more similar to that of honeybees and they support the hypothesis that droneflies are Batesian mimics.

Keywords: Batesian mimicry; droneflies; honeybees; foraging behaviour

1. INTRODUCTION

The mimicry between droneflies (*Eristalis* spp.) and honeybees (*Apis mellifera* L.) has been fooling humans for over 2000 years. In ancient Egypt it was thought that honeybees originated by spontaneous generation from the carcasses of decaying animals, particularly oxen. This myth later became known as the *Bugonia*, meaning ox progeny in Greek. The writings of the Hebrews also mention this myth, but in this instance the carcass was a lion in which Samson is reported to have found a swarm of bees (The Bible, Judges xiv: 8). The myth, which is also frequently mentioned in Roman and Greek literature (Atkins 1948), was finally clarified by the Russian entomologist Osten-Sacken (1898), who identified the dronefly as the false bee of the *Bugonia*. Atkins (1948) cited many more examples of the mimicry fooling beekeepers and entomologists alike. However, the most important question is whether the mimicry fools predators (Whittington 1994). There are a few studies that demonstrate the effectiveness of mimicry by hoverflies (Mostler 1935; Brower & Brower 1962, 1965; Dittrich *et al.* 1993; Heal 1995), although none of these are field studies.

The genus *Eristalis* is widespread and occurs in Holarctic, Oriental and Ethiopian regions with some Neotropical species (Brower & Brower 1965). In their worldwide distribution droneflies have closely followed humans, who provide them with many opportunities of breeding in farmyard drains, manure and polluted ditches.

The most widespread and common *Eristalis* species in Britain are *Eristalis tenax* (L.), which is one of the few hoverflies found throughout the year, *Eristalis pertinax* (Scopoli), which closely resembles *E. tenax*, and *Eristalis arbustorum* (L.) and *Eristalis nemorum* (L.), which are both slightly smaller than *E. tenax* and *E. pertinax* and which are often difficult to distinguish from each other in the field (Stubbs & Falk 1983).

Droneflies are similar to honeybees in their size and shape, a fact which is often referred to though not quantified (Brower & Brower 1962, 1965; Heal 1979) and in their colour pattern (Heal 1982; Holloway 1993). With experience droneflies are quite easy to distinguish from honeybees and so visually droneflies are often described as poor mimics of honeybees (Grewcock 1992), but even imperfect mimics may gain some protection during the period when young birds are learning their hunting skills (Dlusski 1984). Although *E. arbustorum*, *E. nemorum*, *E. tenax* and *E. pertinax* certainly resemble honeybees (Howarth *et al.* 2000), their resemblance is not as precise as that of hoverflies such as *Mallota cimbiciformis* (Fallén) and *Criorhina asilica* (Fallén). The natural predators of droneflies certainly include birds that have quite different and more precise vision from ourselves (Cuthill & Bennett 1993). Dlusski (1984) reported that redstarts (*Phoenicurus phoenicurus*) and spotted flycatchers (*Muscicapa striata*) can find hoverfly prey at a distance of more than 10 m. Thus, if birds can distinguish droneflies by means of their colour, then for mimicry to be effective we might expect their behaviour to resemble that of honeybees. Droneflies have been described as having bee-like flight (Wickler 1968) and Morgan & Heinrich (1987) observed that the mimicry of many hoverflies (including *Eristalis* species) appeared to be most accurate in flight. In addition, droneflies are described as having similar foraging behaviour to honeybees (Holloway 1976). However, these behavioural similarities are based on subjective or anecdotal descriptions; they have never been quantified and no direct comparisons of foraging behaviour have been made between models and mimics in the field.

Most hoverflies are fast adept fliers; *E. tenax* can maintain flight speeds of up to 10 m s⁻¹ for short distances and, presumably, are difficult for predators to catch (Collett & Land 1978). However, when foraging on flowers, they are likely to be easily seen by birds perched in nearby trees or by patrolling insectivorous insects, such as wasps.

The aim of this study was to determine whether there is behavioural mimicry of honeybees by droneflies during foraging. If droneflies are Batesian mimics we predict that

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Table 1. Sites where fieldwork on droneflies was carried out in 1997 and 1998, with the flower species used and their flowering periods

site	species	flowering period
Brock Bottom semi-natural woodland with open grassy areas and river bank in Brock Valley, rural Lancashire grid reference SD 545 423	bramble (<i>Rubus fruticosus</i>) rosebay willowherb (<i>Epilobium angustifolium</i>)	June–July July
Sale Water Park natural carr, water meadows, artificial lakes and open grassy areas in Mersey Valley, semi-urban area in Cheshire grid reference SJ 805 925	snowberry (<i>Symphoricarpos rivularis</i>) Michaelmas daisy (<i>Aster novi-belgii</i>)	August–September September
Sandsend Nature Reserve old quarries and alum workings above coastal cliffs on north-east Yorkshire coast grid reference NZ 859129	knapweed (<i>Centaurea nigra</i>)	August
Wythenshawe Park an urban park in Manchester grid reference SJ 813 896	everlasting daisy (<i>Helichrysum bracteum</i>)	August
Freiburg Botanic Gardens southern Germany	goldilocks (<i>Aster linosyris</i>)	September–October

the time they spend foraging on each flower visit and the time they spend flying between flowers should be more similar to the times of honeybees than to the times spent by other hoverflies or other bees. However, if they do not benefit from mimicry of honeybees, then we predict that the times spent feeding and flying between flowers should be more similar to the times of other hoverflies than to those of hymenopterans.

2. METHODS FOR STUDYING FORAGING BEHAVIOUR

Five contrasting sites were selected in which flowers that attracted both the models (*A. mellifera*) and at least three species of mimics (*E. tenax*, *E. pertinax* and *E. arbustorum* and, possibly, some *E. nemorum* as well) grew. The droneflies were identified to species and sex on two out of the seven flowers (knapweed and goldilocks). A short description of the sites and the flowering period of the flower species used is given in table 1.

Standard-sized patches of flowers of 2 m × 1 m were identified for the study. The models and mimics regularly fed together on these areas alongside other dipterans and hymenopterans, some of which occurred in sufficient numbers to act as controls. A focal watch technique was used to record the behaviour of individual insects whilst they were on the patch. The time the insects spent feeding on each visit to a flower and the time they took to fly between them were recorded using a tape recorder. Behaviour was only recorded whilst insects were on the patch; as far as possible each insect was watched from when it flew onto the patch until it flew off. Observations were made during sunny periods when there were plenty of insects about.

The mean lengths of feeding bouts and flights between flowers were calculated for each species of insect on each species of flower. The data was log transformed to allow parametric analysis and analysed using one-way ANOVAs, followed by Dunnett's test in which comparisons of the mimic can be made with the model and controls. One-way ANOVAs were also carried out on each species in order to detect any differences in behaviour between individuals.

The data from knapweed and goldilocks flowers were analysed further in order to detect any differences between the behaviours

Table 2. Summary of the statistical analysis of the mean times that insects spent feeding and flying between flowers (figures 1 and 2)

(The data were log transformed and a one-way ANOVA applied, followed by Dunnett's comparison test. The dronefly mimics on each flower (column 1) were compared with the honeybee models (column 2) and with the bumble-bee controls (column 3). Feed, comparison of times spent feeding; fly, comparison of times spent flying between flowers. A minus sign indicates no significant difference and a plus sign indicates a significant difference.)

flower	honeybee (model)		bumble-bee (control)	
	feed	fly	feed	fly
bramble (June)	–	–	+	+
bramble (July)	–	–	+	+
snowberry	–	–	no control	
everlasting daisy	–	–	+	–
Michaelmas daisy	+	–	+	+
goldilocks	–	+	no control	
knapweed	–	–	+	–
rosebay	+	–	+	+
willowherb				

of male and female mimics by means of two-sample *t*-tests. A one-way ANOVA was also used to determine whether there were any differences in behaviour between the different species of *Eristalis*.

3. RESULTS

(a) Differences between individuals

One-way ANOVAs were carried out on individuals of each species of insect on each flower, which involved 78 calculations. These showed ten significant differences between the behaviour of individuals, two for feeding times and eight for flight times. The feeding time differences were for honeybees on bramble in June ($F_{8,85} = 2.17$ and $p = 0.038$) and bumble-bees on bramble in July ($F_{31,288} = 2.54$ and $p = 0.000$). The first was only marginally significant, while 'bumble-bees' includes several

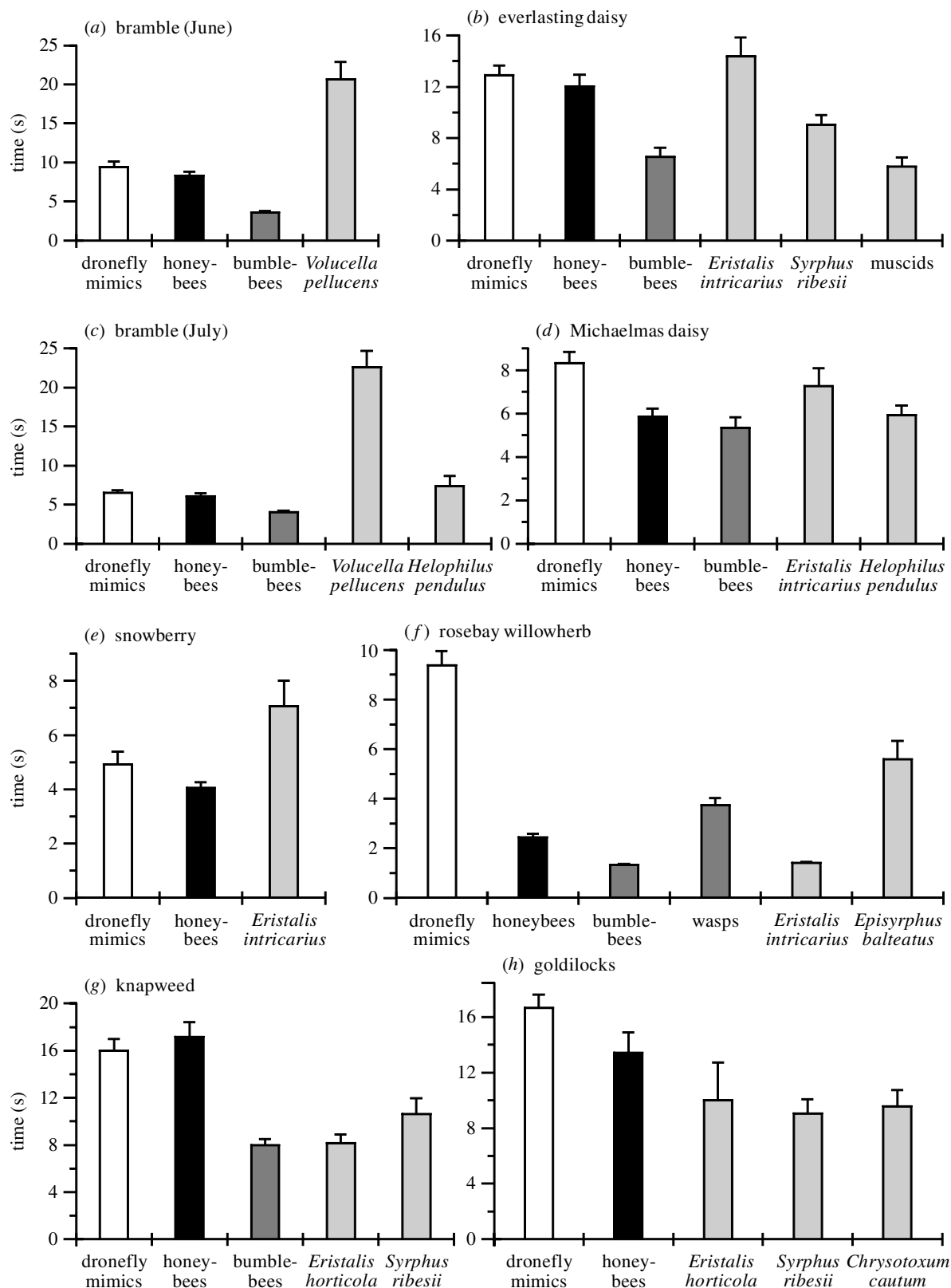


Figure 1. Mean times (with standard errors) spent feeding on flowers by droneflies, honeybees and other insects.

species of black and yellow *Bombus* which differed in their behaviour. The eight flight time differences involved droneflies and honeybees (on three flowers each) and bumble-bees and *Eristalis intricarius* (on one flower each), all of which commonly spent only 1–2 s flying between flowers. For these four species, the significant differences

were less than 1 s, which is less than the level of accuracy of timing in the field, so we considered that they were not biologically meaningful.

Because of the small number of differences between individual insects revealed by the ANOVAs (above) and because we may have inadvertently recorded a returning

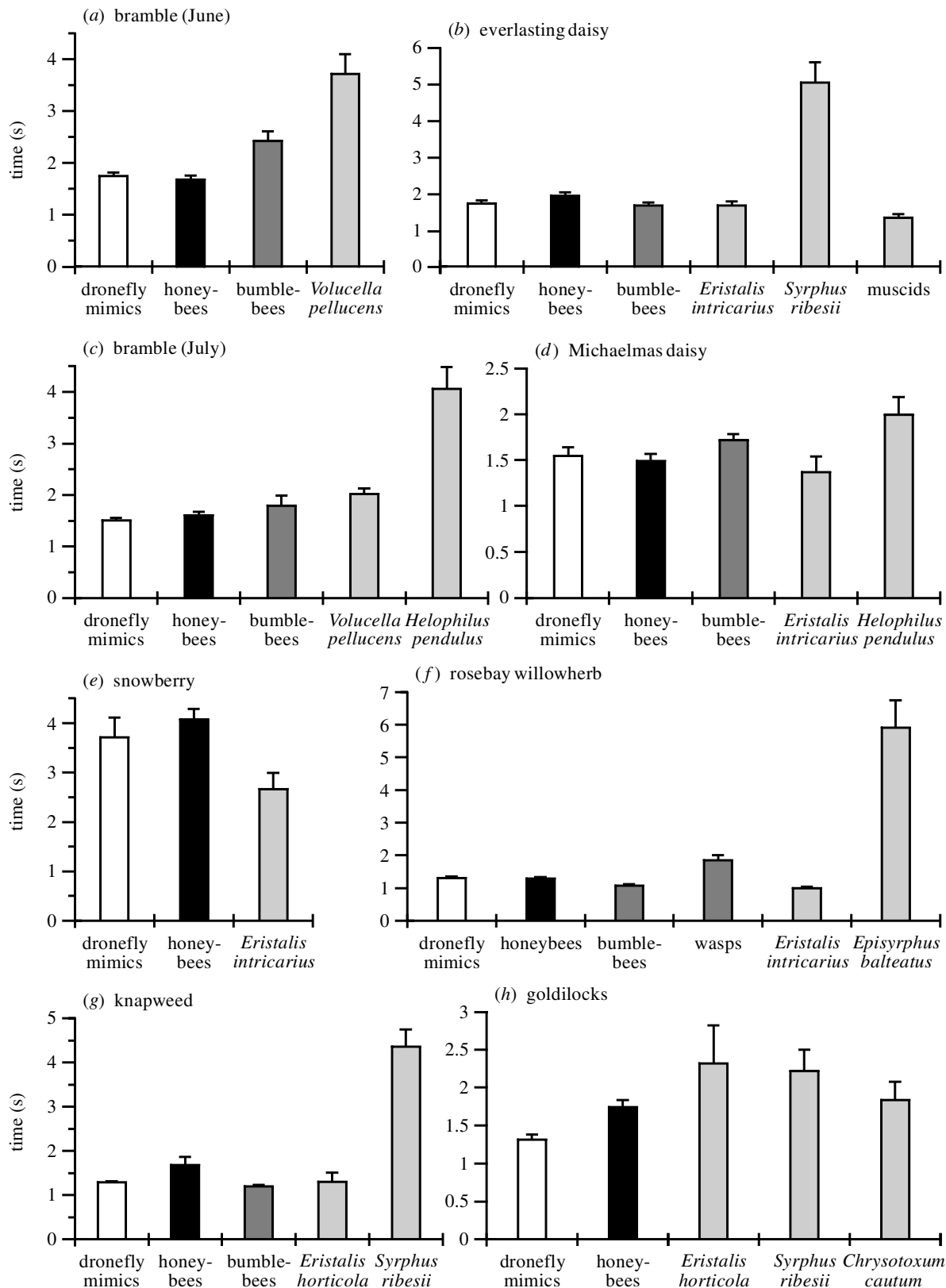


Figure 2. Mean times (with standard errors) spent flying between flowers by droneflies, honeybees and other insects.

insect as a new individual, we decided to include all of the feeding and flight times in subsequent ANOVAs comparing the times of droneflies with those of other insects. Repeating these calculations using mean times for each individual gave similar results but with increased

p-values. We justify our procedure because we were interested in whether dronefly times are more or less similar to those of certain other insects rather than in whether the differences are necessarily statistically significant. This procedure is consistent with the behaviour of

Table 3. Summary of the statistical analysis of the mean times insects spent feeding and flying between flowers (figures 1 and 2)

(The data were log transformed and a one-way ANOVA applied followed by Dunnett's comparison test. The dronefly mimics on each flower (column 1) were compared with the other control flies (column 2). The remaining columns indicate which control fly was used. Two entries under feed or fly in column 2 indicate that two species of control fly were used. Feed, comparison of times spent feeding; fly, comparison of times spent flying between flowers. A minus sign indicates no significant difference and a plus sign indicates a significant difference. The species of other flies are given in figures 1 and 2.)

flower	all Diptera controls		<i>E. intricarius</i>		<i>E. horticola</i>		<i>H. pendulus</i>		other flies	
	feed	fly	feed	fly	feed	fly	feed	fly	feed	fly
bramble (June)	+	+							+	+
bramble (July)	- +	+ +					-	+	+	+
snowberry	+	+	+	+						
everlasting daisy	- + +	- + +	-	-					+ +	+ +
Michaelmas daisy	- +	--	-	-			+	-		
goldilocks	+ + +	+ + +			+	+			+ +	+ +
knapweed	+ +	- +			+	-			+	+
rosebay willowherb	+ +	+ +	+	+					+	+

potential predators which have to make instant decisions rather than assessing mean times for each insect before deciding whether to attack.

(b) Differences between the sexes of mimics

Two-sample *t*-tests showed that, on both knapweed and goldilocks, there were no differences between the sexes in either their mean feeding times or flying times (knapweed feeding times $t_{26} = 1.21$ and $p = 0.24$, knapweed flying times $t_{25} = -0.53$ and $p = 0.60$, goldilocks feeding times $t_{22} = -0.28$ and $p = 0.78$, and goldilocks flying times $t_{24} = 0.14$ and $p = 0.89$).

(c) Differences between the mimic species

The three species of *Eristalis* were not distinguished on every observation and *E. nemorum* may also have been present on some flowers. To identify all species of dronefly would have substantially reduced the sample sizes because of the difficulty in distinguishing them unless the observer was very close and this would have disturbed them. A one-way ANOVA showed that, on knapweed, there were no significant differences between the three mimic species in either their feeding times ($F_{2,243} = 2.95$ and $p = 0.054$) or flying times ($F_{2,243} = 2.06$ and $p = 0.130$). Similarly, on goldilocks, there were no significant differences between the three mimic species in their flying times ($F_{2,253} = 1.05$ and $p = 0.351$) but there were differences in their feeding times ($F_{2,252} = 3.92$ and $p = 0.021$). The mean feeding time for *E. tenax* was 18.96 ± 1.52 s, for *E. arbustorum* 14.88 ± 1.66 s and *E. pertinax* 10.64 ± 2.63 s. The times for *E. tenax* and *E. arbustorum* were more similar to that of the model than to those of control insects, while the time for *E. pertinax* was less than that of the model and very similar to that for *Eristalis horticola*. *Eristalis horticola* differs from *E. pertinax* in having bright orange on its abdomen; it is similar in size to honeybees (*E. horticola* average wing length 9.88 mm and *A. mellifera* average wing length 9.82 mm) and is possibly a mimic of the Italian variety. The times spent feeding for *E. pertinax* and *E. horticola* were intermediate between the time for the model and the times for the control hoverflies.

(d) Comparison of the behaviour of the mimics and models

The means and standard errors of the times the insects spent feeding on a flower and flying between flowers are shown in figures 1 and 2. In all cases, one-way ANOVAs on the log-transformed data showed that there were significant differences between the species. This justified the use of Dunnett's comparison test in which the mimic is compared with the model and controls; these results are shown in tables 2 and 3 and discussed below.

There was no significant difference between the times that the mimics and models spent feeding on each flower visit on all flowers except Michaelmas daisy and rosebay willowherb (table 2). There was no significant difference between the times that the mimics and models spent flying between flowers on all flowers except goldilocks. This supports the hypothesis that droneflies and honeybees have similar foraging behaviour.

(e) Comparison of the behaviour of the mimics and hymenopteran controls

In most cases the behaviour of the mimics was significantly different from that of the hymenopteran controls (table 2). The exceptions were everlasting daisy and knapweed, on which the times mimics spent flying between flowers were also similar to those of bumble-bees. Thus, the feeding and flying times of droneflies were similar to those of honeybees in 13 out of 16 cases, but they were only similar to the times of bumble-bees in two out of 12 instances. This difference was very significant ($\chi^2_1 = 9.05$ and $p < 0.01$) and supports the hypothesis that the mimic has evolved behaviour that is more similar to that of its model than to that of other bees.

(f) Comparison of the behaviour of the mimics and dipteran controls

In all cases the time that the mimics spent feeding on flowers was significantly different from at least one of the dipteran controls, sometimes it was different from two species and, in the case of goldilocks, three species (second column in table 3). Similarly, the time the mimics spent flying between flowers differed significantly from at

least one of the dipteran controls on every flower except for Michaelmas daisy. Thus, the times droneflies spent feeding and flying between flowers were more similar to the behaviour of honeybees than to that of the more closely related Diptera. (For feeding, the mimic times differed from the model in two out of eight comparisons and from other hoverflies in 13 out of 16 comparisons ($\chi^2_1 = 5.00$ and $p < 0.05$). For flying between flowers, the mimic times differed from the model in one out of eight comparisons and from other hoverflies in 12 out of 16 comparisons ($\chi^2_1 = 6.06$ and $p < 0.02$.)

However, syrphids have very diverse habits (Stubbs & Falk 1983), so perhaps it is not appropriate to consider the possibility that droneflies should have behaviour similar to that of any other common syrphid as a null hypothesis. Table 3 separates out the control flies used on the basis of their taxonomic relatedness to the dronefly mimics. The last four columns show that the behaviour of droneflies differed from that of every one of the non-eristaline flies studied (final column), but it did not always differ from the behaviour of species in the same subfamily (*Helophilus*) or in the same genus (*E. intricarius* and *E. horticola*), i.e. the behaviour of droneflies was more similar to that of species in the same genus or subfamily than it was to more distantly related flies. However, the behaviour of droneflies differed significantly from that of *Helophilus pendulus* and *E. intricarius* in six out of 12 cases; in most of these their behaviour was more similar to that of honeybees (figures 1 and 2). This supports the hypothesis that their behaviour has been modified towards that of the model. The third eristaline, *E. horticola*, is problematical. Its behaviour differed from that of the three mimetic droneflies in three out of four cases. However, it is possible that *E. horticola* is also a mimic of honeybees (as previously discussed), but of the Italian variety with a large amount of orange on their abdomens rather than the browner bees which appear to be the model for *E. tenax* and *E. pertinax*.

4. DISCUSSION

The results presented above certainly suggest that droneflies show more similarity to their supposed model in their foraging and flight times than to other related insects. A possible criticism of these results is that the control insects used should have been closely related to the *Eristalis* species studied, preferably a species in the same genus. The congeneric *E. intricarius* is an ideal control which mimics bumble-bees and has been used in some cases. Unfortunately it did not occur on all the flowers, so other species had to be used. Nevertheless, most of these other control species were of a comparable size to droneflies.

Recent work at three sites has shown that many British hoverflies occur at the same time of year and are rarer than their presumed hymenopteran models (Howarth & Edmunds 2000). This phenological pattern is consistent with the hoverflies being Batesian mimics of Hymenoptera. However, *E. pertinax* and *E. tenax* were usually more abundant than honeybees at these sites, which is not consistent with their being Batesian mimics. At four of the five sites used in this study, droneflies were rarer than or of similar abundance to honeybees and it was only at Brock Bottom that they were commoner.

There is also evidence that human disturbance and habitat change have drastically affected the relative numbers of aposematic wasps (*Vespula* and *Dolichovespula* species) and their syrphid mimics (Azmeah *et al.* 1998). Droneflies have also been affected by disturbance. *Eristalis tenax* appears to have followed human populations in its distribution, probably because of the drains, sewers and cesspools associated with humans in which its larvae live. Osten-Sacken (1886) suggested that, in the USA, *E. tenax* was less common in the past when human populations were smaller and this may apply equally in Europe. This would explain why at some sites dronefly mimics are much more abundant than the models, contrary to what one might expect if they are Batesian mimics. It is possible that, at these sites, droneflies no longer gain protection against predators from their mimicry of honeybees. However, the results presented here show that, with only a few exceptions, throughout the season and on a range of flowers, droneflies behave in a way which is more similar to the honeybees they mimic than to other more closely related flies or bumble-bees. This suggests that droneflies may gain protection from their resemblance to bees after all.

It could be argued that droneflies and honeybees spend similar times foraging because they are seeking the same rewards from flowers. This would therefore be a case of convergent evolution, as suggested by Holloway (1976). However, one might then also expect the foraging times of droneflies and other hoverflies to be similar, contrary to the results presented here.

Hoverflies are able to digest pollen which they need for maturation of their sex organs and they feed on nectar for energy (Gilbert 1986). Honeybees also collect nectar for energy, as well as storing it as honey. Although they cannot digest it themselves, they also collect the pollen that adheres to their bodies, transfer it to their pollen baskets and take it back to the hive where the resultant pollen jelly is fed to the young larvae. Thus, hoverflies are foraging for themselves whereas honeybees are foraging for the colony and so are collecting much more pollen and nectar. Therefore, the expectation is that hoverflies will spend less time than honeybees feeding on the same flowers. The results presented here for droneflies show that, in general, this is not the case, although there are two exceptions. The mimics spent a significantly longer time feeding on rosebay willowherb than did all other insects (models, other hymenopterans and control hoverflies) (figure 1). This may be because rosebay willowherb is not a usual foraging flower for *Eristalis*; they soon left this patch to forage on other flowers in the area such as golden rod (*Solidago canadensis*) when they became available. Rosebay willowherb flowers are pink and have very distinct blue-coloured pollen and are thus not typical fly flowers; most flies, particularly *E. tenax*, prefer yellow or white flowers with yellow pollen (Lunau & Wacht 1994). The mimics also spent significantly longer times than the models feeding on Michaelmas daisy flowers, for which we have no explanation, although there was no difference between the mimic and *E. intricarius* on this flower. This is not surprising as these insects belong to the same genus. However, on other flowers such as snowberry and rosebay willowherb, there were differences in both the foraging and flying times between the *Eristalis* honeybee mimics and *E. intricarius*.

The times the mimics spent flying between flowers were also more consistently similar to the times of the models than to the times of other Diptera or Hymenoptera, yet from an evolutionary perspective it would be expected that the flight behaviour of *Eristalis* would most resemble that of other hoverflies rather than bees. Collett & Land (1978) measured the flight velocities of both *E. tenax* and *Volucella pellucens* in the field. Both species can attain velocities of at least 10 m s^{-1} and have similar acceleration speeds, yet on bramble flowers their flight behaviour is different: *V. pellucens* takes longer to fly around flowers than *Eristalis*. However, only flies that are already airborne can reach these speeds; they are likely to fly very much slower between flowers (Dlusski 1984) making them more vulnerable to predation. The results presented here and the impression gained from watching them in the field show that *Eristalis* and honeybees appear very similar when flying around flowers and sometimes it is not possible to identify them confidently until they land. Morgan & Heinrich (1987) confirmed this, suggesting that hoverflies (including *Eristalis* species) are able to maintain a high thoracic temperature by behavioural thermoregulation, which may be important in allowing them to copy the flight behaviour of their endothermic models. The only exception to this behavioural similarity was seen on goldilocks flowers where the mimics differed significantly from the models in flight times, but they also differed from all the control insects. However, there might have been a problem with the accuracy of the flight times on this plant because the flowers are not always discrete, tending to form a loose composite head. Adaptation of flight behaviour has been demonstrated in closely related, tropical mimetic butterflies (Srygley 1999), but not in temperate hoverflies. Certainly these results justify further investigation of the flight behaviour of droneflies in the field, a study of which is currently under way.

In conclusion, the results presented here indicate that dronefly mimics are 'moving' towards their honeybee model in their behaviour and the most likely reason for this is because morphological and behavioural mimicry of a noxious insect has resulted in reduced predation on droneflies.

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