

## DOES THE ABUNDANCE OF HOVERFLY (SYRPHIDAE) MIMICS DEPEND ON THE NUMBERS OF THEIR HYMENOPTERAN MODELS?

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**Abstract.**—We tested the prediction that, if hoverflies are Batesian mimics, this may extend to behavioral mimicry such that their numerical abundance at each hour of the day (the daily activity pattern) is related to the numbers of their hymenopteran models. After accounting for site, season, microclimatic responses, and general hoverfly abundance at three sites in northwestern England, the residual numbers of mimics were significantly correlated positively with their models nine times of 17. Sixteen of 17 relationships were positive, itself a highly significant nonrandom pattern. Several cristaline flies showed significant relationships with honeybees even though some of them mimic wasps or bumblebees, perhaps reflecting an ancestral resemblance to honeybees. There was no evidence that good and poor mimics differed in their daily activity pattern relationships with models. However, the common mimics showed significant activity pattern relationships with their models, whereas the rarer mimics did not. We conclude that many hoverflies show behavioral mimicry of their hymenopteran models.

**Key words.**—Batesian mimicry, generalized linear model analysis, hoverflies, Hymenoptera, Syrphidae.

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Batesian mimicry is the resemblance of a palatable animal (the mimic) to a well-defended animal (the model) such that predators mistake the mimic for the model and so avoid attacking it (Cott 1940; Edmunds 1974). In contrast to the wealth of recent ideas about how Batesian mimicry might work in theory (see Speed 1993, 2001; MacDougall and Dawkins 1998; Mallet and Joron 1999; Servidio 2000; Johnstone 2002; Sherratt 2002), there is still a dearth of realistic experimental or field-based evidence for most of its postulates (Malcolm 1990). Most accounts of mimicry based on natural history cite behavioral mimicry as an adjunct to mimetic resemblance of color patterns, and some do indeed seem extraordinary (see Edmunds 1974). For example, *Temnostoma* hoverflies lack the long antennae of their wasp models, but their anterior tibiae are darkened and they hold them up and wave them about to mimic the appearance of antennae (Waldbauer 1970). Behavioral mimicry has only just begun to be tested in the modern quantitative sense: the flight behavior among heliconiine Müllerian mimics (Srygley 1994, 1999; Mallet and Gilbert 1995; Beccaloni 1997; Srygley and Ellington 1999a,b) and the foraging movements of syrphid Batesian mimics and their models (Golding and Edmunds 2000; Golding et al. 2001) are the only examples known to us. We test here some predictions derived from the hypothesis that behavioral responses to environmental variables have converged between model and mimic.

In the Diptera, the Syrphidae (hoverflies) includes many species that have a close resemblance to bees or wasps and so appear to be Batesian mimics, but there have been no studies in the field demonstrating that predators learn through experience of models to avoid the mimics. The superb work

of Gerhard Mostler (1935) in a laboratory aviary using wild-caught small insectivorous birds demonstrated clearly that hoverflies could be protected via avoidance learning in all three of the main model-mimic systems (*Eristalis* with honeybees; *Volucella bombylans* with bumblebees; *Sericomyia* and *Chrysotoxum* with wasps). It is also widely recognized that whereas some hoverflies have a very precise resemblance to their model (good or specific mimics), others have a much less detailed similarity (poor or nonspecific mimics; summarized in Howarth et al. 2000; Howarth and Edmunds 2000).

Ecological and ethological work in the United States by Waldbauer and his collaborators (see Waldbauer 1988) suggested that mimetic Diptera appear after their hymenopteran models, and furthermore avoid the period of early summer when young inexperienced fledglings are learning how to forage. However, nonmimetic flies show the same phenological pattern, and the Waldbauer hypothesis relies on some critical assumptions that have never been properly tested. A major assumption is that for some early-emerging mimics, returning migrant birds remember the association between noxiousness and color pattern that they learned during the previous summer. This very slow predator forgetting is quite unlike Holling's (1965) results on learning in small mammals, where forgetting rates were very fast. Depending on their experiences, predators are not really forgetting at all, because if they sample mimics they undergo quite a different process, extinction, a learned erasing of the association and its replacement with another (see Shettleworth 1998). The maintenance of the association of the color pattern with noxiousness may require constant reminders (aide-mémoire mimicry, Rothschild 1984), and functionally this may mean that model and mimic must occur together at the same time. We know almost nothing about the learning, forgetting, and extinction processes of relevant bird predators in any realistic model-mimic system.

In a study of the phenology of hoverflies and their supposed models at three sites in northern England, Howarth and Ed-

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munds (2000) showed that most species occur at the same time of the year and in the same habitats as, but are rarer than, their models, as would be expected if they gain protection through Batesian mimicry. But four common taxa are exceptions: *Eristalis* spp., *Helophilus* spp., *Syrphus* spp. (including related genera), and *Episyrphus balteatus*. All of these are often more abundant than their models and frequently occur when models are absent. For classical mimicry theory, this is a problem because Batesian mimics are supposed to be rarer than their models (Carpenter and Ford 1933). There are a number of possible resolutions. For example, it is possible that these species have increased their populations as a result of human-induced environmental changes (Azmeah et al. 1998) such that their protection through mimicry has broken down. However, it is a moot point whether Batesian mimicry does in fact require mimics to be rare relative to their models; more recent studies have suggested that although the protective effect is reduced when mimics become relatively common, some protection can occur at almost any relative abundance, depending on the cost (of attacking a model) to benefit (of attacking a mimic) ratio (Holling 1965; Lindström et al. 1997; Sherratt 2002).

In one of the few quantitative studies of behavioral mimicry, Golding and Edmunds (2000) and Golding et al. (2001) showed that droneflies (*Eristalis* spp.) have flower-visiting behavior that is more similar to that of honeybees (the model) than to that of other syrphids, and they concluded that the behavior of these mimics has evolved toward that of the model. If this is generally true of Batesian mimics (partly because of a requirement to maintain the association of noxiousness by predators), then it seems likely that their behavior has converged with that of their model such that they should coexist more frequently than expected by chance.

Based on the hypothesis of behavioral mimicry, therefore, we have three predictions. First, the numerical abundance of presumed Batesian mimics at each hour of the day (the daily activity pattern) should be related positively to the numbers of their hymenopteran models occurring in the same habitat at the same time. Although such a temporal relationship is not currently thought essential for Batesian mimicry because birds are assumed to remember learned associations over long periods of time (as in Waldbauer's thesis), if it does occur it is difficult to explain other than as an adaptation to improve the mimicry. Second, the daily activity patterns of hoverfly, bee, wasp, and bumblebee mimics within the same subfamily (the Eristalinae) should vary depending on the species mimicked. If they differ from each other, but resemble the activity patterns of their models, then this supports the hypothesis that they benefit from their resemblance to these models. Finally, the daily activity pattern relationship between mimics and models should hold for specific and nonspecific mimics and for common and rare mimics alike.

## MATERIALS AND METHODS

### Data Collection

The study was conducted at three seminatural ancient woodland sites in northwestern England in 1994: Latterbarrow, Cumbria; Gait Barrows, Cumbria; and Brock Bottom, Lancashire. Each site was split into three habitat plots: (A)

woodland; (B) open meadow/pasture surrounded by woodland; and (C) a combination of woodland and open meadow/pasture. Weather permitting, each site was surveyed for seven hours on one day of each week from 13 April until 14 October, with individual plots being visited in sequence so that one plot was surveyed three times on each visit, the other two plots twice (i.e., plots ABCABCA in the first week, BCABCAB in the second week, etc.). In each hour, counts were made of all Syrphidae and Hymenoptera seen. Those species of both taxa that are similar in appearance (and hence presumably difficult for a predator to separate in the field) were grouped under the name of one principal species (for all assumed model-mimic relationships see Howarth and Edmunds 2000), and we refer to these color groups throughout the paper under this name, as if they constitute single species. The commonest such hoverfly color groupings were *Syrphus ribesii* (3230) and *Eristalis pertinax* (2923). Species with fewer than ten records were excluded from the analysis. Each hoverfly was identified as a specific or a nonspecific mimic following Howarth et al. (2000). Temperature was recorded at the beginning, middle, and end of each hour of survey, and the mean was calculated. Time of day had seven classes, 0800–0900; 0915–1015; 1030–1130; 1200–1300; 1315–1415; 1430–1530; and 1600–1700. Further details of the sites, the survey method, and the species of Syrphidae and Hymenoptera are given by Howarth and Edmunds (2000).

### Analysis

Preliminary analysis of the data showed that most of the insect taxa were at peak abundance during the middle of the day and in weak, hazy sunshine. Although other weather variables were recorded, temperature had the highest correlation with insect numbers, and was therefore used as a covariate in all subsequent analyses to account for the influence of weather on general insect activity.

The data were analyzed using a generalized linear model (GLM) implemented by the program GLIM (see Crawley 1993). For rare species we used a Poisson error structure for the counts, which fitted the data well; the data for common species were square-root transformed, and analyzed using normal errors. Every mimic was analyzed according to the same strategy: in an appropriate site (where both model and mimic coexist); with suitable environmental conditions (i.e., temperature permissive); at the right time of year (during the flight season of the mimic); and assuming it is a Batesian mimic, we predicted that its abundance should be positively related to that of its model. Given that there are many factors influencing hoverfly numbers, we used two other covariates (other syrphids, and other Hymenoptera) to control for these factors.

For each mimic species (or group), therefore, the strategy for analysis used the same GLM, consisting of two factors, season (month, with six levels) and site (plot, with eight levels) (but omitting the interaction, which was rarely a significant effect), together with four covariates: the model being mimicked, all other syrphids, all other hymenopterans (excluding the model species), and the mean temperature. In the case of specific mimics, we explored the effects of other taxa of bumblebees, solitary bees, or solitary wasps, as appropriate

TABLE 1. Example of the analysis using the *Eristalis pertinax* group of presumed honeybee mimics. The data were square-root transformed and analyzed with normal errors. For further explanation of the model, see text. The deviances do not add up to the total because they represent the change in deviance upon dropping that component from the full model.

	Deviance	df	<i>P</i>	Slope of covariate
Month	63.6	5	<0.001	
Habitat	177.0	7	<0.001	
Model ( <i>Apis</i> )	7.0	1	<0.01	+0.015 ± 0.009
Other Hymenoptera	29.4	1	<0.001	-0.025 ± 0.007
Other syrphids	119.4	1	<0.001	+0.017 ± 0.002
Temperature	37.8	1	<0.001	+0.154 ± 0.038
Residual	460.7	196		
Total	1306.0	212		

Percentage variance accounted for =  $100 \times (1306 - 460.7)/1306 = 65\%$ .

(see Results). There should have been nine levels of the plot factor, because there were three sites and three plots per site, but one of these (the woodland site in Brock Bottom) was omitted because canopy growth caused deep shade later in the summer, resulting in very few insects of any kind recorded. For the analysis of each mimic, we omitted all months and sites for which no individuals were recorded, because there was no point in including places or times where they were not at least potentially present (i.e., we used times within the flight period and sites that were suitable for the mimic). We adopted a one-tailed approach in testing for the significance of the predicted positive effect of model abundance on mimic abundance, accepting the cost of not being able to claim anything about negative relationships (Kimmel 1957). We predicted no relationship with other Hymenoptera, and therefore adopted a two-tailed significance criterion for these tests.

Where the model is the honeybee, the control model is all Hymenoptera except for honeybees. However, for a presumed specific bumblebee mimic, the model is one particular species (or species group) of bumblebees, so the control model is all other bumblebees. In some cases where the model being mimicked is unclear, we have explored the relationships by running all five bumblebee taxa as separate covariates (*B. terrestris*, *B. pratorum*, *B. lapidarius*, *B. pascuorum*, and unidentified bumblebees comprising bumblebees that were flying too fast to enable them to be identified).

Each model-mimic pairing was defined a priori, and thus each test was independent, requiring no Bonferroni correction. However, where we explored relationships by running several possible models as covariates, we then changed the threshold of significance using a Bonferroni adjustment to the one-tailed *P*-value (because we were still only interested in positive relationships). Table 1 gives an example of our analysis and interpretation of the data for droneflies (*E. pertinax* group, which includes *E. tenax*) with their model, the honeybee. It shows that the numbers of *E. pertinax* varied significantly with month and habitat, neither of which is surprising because the study covered months from spring to autumn and comprised a variety of different habitats. Numbers also varied significantly and positively with temperature and with numbers of other hoverflies. Again, these results might be expected because hoverflies tend to be more active

when it is warm, and droneflies appear to be most abundant when other hoverflies are also abundant.

The deviance in Table 1 is the change in variation that results from dropping each variable from the analysis, and it measures the extent to which that variable predicts the abundance of the mimic after the other factors have been allowed for (e.g., the ability of the numbers of the honeybee model to predict residual *E. pertinax* numbers after the effects of month, habitat, other syrphids, other hymenopterans, and temperature have been included).

The significant relationship between numbers of *E. pertinax* and those of honeybees, with a positive slope, is the crucial test of our prediction based on the hypothesis of mimetic behavior. It does not simply indicate that droneflies are more active when it is warm or under circumstances when other hoverflies are also active, because these factors have been included in the model and hence excluded from this significant effect. We can suggest three possible reasons for this relationship. First, one of the two taxa could have altered its ecology and behavior so as to be more similar to the other. We can think of no reason why it should pay honeybees to resemble droneflies, but it could certainly pay droneflies to resemble a distasteful, stinging honeybee in ecology and behavior (see Golding and Edmunds 2000), just as they do in their physical appearance, through Batesian mimicry. Thus, a significant positive relationship with the presumed model can be regarded as supporting the hypothesis that Batesian mimicry extends to daily activity behavior. Second, dronefly and honeybee numbers could be affected in the same way by some unknown factor, for example, they might forage on the same flowers for reasons quite unrelated to mimicry. Such an effect must only pertain to these two taxa, because the relationship is over and above any commonalities with other syrphids or other Hymenoptera. Third, a predator could control the numbers of *E. pertinax* from hour to hour, day to day, attacking and reducing their numbers when they became too common (and the predator learned that the pattern was palatable), but avoiding them when rarer than a certain proportion of honeybee numbers (because it learned to associate the pattern with noxiousness). Such an explanation seems unlikely because it is unlikely that predators control adult syrphid numbers in such a short-term manner (or indeed in the longer term); and it is unlikely that the learning process operates on such a short-term timescale. Thus, the significant positive effect of honeybee numbers on *E. pertinax* seen in the phenological data is consistent with the hypothesis that droneflies mimic honeybees in their daily activity patterns.

Table 1 also indicates that numbers of *E. pertinax* are significantly negatively correlated with those of other hymenopterans, the control group. This implies that either droneflies avoid certain hymenopterans other than their model (or vice versa), or the two taxa are active under different conditions, or they are attracted to certain resources or environmental factors in different ways. Conversely, a significant effect here with a positive slope would indicate that the two taxa are active under similar conditions. Finally, Table 1 indicates that the variables included in the model account for 65% of the variation in numbers of *E. pertinax*.

TABLE 2. Results from the generalized linear model for supposed hoverfly mimics showing the deviances of covariates, their significance, and slope. Where the error structure was Poisson (P), the deviance is a  $\chi^2$  with 1 df; where it was normal (N), the deviance is an *F*-value with 1 and >100 df.

Mimic	Type	Batesian model	Error	Deviance of model covariate <sup>1</sup>	Slope	Other significant covariates (slope)	Percentage variance accounted for
<b>Bee mimics</b>							
<i>Eristalis pertinax</i>	good	<i>Apis mellifera</i>	N	7.0**	+0.015	syrphids (+), Hymenoptera (-)	65
<i>Eristalis arbustorum</i>	poor	<i>Apis mellifera</i>	P	23.8***	+0.008	syrphids (+), Hymenoptera (-)	70
<i>Cheilosia pagana</i>	poor	<i>Lasioglossum</i>	P	0.7	+		28
<b>Wasp mimics</b>							
<i>Syrphus ribesii</i>	poor	social wasps	N	14.8***	+0.053	syrphids (+), Hymenoptera (+)	68
<i>Episyrphus balteatus</i>	poor	social wasps	N	5.3*	+0.041	syrphids (+)	86
<i>Helophilus pendulus</i>	poor	social wasps	N	39.7 <sup>2</sup>	-0.094	Hymenoptera (+)	71
<i>Sericomyia silentis</i>	good	social wasps	P	0.2	+	Hymenoptera (+)	34
<i>Myathropa florea</i>	poor	social wasps	P	0.8	+	Hymenoptera (+)	67
<i>Xanthogramma citrofasciatum</i>	good	<i>Nomada</i>	P	4.1*	+0.24	wasps (+)	51
<b>Bumblebee mimics</b>							
<i>Cheilosia illustrata</i>	poor	all bumblebees	P	4.2*	+0.03	syrphids (+)	43
<i>Arctophila superbiens</i>	good	<i>Bombus pascuorum</i>	P	0.3	+		57
<i>Criorhina berberina</i>	good	<i>Bombus pratorum</i>	P	1.7	+		48
<i>C. b. var. oxyacanthae</i>	good	<i>Bombus pascuorum</i>	P	2.3	+		27
<i>Criorhina floccosa</i>	good	<i>Bombus pascuorum</i>	P	1.1	+		64
<i>Eristalis intricarius</i> (F)	good	<i>Bombus terrestris</i>	P	5.7**	+0.052	Hymenoptera (+)	56
<i>E. intricarius</i> (M)	poor	<i>Bombus pratorum</i>	P	5.1*	+0.112	syrphids (+), Hymenoptera (+)	73
<i>Volucella bombylans</i> var. <i>plumata</i>	good	<i>Bombus terrestris</i>	P	3.7*	+0.065	bumblebees (+)	52

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

<sup>1</sup> All probabilities were halved in accordance with the one-tailed nature of the hypothesis being tested.

<sup>2</sup> Not significant because one-tailed tests were adopted, and this slope is negative (see text).

## RESULTS

### *Are Mimic Numbers Related to Numbers of Models?*

Table 2 summarizes the results of the GLM on 17 hoverflies that appear to mimic hymenopterans, but omits the relationships with month, temperature, and habitat because these are not informative with respect to a possible mimetic relationship. Column 5 gives the deviances of the model covariate and column 6 indicates if the slope is positive or negative.

After accounting for site, season, and microclimatic responses, as well as for similarity of counts to other syrphids, the residual was significantly correlated positively with the specified model nine times of 17. Furthermore, 16 of 17 slopes were positive, itself a highly significant nonrandom pattern (binomial test  $P < 0.001$ ). The associations themselves are inevitably quite weak, given the nature of the data and the indirect controls involved. The pattern has emerged in spite of these constraints, and therefore these results support our prediction that mimic numbers are positively related to the numbers of their models defined a priori.

In nine of the hoverfly taxa the residual was significantly correlated with the control Hymenoptera, seven positively and two negatively. The two negative relationships were both with eristaline honeybee mimics. Some of the positive relationships may be due to inappropriate controls, for example, *Xanthogramma* may mimic other yellow and black wasps as well as *Nomada*, and *Eristalis intricarius* may mimic more than one species of bumblebee. We explored the relationships of these species further (see below).

### *Bee mimics*

Tables 1 and 2 show that the numbers of both *E. pertinax* and *E. arbustorum* varied significantly and positively with those of their honeybee model, but negatively with other Hymenoptera. Numbers of *C. pagana*, however, showed no significant relationship with those of *Lasioglossum* bees.

### *Wasp mimics*

Numbers of *S. ribesii* varied significantly and positively with those of social wasps (Table 2), and they also showed a significant positive relationship with other Hymenoptera. The relationship between *E. balteatus* numbers and those of social wasps was also positive and significant. However, there was a negative (and therefore non-significant) relationship between the numbers of *H. pendulus* and those of social wasps, and a significant positive relationship with numbers of other hymenopterans.

Neither *S. silentis* nor *M. florea* showed significant variation with numbers of social wasps, but both had significant positive relationships with other hymenopterans. Since *M. florea* has much gray-brown on its body, it could be considered a possible mimic of honeybees rather than of wasps. When the GLM was run with honeybees as the presumed model, the slope was positive but the deviance of 2.1 was again not significant.

The numbers of *X. citrofasciatum* varied significantly and positively both with numbers of *Nomada* and with those of

TABLE 3. Results from the generalized linear model for bumblebee mimics in which the model was run against all five bumblebee taxa separately together with other hymenopterans and other syrphids. All used Poisson errors, and all had Bonferroni-adjusted significance levels.

Mimic	Significant covariates ( $\chi^2$ , and slope)	Percentage variance accounted for
<i>Cheilosia illustrata</i>	none	82
<i>Criorhina berberina</i>	none	48
<i>C. b.</i> var. <i>oxyacanthae</i>	none	27
<i>C. berberina</i> (all)	<i>Bombus pratorum</i> (5.6*, +0.08)	47
<i>Eristalis intricarius</i> (female)	<i>Bombus terrestris</i> (8.3 <sup>1</sup> , -0.2); <i>Bombus pascuorum</i> (8.0*, +0.12); <i>Bombus pratorum</i> (8.0*, +0.13); unidentified <i>Bombus</i> (9.0 <sup>1</sup> , -1.1); syrphids (24.8***, +0.008); Hymenoptera (7.6**, +0.011)	70
<i>E. intricarius</i> (male)	syrphids (4.1*, +0.004); Hymenoptera (17.3***, +0.02)	79
<i>Volucella pellucens</i>	syrphids (11.9***, +0.008)	41
<i>Volucella bombylans</i>	<i>Bombus terrestris</i> (6.2*, +0.07)	76

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

<sup>1</sup> Not significant because one-tailed tests were adopted, and this slope is negative (see text).

other wasps. To further analyze these data, the model was run again with the Hymenoptera separated into *Nomada*, social wasps, yellow and black solitary wasps, black solitary wasps, bees and bumblebees to see if *Xanthogramma* numbers were related to those of any of these groups (Bonferroni adjusted one-tailed threshold = 0.008,  $\chi^2 > 5.8$ ). This time there were two taxa with significant effects and a positive slope: *Nomada* ( $\chi^2_1 = 14.4$ ) and yellow and black solitary wasps ( $\chi^2_1 = 6.7$ ).

#### Bumblebee mimics

Numbers of *C. illustrata* varied significantly and positively with those of bumblebees, but not with those of other hymenopterans. When the model was run with the five bumblebee taxa entered separately (Bonferroni adjusted threshold  $\chi^2 > 5.4$ ; Table 3), there were no significant effects with a positive slope, but *B. pratorum* was close to significance ( $\chi^2 = 4.8$ ).

Numbers of *A. superbiens*, *C. floccosa*, and the two morphs of *C. berberina* showed no significant variation with numbers of their Batesian models (*B. pascuorum* and *B. pratorum*). The model was then run again for *C. berberina*, first, with all bumblebee taxa entered separately (Table 3), and second, with both morphs combined and with all bumblebees as one covariate (both with an adjusted threshold of  $\chi^2 > 5.4$ ), but again there were no significant effects. However, when the two morphs of *C. berberina* were combined and run with all

five bumblebee taxa separately, the effect of *B. pratorum* was significant.

*Volucella bombylans* var. *plumata* numbers varied significantly and positively with numbers of *Bombus terrestris* (Tables 2, 3), and no other covariates were significant. *Volucella pellucens* was run with *B. terrestris* as the most likely model (since both have a pale band on the abdomen) and with the other four bumblebee taxa as well as social wasps entered as separate covariates (Bonferroni adjusted threshold  $\chi^2 > 5.8$ ). Wasps were included because *V. pellucens* is a brood parasite of social wasps. There were no significant effects (Table 3).

Female *E. intricarius* showed significant positive variation with numbers of *B. terrestris*, while males showed significant positive variation with *B. pratorum*. When run with all bumblebee taxa entered separately (adjusted thresholds of  $\chi^2 > 5.4$ ; Table 3), there were no significant model effects for males, but females showed significant effects and a positive slope with both *B. pratorum* and *B. pascuorum*.

#### Are Activity Patterns of Eristaline Flies Similar Irrespective of Their Models?

The results for *Eristalis* spp. when run with separate model groups are shown in Table 4. For *E. arbustorum* there was a highly significant effect with a positive slope with honeybees, as expected from Table 2, but there was also a significant effect with a positive slope with other bumblebees and a possible effect of *B. pratorum*. For *E. pertinax* none of the

TABLE 4. Results from the generalized linear model for *Eristalis* spp. in which the model was run against three bumblebee taxa, honeybees, and social wasps. Each entry is the deviation, its significance (assessed against a Bonferroni-adjusted threshold of  $\chi^2 > 5.4$ ), and slope. Poisson errors were used for *E. arbustorum* and *E. intricarius* and normal errors for *E. pertinax*.

Covariates	<i>E. arbustorum</i>	<i>E. pertinax</i>	Male <i>E. intricarius</i>	Female <i>E. intricarius</i>
<i>Bombus terrestris</i>	2.2 ns	0.02 ns	2.5 ns	2.9 ns
<i>Bombus pratorum</i>	5.1 ns (+0.03)	0.33 ns	5.3 ns (+0.06)	1.1 ns
Other bumblebees	11.5** (+0.05)	0.28 ns	0.86 ns	5.6* (+0.075)
Honeybees	22.9*** (+0.008)	1.7 ns	12.8*** (+0.014)	0.1 ns
Social wasps	38.8 <sup>1</sup> (-0.06)	15.3 <sup>1</sup> (-0.05)	5.5 <sup>1</sup> (-0.14)	97.4 <sup>1</sup> (-0.41)
Other Hymenoptera	8.0 <sup>1</sup> (-0.04)	0.0 ns	0.29 ns	5.5* (+0.045)
Other syrphids	60.1*** (+0.005)	45.3*** (+0.01)	14.8*** (+0.0075)	21.0*** (+0.007)
Variance accounted for	70%	68%	78%	75%

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

<sup>1</sup> Not significant because one-tailed tests were adopted, and this slope is negative (see text).

TABLE 5. Results from the generalized linear model for *Helophilus pendulus* in which the model was run against five hymenopteran taxa. Normal errors were used, and a Bonferroni-adjusted threshold of  $\chi^2 > 5.4$ .

Covariates	Deviation	Significance	Slope
Social wasps	38.4	ns <sup>1</sup>	-0.088
Solitary wasps	2.8	ns	
Honeybees	13.1	<0.001	+0.022
Bumblebees	1.6	ns	
Solitary bees	0.01	ns	
Other syrphids	56.6	<0.001	+0.010
Variance accounted for	63%		

<sup>1</sup> Not significant because one-tailed tests were adopted and this slope is negative (see text).

effects with honeybees or bumblebees was significant, but, as with *E. arbustorum*, the deviance was substantially greater for honeybees than for any of the bumblebee taxa. We assume that the change from a significant effect of honeybees (Table 1) to nonsignificance (Table 4) for *E. pertinax* is caused by the well-known statistical artifact of multiple regression rather than having a biological cause.

For male *E. intricarius* there was an almost-significant effect with a positive slope with *B. pratorum* (as expected from Tables 2, 3), but a very significant effect with a positive slope with honeybees. For female *E. intricarius*, by contrast, the only significant effects with a positive slope were with other bumblebees (presumably *B. pascuorum* judging from Table 3) and with other hymenopterans. The deviance and slope for *B. terrestris* suggests there may be a slight effect here, but it was not statistically significant, while the deviance for honeybees was extremely small, unlike for males.

The results for *Helophilus pendulus* presented in Table 5 show that there was a very significant effect with a positive slope with honeybees, but that no other hymenopteran taxon had a significant effect (apart from social wasps where the slope was again negative).

#### *Do Good Mimics Have a Different Relationship to Models from Poor Mimics?*

Four of what were judged to be good mimics and five poor mimics showed significant positive associations with the numbers of their presumed models (Table 2), so there is no evidence (Fisher's exact test,  $P = 0.64$ ) that one category of mimics has adjusted its behavior toward that of its model better than the other. However, the categorization of mimics as good or poor is subjective (Howarth et al. 2000), and may not coincide with the discriminatory powers of predators. A more interesting pattern is that six of the seven more abundant hoverflies (i.e., with more than 100 insects) showed significant relationships with their models with a positive slope. This is true for *Eristalis pertinax*, *E. arbustorum*, both male and female *E. intricarius*, *Syrphus ribesii*, and *Episyrphus balteatus*. The only exception is *H. pendulus*, where the effect was not significant because of its negative slope. For the 10 or 11 rarer species, however, only three showed significant effects with the model. This pattern of significance is non-random (Fisher's exact test,  $P = 0.025$ ), implying that abun-

dant species are indeed more likely to covary with models than rare species.

## DISCUSSION

Behavioral mimicry has been reported from a variety of insects (Edmunds 1974; Golding et al. 2001), while more detailed studies of flight mimicry have been described by Srygley (1994, 1999) and Srygley and Ellington (1999a,b) in *Heliconius* butterflies and by Beccaloni (1997) in ithomiine butterflies. Mimetic syrphids have long been noted for their behavioral similarity to their models (e.g., Morgan and Heinrich 1987). They often have a slow, measured flight quite unlike the normal syrphid pattern, but similar to the searching behavior of their hymenopteran models, for example, in *Temnostoma* and *Milesia* (Glumac 1962), *Volucella zonaria* (Nickol 1994), *Callicera* (J. Gilbert 2001), *Ceriana* (Haeseler 1976), and *Xanthogramma* (Howarth et al. 2000). Some syrphid mimics hold out their front legs during flight (e.g., *Temnostoma*: Trittler 1984) or at rest (*Spilomyia*, *Temnostoma*, *V. bombylans*: Fincher 1951; Waldbauer 1970; Rupp 1989), imitating the long hymenopteran antennae. These similarities extend further: Mostler (1935, translated from the German) wrote of *Eristalis* that the "tone of the buzz, the type of flight, and the flower visits of the fly and the honeybee are practically the same." These impressions were confirmed by Golding and Edmunds (2000) and Golding et al. (2001) by demonstrating quantitatively the similarity in flight and foraging behavior between model and mimic. Given these similarities in the details of their behavior, our findings indicate that many hoverfly mimics react to their environment in a similar way as their models—and therefore tend to occur in similar habitats and be active at similar times of day.

The dominant pattern of positive associations between hoverfly mimics and their hymenopteran models could be because the two taxa are attracted to similar flowers (or some other resource) for reasons quite unrelated to mimicry, but it could also be because the hoverfly has adapted its behavior to make it more similar to that of its model, and it will thus be encountered by predators (and observers) in similar circumstances to the model. There may be reasons other than Batesian mimicry for two species to converge in behavior, and conversely there may be strong reasons why a morphologically mimetic fly does not alter its behavior toward that of its model. Hence, we should not necessarily expect all mimic species to show significant associations with their models. Nevertheless, if many of them do so, this supports the prediction of behavioral mimicry (derived from assuming that they are Batesian mimics), and if there are many more significant correlations with the supposed model than with the control hymenopterans then it is difficult to reject the Batesian mimicry explanation.

For the bee and wasp mimics, five species showed significant positive associations with their model, and only one of these, *S. ribesii*, also had a significant positive association with the control hymenopterans. This is consistent with these species being Batesian mimics and adjusting their behavior or ecology towards that of their model. Three other wasp mimics, *Helophilus*, *Sericomyia*, and *Myathropa*, had significant positive associations with control hymenopterans but

not with their social wasp model. Two of these are eristalines whose color patterns may be derived from that of honeybee mimicry, the dominant color pattern of the taxon, and there may not have been sufficient selection pressure to decouple their behavioral mimicry. Both *Helophilus* and *Myathropa* had a larger deviance for honeybees than for social wasps, although for *Myathropa* neither value was significant.

The results with bumblebee mimics are more complex but if we look at those with other hymenopterans as control (*C. illustrata*) or with other bumblebees as control (the remaining species in Table 2), and treating *E. intricarius* sexes separately, four had significant effects with positive slopes with the model and two of these also had significant effects with control hymenopterans (the two *E. intricarius*). Further analysis of *E. intricarius* (Tables 3, 4) shows that (in males) this may also be attributed to a possible ancestral mimetic relationship with honeybees.

Although some workers have doubted whether droneflies gain protection through Batesian mimicry of honeybees (Holloway 1976), there is evidence that humans have confused them with honeybees for more than 2000 years (Osten Sacken 1898; Atkins 1948). Droneflies may also have increased in numbers relative to honeybees as a result of human-induced changes to the environment such that they are now often much more abundant than their original Batesian model, including at the three sites studied here (Howarth and Edmunds 2000). More recently Golding and Edmunds (2000) have shown that the foraging behavior of droneflies on several different flowers is more similar to that of honeybees than to that of other hoverflies, and they suggest that droneflies have modified their behavior so as to gain greater protection through mimicry. Golding et al. (2001) have further shown that the flight movements of droneflies are also very similar to those of honeybees, so the mimicry includes both morphological and behavioral similarities. Another example of the behavioral mimicry of *E. tenax* is its habit of rubbing its hind legs together as it flies in a way very similar to that of honeybees cleaning pollen off their legs and storing it in their pollen baskets (Holloway 1976; pers. obs.). Thus, *Eristalis* spp. probably are Batesian mimics of honeybees that have adjusted their behavior in such a way that the numbers visible to a human observer are correlated with those of the honeybee model.

Azmeh et al. (1998) have presented evidence suggesting that common wasp mimics such as *S. ribesii* and *E. balteatus* may have increased enormously in numbers as a result of human-induced changes to the environment, and that it is therefore possible that they no longer gain protection through mimicry of social wasps, a possible explanation for the poor quality of their mimicry. In many habitats they outnumber their supposed social wasp models by five or ten to one (Owen and Gilbert 1989; Howarth and Edmunds 2000), so a predatory bird is likely to attack a palatable fly before it samples a noxious wasp, and hence learn the opposite lesson that such color patterns are good to eat. However, in spite of these considerations, the numbers of these two species are positively related to those of social wasps. This supports the contention that at least in the past they gained protection through mimicry, and the associated behavioral shifts have persisted in spite of recent changes in relative abundance.

There are several possible explanations for the apparent inverse relationship between numbers of the poor wasp mimic *Helophilus pendulus* and numbers of wasps. First, it is possible that these hoverflies avoid flowers with wasps on them because wasps kill many insects on flowers for their brood. All the eristalines except for *Myathropa* showed a negative association, and the avoidance of wasp predation is a likely explanation. Second, the judgment that *Helophilus pendulus* is a poor mimic is based on human perception of its appearance when resting on a flower; when flying, especially when it hovers so that the yellow on the abdomen is blurred, it can appear to be a very good mimic. Thus, human judgment as to the quality of mimicry can be misleading, and the way in which a bird perceives a hoverfly may be quite different, as demonstrated by Dittrich et al. (1993). However, there is a third possible explanation: *Helophilus* and also male *E. intricarius* showed a significant relationship with a positive slope with honeybees, which may be caused by phylogenetic inertia from a honeybee-mimicking ancestor. If honeybees became rare (or alternatively the droneflies expanded their range into an area where honeybees were scarce), then this may have promoted the evolution of bumblebee or wasp mimicry. Clearly, this explanation suggests a particular phylogenetic hypothesis, but there are currently no published phylogenetic hypotheses of any kind for species within the eristalines. If true, it would be an interesting case where behavior shows an evolutionary lag behind morphological change, rather than the more usually cited other way round (e.g., Davies 1999).

A number of very good mimics have no apparent relationship with the numbers of their models (e.g., *Sericomyia*, *Arctophila*, *Criorhina*). Perhaps the numbers of these species are too small for any benefit to be gained from evolving similar activity patterns to their model. Other excellent mimics do show such a relationship. For example, *V. bombylans* is a superb morphological mimic of bumblebees with the typical form resembling *B. lapidarius* and var. *plumata* resembling *B. terrestris*. The typical form was not seen at any of the study sites, but its model, *B. lapidarius*, was much rarer than other bumblebees with only 61 sightings. The results for var. *plumata* support the contention that its mimicry of *B. terrestris* extends to similarity of its daily activity pattern. *Xanthogramma citrofasciatum*, *C. illustrata*, and male *E. intricarius* also showed clear similarities in daily activity patterns with their models. For female *E. intricarius* the results were less clear, while for *C. berberina* there was a similarity to the activity pattern of one of the two models, *B. pratorum*, even though many of the flies belonged to the morph that actually mimicked a different species of bumblebee. We found no evidence for a difference in daily activity patterns between good and poor mimics. We did not expect any a priori, and hence the result is not surprising. However, the categorization of mimetic quality should be regarded as only very rough: this may be because human judgments of the quality of mimicry may be misleading, but some mimics may have evolved to be poor because they are jack-of-all-trades, occupying the average position in pattern space among sets of models (Barnard 1984; Edmunds 2000; Sherratt 2002).

We have shown that abundant mimics have similar daily

activity patterns to their models whereas rarer mimics do not. We know of no previous study of this in other systems, nor any prediction that this should occur. Because more abundant mimics are generally not so faithful in their mimicry of the color pattern of the model (Dittrich et al. 1993; Azmeh et al. 1998), one could view this as representing a trade-off in components of mimicry, behavioral versus visual. However, equally one could argue, as above, that for rare mimics the predators will be more likely to have experienced models beforehand, and therefore be wary; for abundant mimics, predators may be more likely to have experienced mimics beforehand, and therefore the quality of the mimicry needs to be greater for the deception to work. One should bear in mind that the numbers of insects recorded by a human observer may be only crude estimates of the actual encounter rates by bird predators. Dlusski (1984) argued that the fine details of the attack behavior of different species of bird resulted in much greater encounter rates with models than the crude numbers would suggest, mainly because mimics have a rapid escape response, whereas models generally make little attempt to evade contact. Very little is known about these aspects of mimicry in field situations.

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