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**Evolution of Imperfect Mimicry: Explaining Variation in Mimetic Fidelity among  
Syrphid Species**

By  
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In  
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## **ABSTRACT**

The evolution and maintenance of imperfect mimicry has long interested evolutionary biologists, since one might expect that selection would lead to ever higher levels of mimetic fidelity. Many hypotheses have been put forward in an attempt to explain the persistence of imperfect mimicry including eye of the beholder, disequilibrium, kin selection, multi-model/jack of all trades and relaxed selection.

Flower flies (Diptera: Syrphidae) provide some of the most celebrated cases of imperfect mimicry and individual species range greatly in their perceived degree of mimetic perfection. I therefore focused on this group, using comparative analyses to evaluate the validity of the above hypotheses for imperfect mimicry. The first chapter examined the relationship between behavioural mimicry (wing wagging, mock stinging, and leg waving) and visual mimetic fidelity. After behaviourally assaying over 300 individual syrphids with a range of mimetic fidelities and differing models (honey bee, bumble bees or wasps), we found that only intermediate and very good wasp mimics participated in the behaviours.

The second data chapter examined the relationship between abundance and mimetic fidelity, testing whether any such relationship might be mediated by body size. After examining thirteen separate population studies, it was determined that there was no evidence of a relationship between abundance and mimetic fidelity in Syrphidae. There was however, a strong relationship between body size and mimetic fidelity, as body size increases, so does mimetic fidelity.

Collectively, data from the two chapters along with ancillary information allow us to rule out eye of the beholder, disequilibrium, kin selection, multi-model/jack of all trades explanations for imperfect mimicry as they apply to syrphids. However, our results are entirely consistent with the relaxed selection hypothesis. Thus, as mimics become larger they also become more profitable to predators, and the selection pressure towards higher mimetic fidelity becomes stronger.

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## Chapter 1:

### **1.1 Müllerian and Batesian Mimicry**

Mimicry is one of the most celebrated examples of anti-predator defence, having inspired evolutionary biologists for over a century (Bates 1862; Müller 1879). Müllerian mimicry (Müller 1878) arises when two or more unpalatable (and often conspicuous i.e. aposematic) species evolve to resemble each other most likely as a consequence of signal similarity reducing the *per capita* mortality involved in educating predators to avoid them (Sherratt 2008). In classic Müllerian mimicry, the relationship between co-mimics is generally thought to be mutualistic, or at least commensal (Ruxton et al. 2004) in that the presence of members of one co-mimic species reduces (or has no effect on) the *per capita* attack rates on the other co-mimic species.

By contrast, Batesian mimicry (Bates 1862) occurs when a palatable or defenceless species (mimic) resembles an unpalatable or noxious species (the model) (Bates 1862). The relationship between mimic and model is generally considered parasitic because while the mimic is generally protected by the resemblance, the model can be harmed when predators begin to associate the warning signals with palatability (Speed and Turner 1999). The main focus of this thesis will be Batesian mimicry.

Most examples of Batesian mimicry occur in insects, and it is particularly well known in Lepidoptera (butterflies) (Bates 1862), and Syrphidae (hover or flower flies) (Heikertinger 1918). However, Batesian mimicry has also been reported in a range of

other taxonomic groups including other invertebrates such as octopuses (Norman et al. 2001); vertebrates such as snakes (Pough 1988) and fish (Randall 2005); and plants (Augner and Bernays 1998). In the case of insects, most of the research in mimicry has centered on visual signals. However, mimicry of other cues is also possible, such as chemical (Elgar and Allan 2006) and auditory signals (Barber and Conner 2007).

## **1.2 Imperfect Mimicry**

Although theoreticians have tended to assume perfect mimicry (see Ruxton et al. 2004 for review), in some cases the extent of Batesian mimicry appears relatively imperfect, at least to human eyes. An example of differing degrees of mimetic fidelity can be seen in some species of ant-mimicking spiders. Species from the genus *Myrmarachne* tend to be quite convincing mimics, while species from the genus *Cosmophasis* only portray a vague resemblance (Edmunds 2000). Likewise, some species of syrphids, such as *Spilomyia longicornis* (wasp mimic – purported to mimic a yellow jacket – *Vespula vulgaris*) and *Volucella bombylans* (purported bumble bee mimic – *Bombus* sp.) appear as extremely close mimics, while other species such as *Syrphus ribesii* (intermediate wasp mimic – likely a *Vespula* sp) and *Allograpta obliqua* (presumed wasp mimic) have a very limited resemblance (see Figure 1.2). An important question therefore is why natural selection has not acted to improve the degree of resemblance to their models?



Figure 1.2: Examples of a wasp model (a- *Vespula vulgaris*) and three mimics of varying mimetic fidelity; a good mimic (b- *Spilomyia longicornis*), an intermediate mimic (c- *Syrphus ribesii*) and a poor mimic (d- *Allograpta obliqua*). Note these photos have been (approximately) controlled for body size, and as such are not to scale.

My Master's work addressed some of the hypotheses that have been put forward to explain imperfect mimicry, using syrphids as a case example. While a wide range of hypotheses have been put forward (see Gilbert 2005 for a comprehensive review), the following hypotheses are among the most commonly invoked:

### 1.2.1 Hypotheses to Explain Imperfect Mimicry

*Eye of the Beholder* (Cuthill and Bennett 1993):

The eye of the beholder hypothesis suggests that imperfect mimics only appear perfect to our eyes, whereas to their natural predators such as birds or invertebrates, they actually appear near perfect mimics (Cuthill and Bennett 1993).

*Disequilibrium - Imperfect mimicry as an intermediate stage* (Edmunds 2000):

One explanation given for imperfect mimicry is simply that the imperfect mimics are in a state of disequilibrium, in that, they have not yet evolved to be perfect (Edmunds 2000), or they once were perfect and have drifted away. For example, if a

major habitat change brings about a radical change in mimic frequency then there may be a temporary breakdown in the efficacy of mimicry, which in turn reduces selection on the mimetic phenotype (Azmeh et al. 1998).

*Kin Selection* (Johnstone 2002):

The hypothesis that kin selection may play a part in the evolution and maintenance of imperfect mimicry comes from considering situations under which the mimetic trait carried by an individual can also affect the reproductive success of relatives who carry the same mimetic trait. In particular, note that when a mimic is identical to its model then predators should no longer discriminate between mimic and model and so the protection afforded to the mimic is less than a system where the mimic imperfectly resembles a model. Here, despite individual selection for increasing mimetic perfection, inclusive fitness is maximised if individuals maintain imperfect mimicry (Johnstone 2002).

*Jack of all trades/Multi Model* (Edmunds 2000):

It is possible that a mimic appears imperfect because it is simultaneously selected to resemble two or more models; consequently, it is not a perfect or near perfect mimic for any of its potential models but gains more protection from vaguely resembling multiple models (Edmunds 2000). This hypothesis posits that mimics should more closely resemble the model that they share more time or space with. Based on modelling this hypothesis: when all else is equal, the mimic should resemble the less

noxious model (Sherratt 2002), and good mimics should be less common than poor (Edmunds 2000).

*Relaxed Selection* (Duncan and Sheppard 1963; Sherratt 2002):

The “curve of protection” theory for the evolution and maintenance of imperfect mimicry states that if complete protection is given when a mimic vaguely resembles a model, then there is no further selection to improve it. Hence mimics remain imperfect simply as a consequence of mutation-selection balance. This outcome is particularly likely when the model is noxious, because here the predators will act cautiously and generalize their avoidance to less than perfect mimics (Sherratt 2002). As can be seen from the output of a simple signal detection model, when a model has a low level of noxiousness the resemblance of the mimic has to be greater to afford the same protection (Sherratt 2002).

The curve of protection implies a relaxed selection against mimics with highly noxious models. Another factor that needs to be considered is the availability of alternate prey. The presence of an alternate prey item can alter the mimic-model relationship when the alternate prey is of similar profit. The predator will pursue the non-mimetic prey rather than risk mistaking a mimic for a model. The presence of alternate prey reduces the benefit of attacking potential mimics on encounter (Lindström et al. 2009).

### **1.3. Syrphidae**

Syrphids (Diptera: Syrphidae), known colloquially as hover or flower flies, are a diverse group of insects from the order Diptera. The adults feed primarily on pollen and nectar and in so doing they act as pollinators. Syrphids are a good group to study Batesian mimicry for a number of reasons. First, syrphids are common and are easily located in a variety of habitats. Second, syrphids are Batesian mimics of wasps, bumble bees and honey bees (Mostler 1935) allowing us to evaluate the type of mimicry that evolves when many different models are available. Finally the degree to which they resemble their models ranges from very poor to near perfection and this makes them well suited to study the evolution and maintenance of imperfect mimicry (Gilbert 2005), which is the central subject of this thesis.

Syrphids often mimic flying Hymenoptera, including wasps, honey bees and bumblebees. As long ago as 1935, Mostler determined that bird predators learn to avoid Hymenoptera due to their unpalatability, sting, and difficulty of handling due to their exoskeleton. Not all hymenoptera are equally unprofitable, as wasps are much more repellent to avian predators than bees (Mostler 1935). Thus, both wasps and honey bees were determined to be unpalatable, but bumble bees are palatable (but are avoided due to their hard exoskeleton which creates a long handling time) (Mostler 1935).

There have been many hypotheses proposed to explain the variation in mimetic fidelity in hover flies. Some have even gone so far as to suggest that hoverflies are

Müllerian mimics (Gilbert 2005), or not mimics at all (Drees 1997); rather than Batesian mimics. After considering all the literature and arguments for each general theory, I argue (as many do) that the evidence in support of Batesian mimicry is overwhelming.

It has been suggested that syrphids are not mimics at all, and that the yellow and black coloration occurs for another reason such as an aposematic signal or a consequence of thermoregulation (Drees 1997). The hypotheses that syrphids are not mimics at all, or that they are Müllerian mimics can be rejected. For example, even a vague resemblance to Hymenoptera provided some protection against avian predators (Mostler 1935). When offered in a mimic - model - mimic sequence, the mimic was eaten at first, but after coming in contact with the model, the birds avoided both the model and the mimic in subsequent trials (Mostler 1935). Syrphids were readily eaten until the bird came into contact with the model. Moreover, pigeons trained to attack non-mimetic flies pecked mimetic flies less often than non-mimetic flies, and pigeons trained to attack wasps pecked mimetic flies more often than non-mimetic flies (Dittrich et al. 1993). Finally, a number of mimetic syrphids also engage in behavioural mimicry (See Chapter 2), a phenomenon that is challenging to explain on the basis of thermoregulation or aposematism.

The hypotheses that syrphids are not mimics at all, or that they are Müllerian mimics can be rejected based on previous studies, because they do not explain why many syrphids are behavioural mimics. The remaining hypotheses for imperfect mimicry—eye of the beholder, disequilibrium, kin selection, multi model, and relaxed

selection, will each be examined in turn, and their validity evaluated in the light of data presented in my two data chapters. A discussion of each of these hypotheses will be completed in the fourth chapter of my thesis.

While Gilbert (2005) wrote a very thorough and insightful review on imperfect mimicry in syrphids, little direct comparative evidence was provided to support several key claims, such as: imperfect mimics are more common than more perfect mimics and that some wasp mimics have lower a mimetic fidelity than bee mimics. This thesis attempts to seek quantitative support for these claims and in so doing move us closer to understanding the evolution and maintenance of imperfect mimicry. My approach will capitalise on the wide array of mimetic fidelities represented in the Syrphidae, and I will employ, for the first time, a quantitative comparative approach to systematically evaluate each hypothesis, evaluating support for or against each hypothesis in the following two chapters.

## **Chapter 2:**

### **Is there a relationship between morphological mimetic fidelity and behavioural mimicry?**

#### **2.1: Introduction**

When researchers study Batesian mimicry they usually investigate morphological mimicry (see Gilbert, 2005 for a review). However, mimicry can also occur in other sensory modalities such as olfaction (Ceccarelli 2008; Ruxton et al. 2008), audition (Rashed et al. 2009), and behaviour (Gilbert 2005; Rashed et al. 2009; Waldbauer 1970). Behavioural mimicry occurs in multiple mimicry systems including the *Myrmecarachne* spider-ant complex (Ceccarelli 2008), the syrphid-hymenopteran complex (Waldbauer 1970) and even in masqueraders such as leaf or twig mimics (Bradburne 1995). For example, myrmecomorphs increase their resemblance to their ant models by running in a zig-zag motion and tap their abdomens in a similar manner as their ant models. They also run on their back three pairs of legs with their first pair of legs sticking straight out which has been hypothesized to mimic the ant's antennae (antennal illusion). Resembling a model in multiple sensory modalities can increase the likelihood predators will be deceived, and potentially protect against multiple predators that may use different sensory modalities to detect their prey (Ceccarelli 2008). However, these behaviours are seriously understudied.

In the syrphid-hymenopteran mimicry system behavioural mimicry is present in some species. For example Golding et al.(2001) reported that the honeybee mimic *Eristalis tenax*, resembled its model in flight behaviour. Syrphids have also been observed to mock sting, wing wag and leg wave (presumably to resemble the hymenopteran antennae) (Gilbert 2005; Waldbauer 1970). These behaviours may reinforce morphological resemblance to their models. While a number of studies have evaluated the extent of behavioural mimicry, (Rashed et al. 2009; Waldbauer 1970), or described general observations behavioural mimicry (Gilbert 2005; Shorter and Drew 1976) systematic empirical evidence, particularly of a comparative nature, has not been generated.

The purpose of this chapter of my thesis was to systematically and empirically study the patterns of behavioural mimicry in relation to their mimetic fidelity. Behavioural mimicry may be beneficial for syrphids, however, it has been noted that only certain syrphids participate in these mimetic behaviours (Waldbauer 1970). The question remains as to whether the behaviour is additive to the species that are already good mimics, or compensatory for the imperfect mimics to make up for their poor mimetic appearance. If high fidelity mimics participate in the behaviour then it would be seen as additive to their morphological mimicry, and thereby it enhances its resemblance to its model. If low fidelity mimics participate in the behaviour to compensate for poor mimicry then behavioural mimicry can be seen as compensatory. Moreover, any association between morphological mimicry and behavioural mimicry (which can be ascribed unambiguously) would imply that the morphological mimicry

represents a valid metric, and is not simply a reflection of human perception. If there is no relationship between mimetic perfection and behavioural mimicry then we would need further hypotheses to understand why the two are unrelated.

We predict that there is a relationship between morphological mimicry and behavioural mimicry. Specifically we predicted that high fidelity morphological mimics might use behavioural mimicry as an additive quality to enhance the protection against predation, while low fidelity mimics would not be able to compensate for their poor morphological mimicry by being a good behavioural mimic alone. One reason for the underlying variation in behavioural mimicry may be body size. There is a relationship between size and mimetic fidelity (see Chapter 3), with smaller syrphids tending to be poorer mimics. At smaller size, it is unlikely that adding behavioural mimicry will help for two reasons. Firstly, predator perception of the behaviours may be reduced because of the small size of the poor mimics. Secondly, because the morphological mimicry is of low fidelity, adding behavioural mimicry is not guaranteed to increase the chances of a predator mistaking a mimic for a model.

In conducting our comparative analysis, we also make an additional prediction. Syrphids that have evolved the leg waving behaviour are predicted to have black front legs. The evolution of darkened frontal tibia may aid the effectiveness of the behavioural mimicry in convincing predators that the antennal illusion is in fact antennae. While not all wasps have dark antennae (the paper wasp for example – *Polistes dominula*), many *Vespula* models have thick, black, obvious antennae; and

modifying the color in the frontal tibia may enhance the illusion and thereby confer greater protection from predators because of the behavioural mimicry is more convincing.

## 2.2: Methods

### 2.2.1: Field work

Syrphid flies with varying degrees of mimetic similarity were captured throughout the field season (April to September) in 2010. Flies were captured at Fletcher Wildlife Garden, Ottawa, ON (45°23'08N, 75°42'15W); Uxbridge, ON (44°14'30N, 79°10'41W); Queens Biological Field Station, Chaffey's Locks, ON (44°34'22N, 76°20'05); Gatineau Park, Gatineau, QC (45°30'31N, 75°48'59W); and Mont Rigaud, Rigaud, QC (45°27'06N, 74°19'33W). Flies were sought and caught between 9 am and 4 pm local time. When possible, all flies that were detected were captured using a large insect net and only captured flies were included in the analysis. To allow for comparison, a mixture of mimetic (including honey bee mimics, bumble bee mimics, and wasp mimics) and non-mimetic flies were caught and tested.

The behavioural mimicry traits that we were interested in have been generally reported in wasp mimicking syrphids; however all syrphids (independent of the model they resembled) that were caught were tested for the following behavioural traits. The **mock sting** was defined as tapping the tip of the abdomen in an aggressive manner. If the fly did not exhibit the mock sting when faced with the avian predator, it was lightly grasped between the thumb and forefinger of the researchers in an attempt to illicit the

behaviour. **Wing wagging** was described as holding and wagging the wings in a wasp-like rather than fly like manner. **Leg waving** was defined as resting on their mid and hind legs and waving their forelegs in front of their head. The leg waving movement was distinct from a washing movement, and was an obvious leg waving behaviour. As noted above, some researchers have informally noticed that leg waving syrphids tend to have black tibia on the front pair of legs, while the mid and hind legs remain yellow. Therefore, leg color was noted on each specimen.

On capture, specimens were placed in small, clear plastic vials and kept until they were tested (within 10 minutes on hot days (above 30 degrees Celcius), but within 2 hours maximum on milder days). On testing, the fly was then placed in a mesh cage (30 cm cubed), and was allowed time to settle and acclimatize to the cage. After acclimatization, the syrphids were behaviourally assayed by prodding them with a simulated avian predator (a stuffed blue jay – *Cyanocitta cristata*). They were prodded with the beak of the predator up to five times, and all behaviours of the fly, (wing wagging, mock stinging, leg waving, or no behaviour) were recorded. They were then killed (using either cyanide or freezing), pinned, and identified to genus. When it was possible, specimens were identified to species level (in genera such as *Syrphus* and *Sphaerophoria* identification to species in females is not possible with the current key). All specimens were deposited in the Canadian National Collection of Insects, Arachnids and Nematodes in Ottawa, ON. Labels were added to each specimen with a unique voucher number (HP1 to HP382).

### 2.2.2: Human Ranking System

In order to obtain a ranking of the mimetic similarity of our captured specimens, a human computer ranking system was created. The ranking system ran in MS Visual Basic 6. Thirty representative syrphid species were selected from the 59 species that were collected throughout the summer. The syrphids were from a range of mimetic fidelities including wasp and bee mimics and non-mimetic flies. Photographs from the dorsal view were taken of 3 individuals for each of the 30 species. Photographs of 3 separate model species were also taken. All the photos were taken using a Canon EOS 50D. The camera had a Canon macro lens (100 mm). An 80 LED microscope ring light (KD-200) was used to illuminate the insects and prevent shadows. Human participants ranked each mimic photo on a scale of 1 (very poor) to 10 (very good) separately for each of the 3 potential models: a bumble bee (*Bombus affinis*), and two vespid wasp species – a yellow jacket (*Vespula vulgaris*) and a potter wasp (*Ancistrocerus parietum*). Photographs of each of the models were also included for participants to rank (but the photos were of separate individuals than the model photo). There were three participant blocks with 10 participants in each block (a, b and c). Each block contained a photo from each of the 30 syrphid species (presented in random order) and 1 photo for each model for comparison. The species photos (for models and mimics) were changed for each block. The rankings for each photo were averaged for potential model, and

then the species from separate blocks were combined for an average ranking of the species itself.

### 2.2.3: Statistical Analysis

A chi-square test was conducted to determine whether being a behavioural mimic was independent of being a good morphological mimic. The syrphids were classified into categories of morphological mimetic fidelity using the human rankings from Chapters 2 and 3 combined. The human experiments from Chapters 2 and 3 evaluated the similarities of different syrphid mimics to different potential models. The models in this Chapter (2) were a bumble bee (*Bombus affinis*), a yellow jacket wasp (*Vespa vulgaris*), and a potter wasp (*Ancistrocerus parietum*). The models for Chapter 3 were a bumble bee (*Bombus impatiens*), a honey bee (*Apis mellifera*) and a yellow jacket (*Vespa vulgaris*). For 30 of the 59 syrphid species we had behavioural data for, the mimetic fidelity could come directly from our human rankings. If a species similarity to models was not rated however (29 of 59 potential mimics) it was given the same ranking as other members in its genus (or the average if there were more than two species per genus) in our data set. If the genus was not represented, it was rated based upon related genera or other species with a similar appearance (see Table A1 in the Appendix for species lists and rankings).

Due to the lack of overlapping models for the human ranking experiments in Chapters 2 and 3, syrphids were classified as either a wasp (*Vespa vulgaris* and *Ancistrocerus parietum*), or a bee (*Bombus sp.*, and *Apis mellifera*) mimic. These

combinations are justified because the rankings tend to be very close among (wasp and among bee) models because the models look similar.

Species were categorized, based on the human rankings from Chapters 2 and 3, as good (above 6), intermediate (between 4 and 6), poor (between 2 and 4) or non-mimetic (below 2) for their respective models (wasp or bee) (see Table A1 in the Appendix). Another chi square was conducted to determine whether the leg waving behaviour was independent of leg color. A comparative analysis on the behavioural data was not conducted because it was only present in 2 genera, with 3 species per genus – making the trait highly clustered within the phylogeny.

An ANOVA was performed on the average human rankings for bumblebee mimics and wasp mimics (which were separated by behavioural and non-behavioural mimic categories) that we had direct data for. Yellow jacket and potter wasp mimics were combined to form all wasp mimics due to rankings being very similar for each. The analyses were performed with and without *Spilomyia fusca* because their purported model (Bald faced hornet: *Dolichovespula maculata*) was not included for the participants to compare against, giving the species a much lower ranking than its generic counterparts. *Spilomyia fusca* is unique in that it very closely resembles a bald faced hornet, particularly with its facial markings

### **2.3: Results**

All individuals (from 29 species, 359 total specimens – see Appendix Table A1 for sample sizes of each species) were assayed for behavioural mimicry. There was no

within-species variation of behavioural mimics. In other words, if one individual did or did not do the behaviour, then all individuals of the species would do the same. There were only six species (*Spilomyia sayi*, *S. fusca*, *S. longicornis*, *Tenostoma alternans*, *T. barberi*, and *T. obscurum*) that exhibited behavioural mimicry (see Table 2.1) and all six species mimic wasps (as determined by our human ranking system). Most behaviourally mimetic species did all three behaviours, while *S. sayi* only engaged in the mock sting and the wing wag.

Table 2.1: The number of species for each category for each mimic's model (non-mimetic, good, intermediate, or poor wasp or bee mimic) and whether they were behavioural mimics (used the mock sting, wing wag or leg wave) or not. Being good was defined as a human ranking above 6, intermediate was between 4 and 6, and poor was between 2 and 4, and non-mimetic was below 2. Being a wasp or bee mimic was determined by which ranking was higher.

Category	Not a behavioural mimic	Behavioural mimic
Good Wasp Mimic	6 species	4 species
Intermediate Wasp Mimic	21 species	2 species
Poor Wasp Mimic	12 species	0 species
Good/Intermediate Bee Mimic	12 species	0 species
Non-Mimetic Syrphid	2 species	0 species

A chi-square test was conducted, and it was determined that behavioural mimicry was not associated with visual mimetic fidelity when examining all mimics (non-mimetic syrphids were not included) in which good and intermediate categories (for bee mimics) were necessarily combined to generate sufficiently high expected values (Yates'  $\chi^2=7.393$ ,  $df=3$ ,  $p=0.06$ ). A Yates' correction had to be applied because one of the

frequencies was less than 5. As seen in Table 2.2, only wasp mimics that were either good or intermediate participated in behavioural mimicry. When examining wasp mimics alone (3 levels of mimicry), it was determined that behavioural mimicry was associated with visual mimicry ( $\chi^2=8.428$ ,  $df=2$ ,  $p=0.01$ ).

Table 2.2: The number wasp mimics that were leg wavers and non-leg wavers with color patterns (all the same color or dark forelegs and light back legs).

	All same color	Dark forelegs, light hind legs
Leg waver	0	5
Non leg waver	27	1

A chi-square test was conducted to determine whether being a leg waving behavioural mimic was independent of leg color in wasp-mimicking syrphids. When examining only the good and intermediate fidelity wasp mimics, a clear relationship between leg waving and leg color can be seen (Yates'  $\chi^2$ : 20.432,  $df=1$ ,  $p<0.0001$ ). A Yates' chi square was used because one of the expected values was below 5. Leg wavers all had dark forelegs and lighter mid and hind legs. With the exception of *Spilomyia sayi* all non-leg wavers had all the same color legs (either all yellow or all dark).

An ANOVA was conducted on the human rankings for the species assessed for behavioural mimicry. Mimics were categorized as wasp or bumble bee mimics based on their highest human ranking. The average human ranking for each group of mimics was calculated (Figure 2.1). Bumble bee mimics (mean ( $M$ )= 6.35, standard error (SE)= 0.554) and behavioural wasp mimics ( $M$ = 6.12, SE=0.62) had means that were not significantly

different from each other ( $t=0.295$ ,  $df=12$ ,  $p=0.773$ ). Both of them were higher in mimetic fidelity than the non-behavioural wasp mimics ( $M=5.05$ ,  $SE=0.22$ ). There was a marginally significant difference among means of the bee and wasp (behavioural and non-behavioural) mimics ( $F= 3.99$ ,  $df=2, 27$ ;  $p=0.03$ ). When *Spilomyia fusca* was removed from the analysis due to a lack of the correct model (*Dolichovespula maculata*) the difference among means of bees ( $M= 6.35$ ,  $SE= 0.554$ ), non-behavioural ( $M=5.05$ ,  $SE=0.22$ ) and behavioural wasp mimics ( $M=6.49$ ,  $SE= 0.51$ ) is also significant ( $F=5.272$ ,  $df=2,26$ ;  $p=0.012$ ). Behavioural and non-behavioural mimics were significantly different from each other ( $t=-2.89$ ,  $df=19$ ,  $p=0.009$ ).

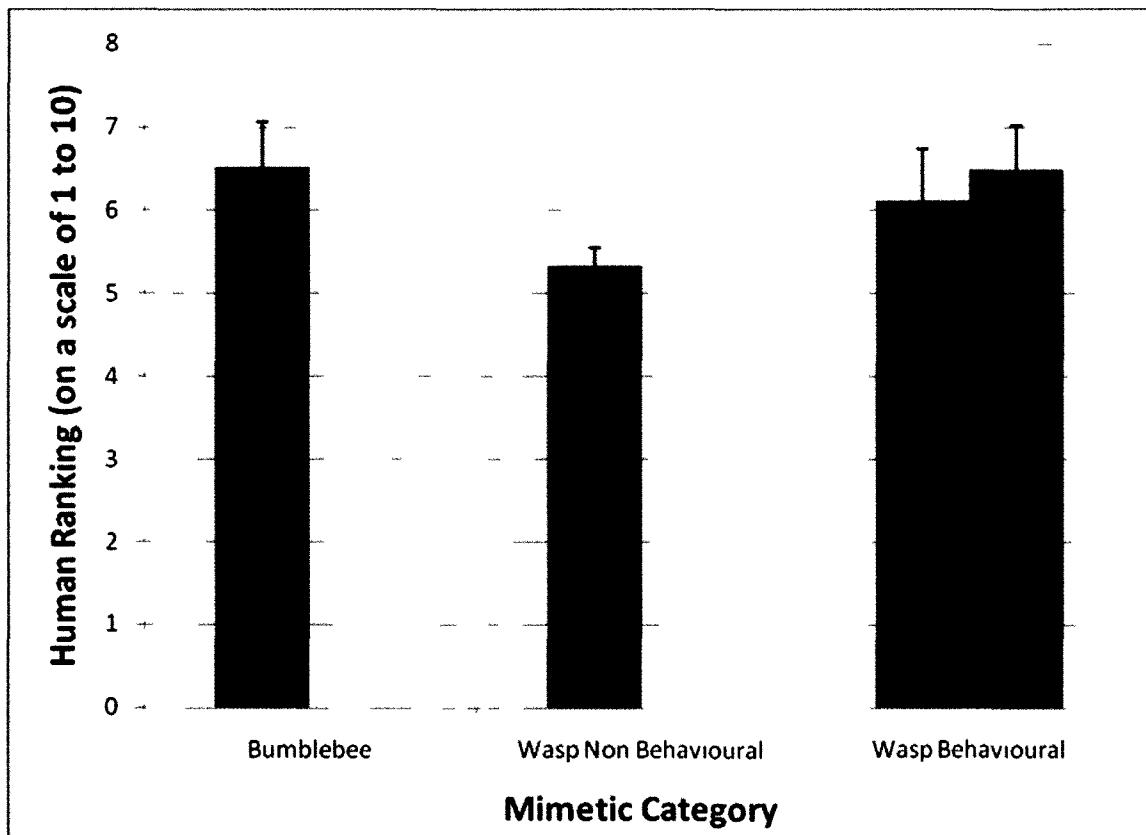


Figure 2.1: Average human ranking for bumblebee mimics, wasp mimics – both behavioural and non-behavioural mimics. In the wasp behavioural category it includes

(blue) and does not include (red) *Spilomyia fusca*. The error bars represent 1 standard error.

## 2.4: Discussion

After empirically and systematically testing syrphids from a range of mimetic fidelities it was determined that there is indeed a relationship between morphological mimetic fidelity and behavioural mimicry. To humans, behavioural mimics were always good or intermediate mimics, but not all good or intermediate mimics are behavioural mimics. There was a marginally significant difference in the similarity of behavioural and non-behavioural wasp mimics to their models, with behavioural mimics being better mimics on average. There were no examples of a behavioural mimic that received a low human mimetic fidelity ranking, when *S. fusca*'s lack of an appropriate model to compare to in the human experiment was taken into account.

All leg wavers had the same coloration pattern (dark forelegs and light mid and hind legs). Non leg wavers always had a different color pattern (such as all dark, all light or other variations such as light or dark tibia on various legs). *Spilomyia sayi* was the only syrphid with the leg waver's color pattern that was not a behavioural mimic. When examining *S. sayi* ( $M= 0.437 \pm 0.008$  (SE)) it can be noted that they have longer antennae than other members of their genus such as *S. fusca* ( $M= 0.266 \pm 0.002$  (SE)) and *S. longicornis* ( $M=0.318 \pm 0.007$  (SE)). It is quite possible that *S. sayi* has vestigial leg waving coloration, left over from a time in their evolutionary life when they had shorter antennae and participated in leg waving. Another possible explanation is that it is an

artefact of phylogeny, in that, *S. sayi* had a leg waving common ancestor and the leg color remained due to lack of selection against it (phylogenetic inertia).

Intriguingly, behavioural mimics were only present in the intermediate and good wasp mimic category. There were no poor wasp mimics, bee mimics or non-mimetic syrphids that were behavioural mimics. However, it has been previously noted that *Volucella bombylans* (a bumble bee mimic) does participate in leg waving behaviour (Waldbauer 1970). Nevertheless, *Volucella* females lay their eggs inside of bumble bee nests, and use the behaviour to gain entry to the nest (they are aggressive mimics), which differs from wasp mimics, which use leg waving as a predator defence that enhances their mimicry (Waldbauer 1970). We tested a number of *Volucella bombylans* for behavioural mimicry, however, they were classified as being non-behavioural. The fact that *Volucella* participates in the behaviour only in the presence of bumble bees as aggressive mimicry (instead of predators) may explain why we did not observe the leg waving behaviour during the simulated avian attack.

Behavioural mimicry can be additive or compensatory to morphological mimicry. For the mock sting and wing wag at least, it seems that these behaviours are additive in that they are only present in higher fidelity mimics. Thus, the behavioural mimics are using mock sting and wing wag as a means to visually enhance their high fidelity morphological mimicry. However, it seems that the leg waving behaviour is a compensatory trait. There were five species out of the six behavioural mimics that were leg wavers. All five leg wavers all had short antenna in comparison to the non-leg waving

behavioural mimic (*Spilomyia sayi*). The leg waving behaviour is likely a compensation for the syrphid's short antennae.

The species data are not independent of one another due to a shared phylogeny. Controlling for phylogeny for the behavioural assays is not appropriate because there are too few examples of behavioural mimics. Behavioural mimicry arose in only 2 unrelated genera (6 species) both of which have species that are high fidelity wasp mimics; this pattern in itself is indicative of a broad relationship between morphological mimetic fidelity and behavioural mimicry, but clearly any phylogenetically-controlled test would be of insufficient power to allow us to reject the null hypothesis of no association.

The length of antennae is an important discriminating factor between syrphids and hymenopterans. In the analysis of Chapter 3 I shall demonstrate that antenna length alone is an important trait in distinguishing syrphids from hymenopterans. This feature has also been shown to be an important discriminating factor in a neural network for avian predators (Bain et al. 2007). Hence, when predators are motivated to discriminate it seems likely that leg waving behaviour will significantly reduce the degree of discriminability.

For the first time, an empirical, systematic assessment of the relationship between behavioural mimicry and morphological mimetic fidelity was completed. It was determined that, in wasp mimics, behavioural mimics are good mimics. Behavioural

mimics have additive protection by combining good morphological mimicry and behavioural mimicry.

## **Chapter 3:**

### **How are abundance, body size, and mimetic fidelity related in flower flies (Diptera: Syrphidae)?**

#### **3.1: Introduction**

Syrphids frequently resemble Hymenoptera such as wasps, honey bees and bumble bees. However, the extent of their perfection (i.e. their mimetic fidelity) appears to vary significantly among species (Dittrich et al. 1993; Rashed et al. 2009) to human eyes and those of pigeons (Dittrich et al., 1993), syrphid mimetic fidelity ranges from near perfect to very poor. Researchers have argued that this variation in mimetic fidelity can be explained by variation in factors such as model noxiousness (Sherratt 2002) and abundance (Gilbert 2005), but so far there have been no quantitative evaluations of these theories. In particular, researchers have consistently argued that good mimics tend to be rarer than their poor mimic counterparts (Gilbert 2005; Johnstone 2002). While this statement may well be true, so far all of the support for this argument has been entirely anecdotal; for example, it has simply been noted that near-perfect mimics (such as *Spilomyia fusca*) tend to be less common than more imperfect ones (such as *Toxomerus marginatus*) (Gilbert 2005).

Here we begin by formally evaluating the evidence for an abundance-fidelity relationship. If true, then we argue that this abundance-fidelity relationship may be mediated by body size, and we set out to test this supplementary hypothesis. General body size-abundance relationships, with smaller species being more abundant, have

been shown across taxa such as mammals, fish and insects (Schmid et al. 2000), but not yet examined in detail in syrphids. Indeed, the closest examination in syrphids was completed by Owen and Gilbert (1990). They did not find a relationship between morphological characteristics (not body size per se) and population density. Body size may play an important mediating role because it may reflect the profitability of the meal to predators and therefore the intensity of selection on mimetic fidelity (Sherratt 2002). If large species also tend to be rarer than small species, and large species also tend to face more intense selection for mimetic fidelity, then any abundance-mimetic fidelity relationship referred to in the literature may arise simply as an indirect consequence of selection for mimetic fidelity based on body size. We set out to evaluate this hypothesis.

One challenge in this general field that must be addressed at the outset is quantifying the extent of mimetic fidelity. To date, when the degree of mimetic fidelity has been quantified, the measures used to determine the quality of mimicry have been largely subjective, generally using humans (Golding et al. 2005). A necessary first step to testing predictions based on inter-specific variation in mimetic fidelity was therefore to obtain an objective, quantitative value for degree of mimetic fidelity, which we can, as necessary, compare directly with human-based indices. In a study in 2007, Bain et al. used a neural network to analyze the pigeon data from Dittrich et al. (1993). The neural network was used to ascertain which features of flies and wasps are important for discrimination. The variables that were deemed important by the Bain et al (2007) study

were the variables selected for the development of a more objective quantitative measure of mimetic fidelity for my thesis.

### **3.2 Methods**

#### *3.2.1 Abundance:*

Multiple datasets from the literature were used to determine if there are relationships between abundance and body size, and abundance and mimetic fidelity. The data comprised 13 separate studies that included syrphid abundance numbers (see Table 3.1 for further information about each study). To control for variation in trapping time, the abundance used was relative abundance compared to all species that were collected in that study. There were 35 species (from a total of 40) selected from the Gilbert and Owen (1990) dataset that were used in the analysis of body size and mimetic fidelity. There were 40 species that were collected in the Gilbert and Owen 1990 study, of those, the CNC had 37 species. Two of those species did not have a high enough sample size to be included in the analysis leaving 35 species in the analyses (see Appendix for the species list). Body size was estimated using the morphological data collected (the PCA of body size).

**Table 3.1: Thirteen studies that were examined for abundance data – examining location, season, sampling method and total number of syrphids caught for comparative analysis.**

Dataset	Location	Season	Sampling Method	Total # of Syrphids Caught (species)
(Leinon et al 2006)	Finland, Western Russia, Estonia, Latvia and Lithuania	May to Sept, 1997 to 1999	Yellow traps (type Russell, pheromone trap)	246 (35)
(Marshall and West 2007)	England (31 arable fields)	3 weeks in June and July 2004	Window and water traps	1060 (28)
(Haenke et al 2009)	Germany (5 habitat types)	June and July, 2006	Sweep netting -100 m transects	829 (20)
(Kleijn and van Langevelde 2006)	Netherlands (16 stream beds)	April to mid August, 2002	30 25x2m subplots All syrphids seen in 5 min interval were caught Sampled 3 times in the season	2017 (40)
(Meyer et al 2009)	Germany (32 grasslands)	April to September, 2004	6 transect walks Syrphids in the 4m corridor were IDed in the field or caught	3560 (75)
(Moron et al 2009)	Poland	April to September, 2007	20 200m transects Walked slowly, 500 net sweeps	200 (21)
(Ouin et al 2006)	France (Woodland)	May 10- June 10 and Sept 13 to Oct 13, 2000	Malaise traps	3317 (100)
(Owen 1981)	England (one backyard)	April to October, 1972-1979	Malaise trap	28924 (85)
(Ricarte et al In press)	Spain (3 vegetation types)	May to Nov 2004, April to Sept 2005	Hand net, 2hr/month at each sampling site	2356 (72)
(Fayt et al 2006)	Belgium	March to October, 2002-2003	Malaise, stump emergence, free hanging window traps	3020 (106)
(Gilbert 1985)	England (two urban and one ancient woodland site)	1979 and 1980	Standard census walks	802 (57)
(Taki et al 2010)	Central Japan	May to Sept, 2005 and 2007	Malaise traps	990 (57)
(Gilbert and Owen 1990)	England	April to October, 1979 -1986	Malaise trap, one backyard	43359 (40)

The abundance data that was used most intensively in this chapter was collected over a 15 year period in England (Gilbert and Owen 1990). Therefore, much of the analysis (including the assessment of mimetic fidelity) has focused on the morphological attributes of species included this data set. However, included in this chapter is an

analysis of a number of other data sets that allow us to test for a general relationship between body size and abundance in Syrphidae.

### 3.2.2: Photography

Photographs of individual syrphids were taken from specimens held at the Canadian National Collection of Insects, Arachnids and Nematodes (CNC). It was noted that there were no representatives of what we might consider high fidelity mimics so three additional species (*Spilomyia longicornis*, *S. fusca* and *Temnostoma alternans*) were also photographed. Eleven hymenopteran (3 bumble bee species, honey bee, a polistine wasp, and 6 vespid wasp species) species were used as potential model species. Photos were taken of 10 individuals (5 males, 5 females) for each syrphid species (when such numbers were available) and 10 females for each hymenopteran species (all photographed individuals were female). The potential models were selected based upon overlapping geographic range (Palearctic species) and were chosen to represent a variety of model appearances. Each individual was photographed at multiple angles (dorsal and lateral views) to help ensure that, when possible, the traits to be measured were in the plane of the photo. All the photos were taken using a Canon EOS 50D that was mounted on a copy stand. The camera had a Canon macro lens (100 mm), and microtwin light (MT-243X). The intensity of the flash and the light in the room where the photography took place was held constant.

### 3.2.3: Variable Measurement

#### *3.2.3a Mimetic Fidelity:*

Mimetic fidelity was measured in two ways. The first was analyzing morphological data using multivariate statistics, and the second was using a human ranking system.

#### *3.2.3b Morphological measurements:*

Using ImageJ (Rasband 1997-2011), the photographs of the syrphids and hymenopterans were measured for multiple variables namely: antenna length, abdomen length, abdomen width, thorax width, wing length and head width. The assessments of similarity between models and mimics needed to be independent of body size, so all of the values in our analyses were first divided by the width of the head to create a relative measurement. The number and color (classified by the observer as white, grey, silver, yellow, orange or brown) of patches and/or stripes were recorded. Wing transparency (which ranged from 0 being completely translucent to 4 being opaque) was determined. The red, green, blue (RGB) colour and the standard deviation of RGB of the abdomen were measured using COREL PhotoPaint X3.

#### *3.2.3c Human ratings*

Photographs (all were dorsal view) were taken of 2 individuals for each of the 38 (35 + 3 additional) syrphid species and 2 individuals of each of 3 hymenopteran species (were chosen as controls-a bumble bee, a honey bee and a vespid wasp) that were

this relationship, although arguably phylogenetic control may not be necessary in this instance.

To elucidate the relationship between body size and abundance, relative abundance estimates from eleven separate studies were compared (using a Pearson's correlation) to a PCA of body size based on species from (Gilbert and Owen 1990; Gilbert and Owen 1991). A Bonferroni correction was applied because of the high number of tests.

It was apparent that there was a need for phylogenetic control when examining the species included in the dataset from Gilbert and Owen (1990) because each species is not an independent data point (see Figure A1 in Appendix). Of the 38 species of interest, only 15 had genetic information on GenBank or BOLD (both of which are online genetic databases). A phylogenetically independent contrast (PIC) requires a dichotomous tree (all nodes resolved and no polytomy) in order to contrast pairs of sister species. Since a fully dichotomous tree was unavailable a PIC was not possible, so a generalized estimating equation (GEE) was instead fitted. The fit of the GEE was implemented using the ``compar.gee`` function in the ape library (Paradis et al. 2004) in R (R: Development Core Team 2011) and effectively helps test for significance while controlling for phylogenetic autocorrelation. Each of the GEE's fitted in this chapter used a phylogenetic tree with branch lengths was set to 1 (the tree was based on subfamily, tribe, genus and species relationships).

When conducting a comparative generalized estimating equation (GEE), phylogenetic degrees of freedom (pDF) are used instead of regular degrees of freedom. Degrees of freedom assume that each data point is independent of all other data points. However, when dealing with species that vary in relatedness, phylogenetic degrees of freedom must be used to control for phylogenetic autocorrelation (pDF). pDF's are estimated based on genetic dissimilarity between species.

### **3.3: Results**

#### 3.3.1: Multivariate analysis of Mimetic Fidelity

To analyze multivariate mimetic fidelity a generalized canonical discriminant analysis (GCDA) was completed with (Figure 3.1) and without (Figure 3.2) antenna length, and with an increased antenna length in the leg waving behavioural mimics (Figure 3.3). When antenna length was included in the analysis, syrphids and hymenopterans cluster with their respective orders (syrphids with syrphids and hymenopterans with hymenopterans). Alternately, when antenna length was not included in the analysis the syrphids cluster closer to the hymenopterans. This implies that antenna length is a very important discriminating factor between syrphids and hymenopterans. Another indicator of the strength of a variable in differentiating among species is the length of the arrow on the graph. As noted in Figures 3.1 and 3.3, relative antennae length is the longest arrow, indicating it is the strongest predictor variable.

Behavioural mimics use their forelegs to resemble hymenopteran antennae, which artificially increases the apparent length of their antennae. When antenna length

was increased in the species known to be behavioural mimics (*Temnostoma obscurum*, *Spilomyia longicornis* and *Spilomyia fusca*, Chapter 2), these species shift closer to their models in multivariate space.

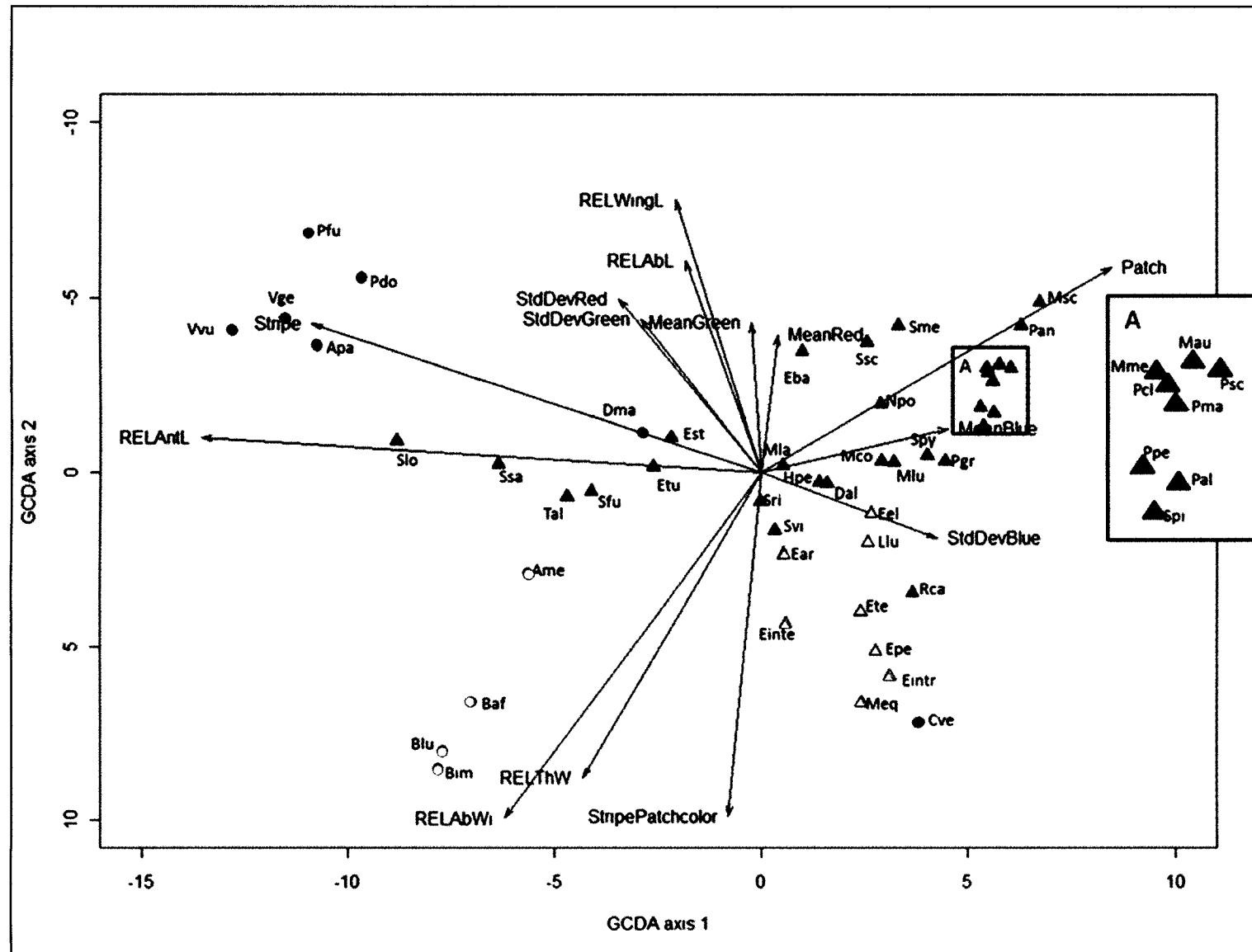
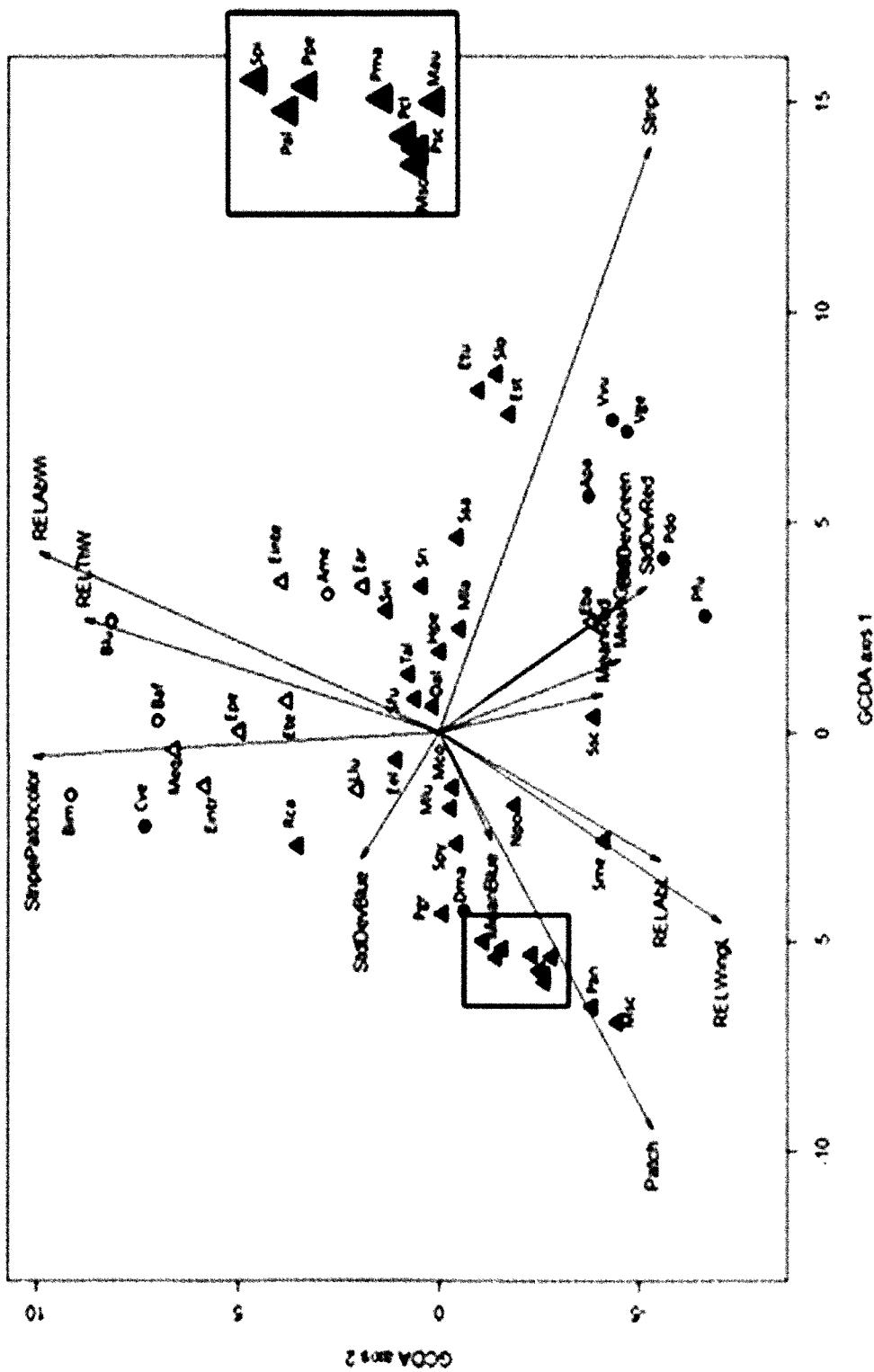


Figure 3.1: Generalized canonical discriminant analysis plot without modifications to antennae length. (Circles are models, triangles are mimics. Blue are wasps or wasp mimics, yellow are bees or bee mimics. The solid black circle is the non-mimetic syrphid). Note that each group clusters with other members of its group more so than their model or mimic – bees look like bees, wasps look like wasps, wasp-like syrphids look like wasp-like syrphids and bee-like syrphids look like bee-like syrphids. Wasp- and bee-like syrphids look more like each other than their respective models.

Bees: *Apis mellifera* (Ame); *Bombus affinis* (Baf); *Bombus impatiens* (Bim), *Bombus lucorum* (Blu)

Wasps: *Ancistrocerus parietum* (Apa); *Dolichovespula maculata* (Dma); *Polistes dominula* (Pdo); *Polistes fuscatus* (Pfu), *Vespula germanica* (Vge); *Vespula vulgaris* (Vvu)

Syrphids: *Cheiobia vernalis* (Cve); *Dasysyrphus albostriatus* (Dal); *Epistrophe eligans* (Eel); *Episyrrhus balteatus* (Eba); *Eristalis arbustorum* (Ear); *Eristalis interrupta* (Einte); *Eristalis intricaria* (Eintr); *Eristalis pertinax* (Epe); *Eristalis tenax* (Ete); *Eumerus strigatus* (Est); *Eumerus tuberculatus* (Etu); *Helophilus pendulus* (Hpe); *Leucozona lucorum* (Llu); *Melanostoma mellinum* (Mme); *Melanostoma scalare* (Msc); *Meliscaeva auricollis* (Mau); *Merodon equestris* (Meq); *Metasyrphus corolliae* (Mco); *Metasyrphus latifasciatus* (Mla); *Metasyrphus luniger* (Mlu); *Neoascia podogrica* (Npo); *Platycheirus albimanus* (Pal); *Playcheirus angustatus* (Pan); *Platycheirus clypeatus* (Pcl); *Platycheirus granditarsa* (Pgr); *Platycheirus manicatus* (Pma); *Platycheirus peltatus* (Ppe); *Platycheirus scutatus* (Psc); *Rhingia campestris* (Rca); *Scaeva pyrastri* (Spy); *Sphaerophoria menthastris* (Sme); *Sphaerophoria scripta* (SSc); *Spilomyia fusca* (Sfu); *Spilomyia longicornis* (Slo), *Spilomyia sayi* (Ssa); *Syritta pipiens* (Spi); *Syrphus ribesii* (Sri); *Syrphus vitripennis* (Svi); *Temnostoma alternans* (Tal)



**Figure 3.2:** Generalized canonical discriminant analysis plot without antennae length. (Circles are models, triangles are mimics. Blue are wasps or wasp mimics, yellow are bees or bee mimics. The solid black circle is the non-mimetic syrphid). When antenna length is not included in the analysis, syrphids and hymenopterans tend to cluster closer together and some species that are closely related and look very similar no longer cluster together. The species abbreviations are explained in the legend for Figure 3.1.

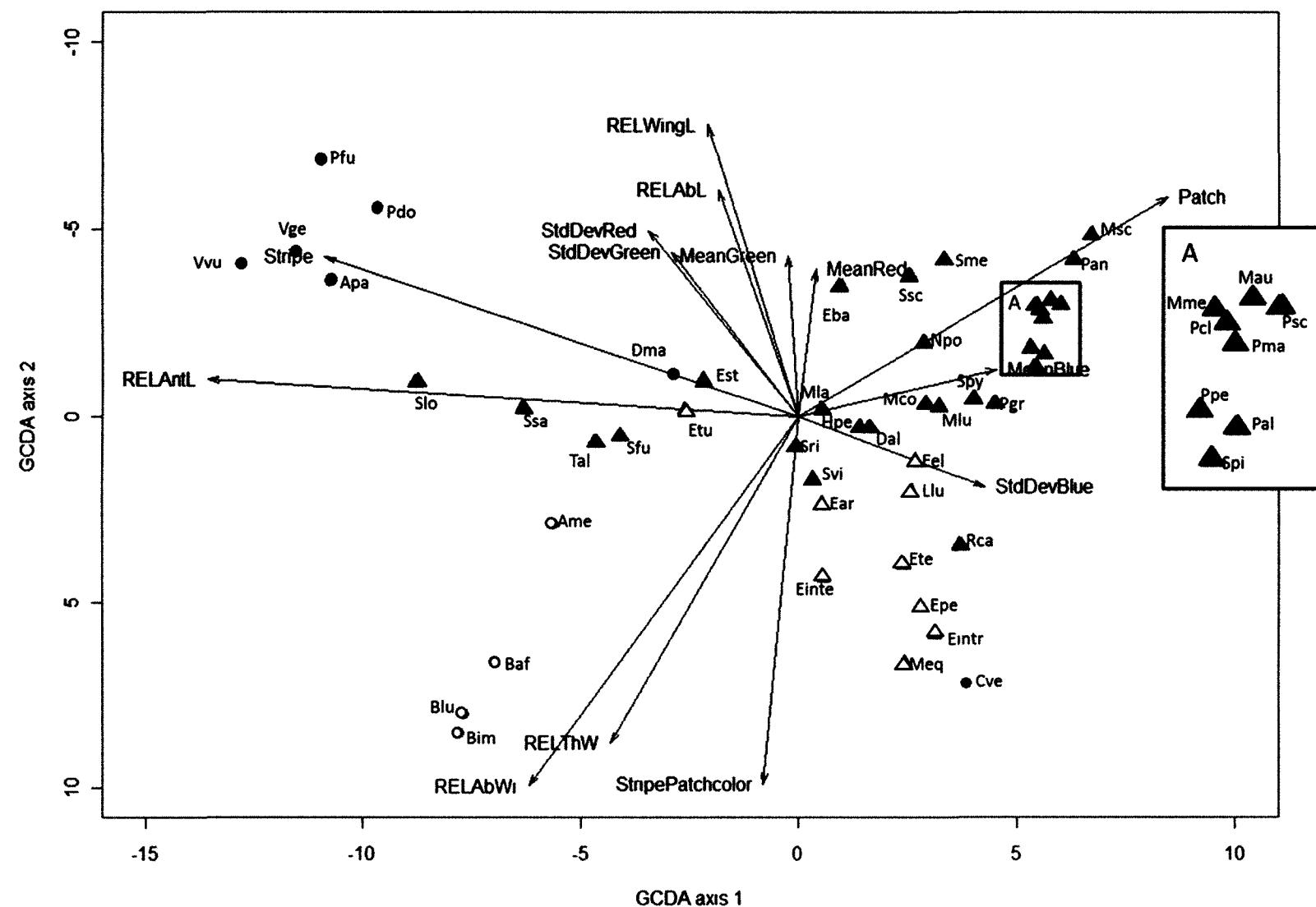


Figure 3.3: Generalized canonical discriminant analysis plot with enhanced antennae for the syrphids that are behavioural mimics. (Circles are models, triangles are mimics. Blue are wasps or wasp mimics, yellow are bees or bee mimics. The solid black circle is the non-mimetic syrphid). It can be noted that, in comparison to the GCDA plot without antennae modification, the behavioural mimics - *S. fusca* (Sfu), *T. alternans* (Tal) and *S. longicornis* (Slo) shift much closer to the hymenopteran models. The species abbreviations are explained in the legend for Figure 3.1.

### 3.3.2: Mimetic Fidelity - Multivariate vs Human rankings

The Mahalanobis distances from the regular GCDA (including non-modified antennae lengths) and the human rankings were compared for consistency. A Pearson correlation was conducted. There was a marginally significant negative relationship between Mahalanobis distances and the human rankings ( $r=0.399$ ,  $p=0.013$ ) – thus species ranked as close mimics (high human scores) tended to have low Mahalanobis distances. To control for phylogeny a comparative generalized estimating equation (GEE) was fitted when characterizing the correlation. The relationship between the Mahalanobis distances for mimetic fidelity and the human rankings of mimetic fidelity was marginally non-significant after controlling for phylogeny ( $t=-2.021$ ,  $pDF=16.25$ ,  $p=0.063$ ; see Figure 3.4).

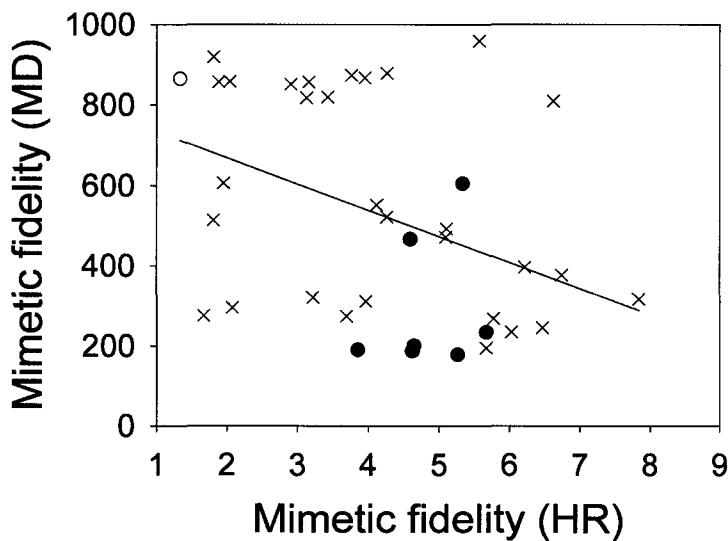


Figure 3.4: The relationship between mimetic fidelities – average Mahalanobis distance (MD) and human rankings (HR). Circles are bee mimics, crosses are wasp mimics, and the open circle is the non-mimetic syrphid – *Cheilosia vernalis*. The line shows a linear regression, see text for statistics.

### 3.3.3: Abundance vs Body Size

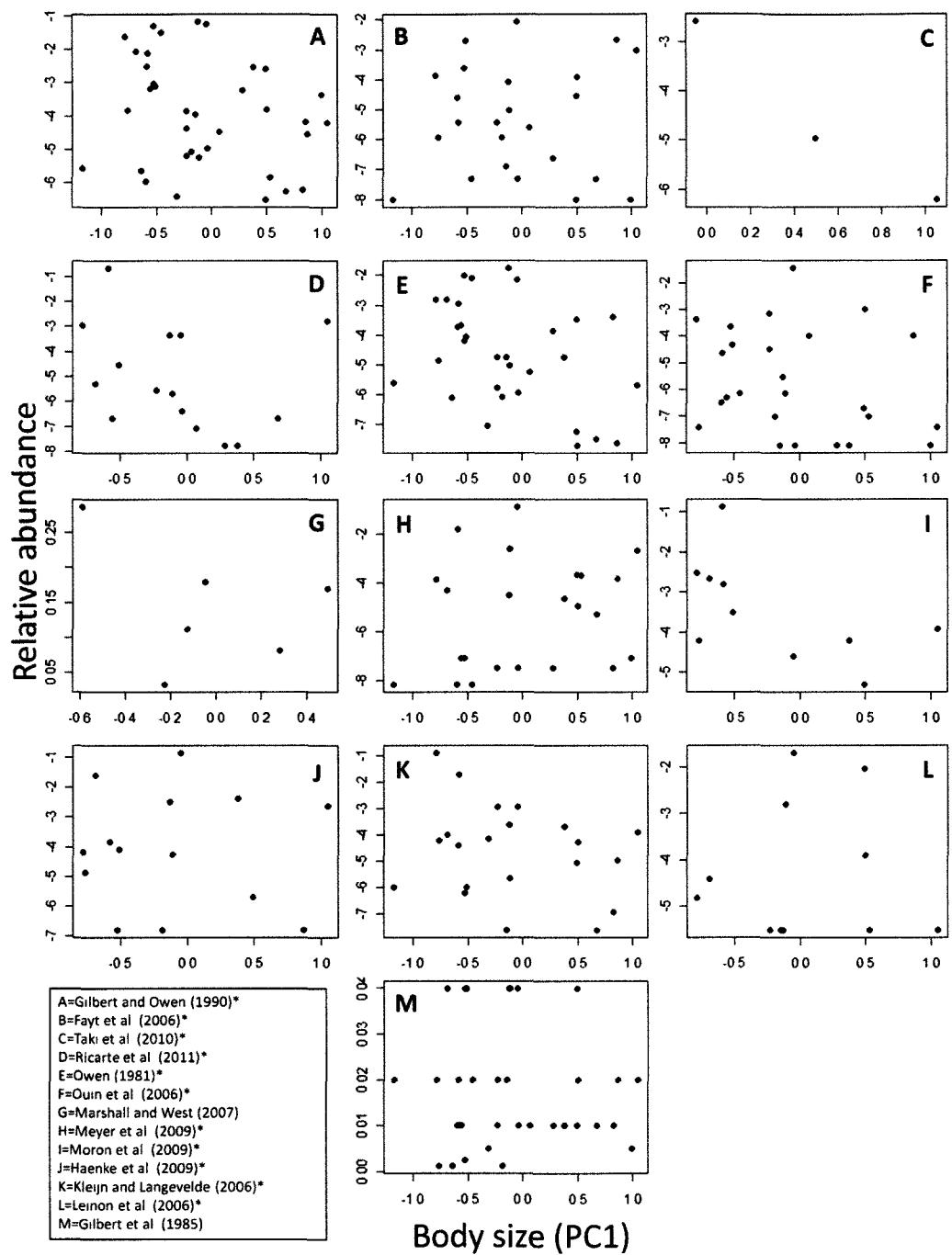
The relative abundances and body size relationships were examined for 13 separate studies (see Table 3.2).

Table 3.2: Relative abundance and body size (PCA) relationship for thirteen studies compared using Pearson correlations (n is the number of species that were present in the (Gilbert and Owen 1990) study). \* used logged relative abundance.

Dataset	n	r	p	t	p
(Leinon et al. 2006)*	11	0.023	0.947	0.467	0.659
(Marshall and West 2007)	6	-0.362	0.480	-1.086	0.377
(Haenke et al. 2009) *	14	0.034	0.895	0.234	0.824
(Kleijn and van Langevelde 2006)*	21	-0.254	0.268	-0.808	0.443
(Meyer et al. 2009)*	24	-0.213	0.319	-0.466	0.652
(Moron et al. 2009)*	10	-0.570	0.086	-0.332	0.758
(Ouin et al. 2006)*	25	-0.247	0.235	0.351	0.733
(Owen 1981)*	32	-0.391	0.030	-1.094	0.297
(Ricarte et al. In press)*	15	-0.272	0.326	<b>-3.190</b>	<b>0.019</b>
(Fayt et al. 2006)*	25	0.036	0.866	0.540	0.602
(Gilbert 1985)	34	-0.066	0.716	0.939	0.366
(Taki et al. 2010)*	3	-0.983	0.118	-2.31	0.471
(Gilbert and Owen 1990)*	34	-0.251	0.140	0.204	0.842

When each of the studies was examined graphically, it became apparent that many relationships needed to be logged. With the exception of Taki et al. 2010 which only had 3 representative species for which we had mimetic fidelity estimates, all of the other studies had a great deal of variation in their data (see Figure 3.5). Thirteen studies were examined for an abundance-mimetic fidelity relationship. A Pearson correlation was conducted for all 13 studies, and there were no significant correlations. GEE's were performed for all 13 studies, and there was only one significant relationship Ricarte et al (in press) between abundance and mimetic fidelity among the 13 studies (Table 3.1). However, after conducting a Bonferroni correction to help control for the high number

of tests, the significant result becomes insignificant. With 10 negative correlations and 3 positive correlations, we cannot reject the null hypothesis that positive and negative correlations arise with equal frequency (sign test,  $P = 0.0923$ ).



**Figure 3.5:** Graphical representation of the relationship between relative abundance and a principal components analysis of body size for each of the eleven studies examined in Table 3.2.

\*relative abundance was logged for these studies

### 3.3.4: Body size vs Mimetic Fidelity

The relationship between body size and mimetic fidelity was examined without (Pearson correlation) and with phylogenetic control (generalized estimating equation-GEE). Each test was conducted to compare body size and mimetic fidelity (both the human rankings and the Mahalanobis distances). Each GEE was based on a phylogenetic tree where all branch lengths equalled 1. The GEE yielded an estimated scale parameter of 1.595 the 16.25 pDF. Since the uncontrolled DF was 32 this highlights the need to control for phylogenetic autocorrelation. There was a highly significant relationship between body size (PCA of body size) and mimetic fidelity (human rankings) both before controlling for phylogeny ( $r=0.680$ ,  $p<0.001$ ) and after controlling for phylogeny ( $t=6.889$ ,  $p<0.001$ ). The relationship between body size and mimetic fidelity based on Mahalanobis distances is significant (and in a consistent direction) before controlling for phylogeny ( $r=0.632$ ,  $p<0.001$ ), and remains significant after controlling for phylogeny ( $t=4.176$ ,  $p<0.001$ ).

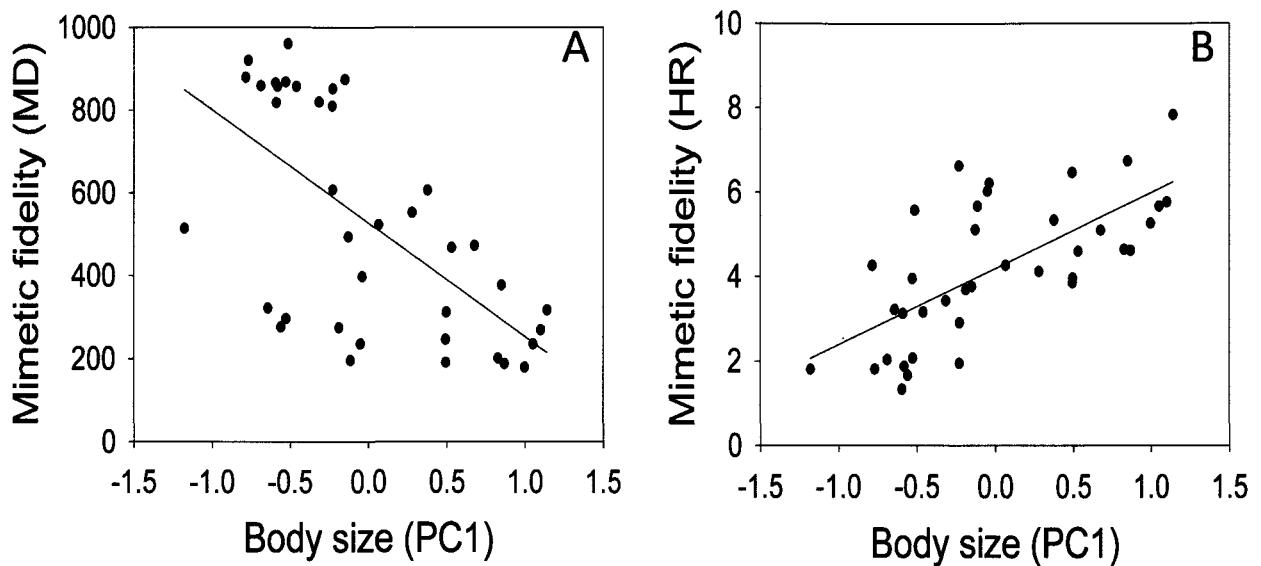


Figure 3.6 – Relationship between body size and (A) human ratings of mimetic fidelity (HR), and (B) objective measures of fidelity based on Mahalanobis distances (MD). Lines show linear regressions, see text for statistics.

### 3.4: Discussion

This chapter of my thesis established four key results: (i) mimetic fidelity is strongly associated with body size, but not with abundance, (ii) there was no relationship between body size and abundance, (iii) mimetic species are readily distinguishable from their models using multivariate methods, and (iv) it seems that the key feature in distinguishing models and mimics is antennae length, which has a role in behavioural mimicry. Each of these findings will now be discussed.

We predicted that there would be a relationship between abundance and mimetic fidelity that was potentially mediated by body size. However, the only significant relationship that was predicted and empirically supported by our results was

the relationship between body size and mimetic fidelity. When examining the relationship between human rankings and the PCA of body size there was a significant positive relationship between body size and mimetic fidelity. Larger syrphids tended to be better mimics, while smaller syrphids tended to be poorer mimics.

Researchers have long stated that there is a relationship between abundance and body size among other taxa (Schmid et al. 2000). As such it has been suggested that this relationship exists in syrphids, in that, as abundance increases body size decreases (common syrphids tend to be small, rare syrphids tend to be big) (Gilbert 2005). However, through empirical examination, we determined that in the set of syrphids investigated, there is no significant relationship between body size and abundance. Similarly, Owen and Gilbert (1990) measured various morphological traits (not body size) and they found that there was no relationship between these features and population density. Our measure of body size was based on a principal component analysis on various body size measures. It should be mentioned however, that the general abundance-body size relationship that has been previously shown in mammals (Damuth 1981; Damuth 1987) has generally been shown by measuring population density (rather than abundance), and mass (Hendriks 2007) as the body size measurement (rather than length measures). Future consideration should be given to examine whether a population density-mass relationship exists in syrphids.

In our analysis of thirteen different data sets (after applying a Bonferroni correction for the high number of tests), there was no relationship between abundance

and mimetic fidelity. More research should be done however, because most of the trap data in Gilbert and Owen (1990) was based on relatively imperfect mimics. Thus, it is possible that some species of syrphids are so rare that they do not appear in any of the tested datasets. The available data may therefore ignore a large portion of the full range of abundance.

Further complicating the issue is that in each of the eleven studies, there were different methods of capturing syrphids, and the syrphids were captured in different habitat types (farmland to wooded areas) in different geographic locations (including Japan, Germany, France, England, Poland, Belgium and the Netherlands) (See Table 3.1). Moreover, it should be noted that Gilbert and Owen (1990) and Gilbert (1981) are not independent of each other. Owen (1981) has the first 8 years of the data set, while Gilbert and Owen (1990) continued the same study and also includes the first eight years of data. Among studies, there were some significant abundance correlations, and some were not (see Table A2 in the Appendix). In the analysis some studies used transects - catching every syrphid encountered along a transect (Haenke et al. 2009; Meyer et al. 2009; Moron et al. 2009), while others used an observer identifying syrphids as they proceeded through the transect in tandem with collecting individuals that they were not able to ID in the field (Kleijn and van Langevelde 2006), emergence traps, free hanging window traps (Fayt et al. 2006) and some of the studies used Malaise traps (Fayt et al. 2006; Gilbert and Owen 1990; Ouin et al. 2006; Owen 1981). Malaise traps have inherent biases in them, and tend to skew the relative abundance. Syrphids that travel farther, (which tend to be larger), are more likely to be captured in a Malaise

trap (Arneberg and Andersen 2003). According to the Arneberg and Andersen, the tendency of researchers to not find a relationship between body size and abundance may be explained by the biases in these common sampling techniques. This causes some concern because many of the studies that were examined, including the main study (Gilbert and Owen 1990), used Malaise traps to obtain a measure of abundance, without accounting for the size bias.

Researchers typically use a subjective ranking system (such as human rankings) for assessing a degree of mimetic fidelity, although Dittrich et al. (1993) used pigeons to obtain (and informally compare with human rankings) for a more objective ranking system. In this study a measure of mimetic fidelity (Mahalanobis distance) was created using objective measurements and multivariate statistics. The Mahalanobis distances were related to human rankings of the same mimics. This confirms the consistency of multivariate measures of mimetic fidelity, indicating that the indices obtained are comparable with human-based assessments.

After conducting the multivariate generalized canonical discriminant analyses (GCDA; see Figure 3.1), it was determined that models and mimics are readily distinguishable from each other, at least in multivariate space. Syrphids look like syrphids and hymenopterans look like hymenopterans. This is not unexpected – despite their coarse similarity the two sets of species derive from very different taxonomic orders.

The multivariate statistics were able to discriminate between a syrphid and a hymenopteran on antenna length alone, and this was the strongest predictor variable (antennae length had longest arrow in the GCDA plots). This fact might be predicted because a major morphological difference between the orders is antennae length. Because of this obvious difference between the orders some syrphids use a leg waving behaviour to enhance their perceived antenna length (see Chapter 2). Likewise, when Bain et al. (2007) “reverse-engineered” the pigeon data from Dittrich et al (1993) to determine which variables were most important in discriminating between hymenopterans and syrphids, antenna length was one of the most important factors. This emphasizes the importance of perceived antennae length on the protection afforded to mimetic syrphids.

A relationship between body size and mimetic fidelity has been supported by the work completed in this chapter, in that as body size increases mimetic fidelity increases. According to the curve of protection hypothesis, protection afforded to a mimic is inversely related to the benefit of correctly choosing a mimic and directly related to the cost of accidentally choosing a model (Sherratt 2002). In order for large mimics (which are more profitable to predators) to be afforded the same amount of protection as a smaller mimic then they may well need to have a higher mimetic fidelity. The pattern of large mimics having a higher mimetic fidelity than small mimics therefore supports the curve of protection hypothesis.

The implications of this finding, along with my behavioural work, will be discussed in the fourth chapter of my thesis.

## Chapter 4:

### Final Discussion

The results of the two previous chapters help us explain why imperfect mimicry has evolved and how it is maintained. I will now re-examine some of the hypotheses put forward in Chapter 1 to explain imperfect mimicry, and evaluate their validity in the light of data presented in Chapters 2 and 3.

*Eye of the Beholder* (Cuthill and Bennett 1993):

The eye of the beholder hypothesis suggests that imperfect mimics only appear perfect to our eyes, whereas to their more common predators such as birds or invertebrates, they are actually near perfect mimics (Cuthill and Bennett 1993). For example, the non-venomous scarlet kingsnake (*Lampropeltis elapsoides*) is considered a Batesian mimic of the coral snake (*Micrurus fulvius*), yet the order of the coloured rings that circle their bodies differ. Using polymer clay replicas, Kikuchi and Pfennig (2010) found that while certain aspects of the phenotype were important in providing protection from predators, the ordering of colors was immaterial and therefore not subject to selection.

The propensity to engage in behavioural mimicry (mock stinging, wing wagging, leg waving) could be unambiguously ascribed to syrphid species and was significantly associated with the human based assessment of perfection of mimicry (Chapter 2). Since the human-based assessment of perfection of mimicry associated with a completely independent set of mimetic traits, this suggests that the human-based

categorization of the perfection of mimicry carries wider significance and is not simply a reflection of human perception, as the “eye of the beholder” hypothesis assumes.

*Dis-equilibrium - Imperfect mimicry as an intermediate stage* (Edmunds 2000):

One explanation given for imperfect mimicry is simply that the imperfect mimics are in a state of dis-equilibrium, in that, they have not yet evolved to be perfect (Edmunds 2000), or they have temporarily evolved away. For example, if a major habitat change brings about a radical change in mimic frequency then there may be a temporary breakdown in mimicry, with a consequential effect for the mimetic phenotype (Azmeh et al. 1998).

If the dis-equilibrium hypothesis was correct, then one would not necessarily expect a consistent relationship between body size and mimetic fidelity as detailed in Chapter 3, unless somehow the smaller species were more likely to be at disequilibrium. One reason for this might be an enhanced local abundance of smaller species due to changes, for example, in farming practice. However data presented in Chapter 3 indicate no consistent relationship between body size and abundance. We therefore find that the dis-equilibrium hypothesis is unlikely as an explanation for the evolution of imperfect mimicry.

*Kin Selection* (Johnstone 2002):

The hypothesis that kin selection may play a part in the evolution and maintenance of imperfect mimicry comes from considering situations under which the

mimetic trait carried by an individual can also affect the reproductive success of relatives who carry the same mimetic trait. In particular, when a mimic is identical to its model then predators should no longer discriminate between mimic and model and so the protection afforded to the mimic is less than a system where the mimic imperfectly resembles a model. Here, despite individual selection for increasing mimetic perfection, inclusive fitness is maximised if individuals maintain imperfect mimicry (Johnstone 2002).

In the case of syrphids, it is highly unlikely that individuals carrying the same sets of mimetic traits remain in close proximity to one another because of their high rates of dispersal and movement. For example, in a study on pollinator movement, it was determined that syrphids had very high rates of dispersal- on average they moved greater distances than hymenopterans or lepidopterans throughout the course of the study (Lysenkov 2009). In flower rich areas, between flower flight is very short (Kevan and Baker 1983), however based on pollen analyses, syrphids have been found to disperse over one to two kilometers in a single day to find adequate resources, oviposition sites or overnight shelter (Schneider 1962). Due to high dispersal of individual syrphids, kin selection is a highly unlikely driving force behind the maintenance of imperfect mimicry in syrphids.

*Jack of all trades/Multi Model* (Edmunds 2000):

The explanation that the jack of all trades hypothesis provides is that a mimic looks imperfect because it resembles two or more models, consequently, it is not a

perfect or near perfect mimic for any of its potential models alone but gains more protection from vaguely resembling multiple models (Edmunds 2000). This hypothesis posits that mimics should more closely resemble the model that they share more time or space with. Based on modelling this hypothesis: when all else is equal, the mimic should resemble the less noxious model, and good mimics should be more common than poor (Edmunds 2000).

This hypothesis can be refuted based on both previous observations, and empirical evidence from the third chapter of my thesis. According to the multi model hypothesis, a mimic resembles more than one model, and therefore gains overlapping protection not afforded to the mimic if it only resembled one model. When plotting phenotypic traits in multivariate space, the multi model mimic should sit near the cluster of models, somewhere near the middle. However, when examining the GCDA it can be seen that none of the mimics sits near the models. Hymenopterans tended to look, and cluster with other hymenopterans, while syrphids tended to look, and cluster with other syrphids, so there is little direct evidence for the multi-model hypothesis. Moreover, my thesis casts doubt on the assertion that good mimics should be less common than poor mimics (Chapter 3).

*Relaxed Selection* (Duncan and Sheppard 1963; Sherratt 2002):

The relaxed selection hypothesis for the evolution and maintenance of imperfect mimicry states that if complete protection is given when a mimic vaguely resembles a model, then there is no further selection to improve it. Hence mimics remain imperfect

simply as a consequence of mutation-selection balance. This hypothesis was originally founded in 1963, and further refined in 2002. While there have been multiple studies **modelling** the curve of protection, Sherratt 2002, for example, however, there have been no studies that have set out to **test** it in the context of Batesian mimicry with empirical evidence.

Both of my data chapters lend support for the relaxed selection hypothesis. In Chapter 3 it was determined that there is a significant positive relationship between body size and mimetic fidelity, in that, as body size increases so does mimetic fidelity. As body size increases, so does profitability (or benefit) of the organism for a predator. This means, that with increasing body size, there is an increased selective pressure towards mimetic fidelity because the cost-benefit ratio becomes lower, making predators more likely to risk sampling a potential mimic. When a model is particularly noxious even imperfect mimics are protected. We see that small mimics are also more likely to be imperfect mimics because there is no further selection to improve their morphological mimicry. It is possible that these small syrphids have low selective pressure in comparison to a syrphid that is three or four times its size, making its curve of protection much larger than that of the bigger syrphids.

Honey bees and bumble bees have been shown to be less noxious than wasps (Mostler 1935). The curve of protection states that with decreasing model noxiousness, there is a greater selective pressure towards perfection (Sherratt 2002). When examining the bee mimics, we find that a greater proportion of them are large with

fairly good rankings of mimetic fidelity, while wasp mimics have a wider range of size and mimetic fidelity (see Table 3.6). The wasp's high level of noxiousness gives the small, imperfect flies protection from predators, with little selection to improve their mimetic fidelity.

In Chapter 2 it was determined that behavioural mimics were also good morphological mimics. The otherwise good morphological mimics used behavioural mimicry as a means to enhance their resemblance to their models. This may indicate that the larger, higher fidelity mimics are under greater selective pressure to enhance their resemblance to their model than their smaller, lower fidelity counterparts due to their increased profitability as a consequence of being large. Also, predator visual acuity (in vertebrate predators at least) may not detect variables such as behavioural mimicry in syrphids that are very small, so there is no selection for behavioural traits in small syrphids. In large, high fidelity syrphids, behavioural mimicry is very important because, as a product of being large, they are more noticeable, and predators can detect differences between them and their models due to scale.

When a human or a pigeon (Bain et al. 2007) attempts to discriminate between a syrphid and one of its models, some variables are more important than others. One of these variables has been found to be extremely important. A GCDA can discriminate between a hymenopteran and a syrphid based on antenna length alone. This means that antenna length is a very important variable, and as a result, selection has acted on syrphids to enhance their resemblance, which has to include an increased antennae

length, or at least the appearance of one. Various syrphids have evolved longer antennae (e.g. *Sphiximorpha* sp, *Ceriana* sp) as a means to enhance their resemblance to wasp models. *Spilomyia* (most) and *Temnostoma* have not evolved longer antennae, but some participate in leg waving behaviour. In fact, all of the leg waving syrphids tested in this study had yellow back legs, and darkened front tibia and tarsi. This darkened frontal tibia likely aides in the resemblance of the legs to a hymenopterans antenna, which as we know is an important discriminating factor.

In conclusion, throughout my thesis we were able to tentatively reject a number of hypotheses that were put forward to explain the evolution and maintenance of imperfect mimicry in the syrphid – hymenopteran system. More importantly, for the first time, direct comparative empirical evidence has been provided to lend support to the relaxed selection hypothesis as the explanation for the persistence of imperfect mimics. A curve of protection is created using the costs of attacking a model (noxiousness) and benefits (profitability) of attacking a mimic. Empirical evidence was found to discount a number of competing hypotheses to explain the evolution and maintenance of imperfect mimicry. More importantly, empirical evidence supporting the curve of protection as the hypothesis that explains imperfect mimicry was found in my two previous chapters.

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**Appendix:**

Table A1: Species list with the number of individuals assayed, their human rankings from Chapter 2 or 3 (if available), their classification as a non-mimetic, good, intermediate, or poor bee or wasp mimic, and whether they were behavioural mimics (LW: Leg wave, WW: wing wag, MS: mock sting)

Species	Number of individuals	Model	Ranking (from Ch 2)	Ranking (from Ch 3)	Classification	Behavioural Mimic?
<i>Allograpta obliqua</i>	7	Wasp	5.65		Int wasp	No
<i>Ceriana abbreviata</i>	1	Wasp	6.7		Good wasp	No
<i>Chalcosyrphus curvaria</i>	5	Wasp	3.83***		Poor wasp	No
<i>Chalcosyrphus libo</i>	1	Wasp	3.83***		Poor wasp	No
<i>Chalcosyrphus piger</i>	3	Wasp	3.83***		Poor wasp	No
<i>Chalcosyrphus plesia</i>	1	Wasp	3.83***		Poor wasp	No
<i>Chalcosyrphus vecors</i>	1	Wasp	3.83***		Poor wasp	No
<i>Cheilosia pontiaca</i>	6	Non mimetic		1.33 *	Non Mimetic	No
<i>Dasybasis venustis</i>	2	Wasp		6.2 *	Good wasp	No
<i>Epistrophe emarginata</i>	13	Wasp	4.97	4.97 *	Int wasp	No
<i>Epistrophe grossulariae</i>	7	Wasp	4.97 *	4.97 *	Int wasp	No
<i>Eristalis anthophorina</i>	2	Bumble bee?			Int Bee	No
<i>Eristalis arbustorum</i>	17	Bumble bee	5.68		Int Bee	No
<i>Eristalis dimidiata</i>	1	Bee?			Int Bee	No
<i>Eristalis flavipes</i>	11	Bumble bee	4.3		Int Bee	No
<i>Eristalis stipator</i>	1	Bee?			Int Bee	No
<i>Eristalis tenax</i>	12	Honey bee		5.67	Int Bee	No
<i>Eristalis transversa</i>	7	Bumble bee	8.03		Good Bee	No
<i>Eupeodes latifasciatus</i>	4	Wasp			Int wasp	No
<i>Eupeodes sp</i>	7	Wasp			Int wasp	No
<i>Eupeodes volucris</i>	5	Wasp	5.4		Int wasp	No

<i>Helophilus fasciatus</i>	3	Wasp	4.93		Int wasp	No
<i>Lejops sp</i>	3	Wasp	4.17		Int wasp	No
<i>Mallota bautias</i>	1	Bumble bee	7.76*		Good Bee	No
<i>Mallota posticata</i>	4	Bumble bee	7.76		Good Bee	No
<i>Melangyna sp</i>	1	Wasp			Poor wasp	No
<i>Melangyna umbellatarum</i>	2	Wasp			Poor wasp	No
<i>Melanostoma mellinum</i>	4	Wasp	4.33	4.11	Int wasp	No
<i>Parhelophilus sp</i>	6	Wasp			Int wasp	No
<i>Platycheirus confusus</i>	1	Wasp		2.98**	Poor wasp	No
<i>Platycheirus hyperboreus</i>	1	Wasp		2.98**	Poor wasp	No
<i>Platycheirus nearcticus</i>	2	Wasp		2.98**	Poor wasp	No
<i>Platycheirus obscurus</i>	16	Wasp	3.9	2.98**	Poor wasp	No
<i>Platycheirus sp</i>	9	Wasp		2.98**	Poor wasp	No
<i>Rhingia nasica</i>	1	Non mimetic		1.95	Non mimetic	No
<i>Sericomyia chrysotoxoides</i>	7	Bumble bee	4.83		Int bee	No
<i>Sericomyia lata</i>	1	Wasp	4.87		Int wasp	No
<i>Sericomyia militaris</i>	2	Bumble bee	5.14		Int bee	No
<i>Sphaerophoria contigua</i>	1	Wasp	5.09**		Int wasp	No
<i>Sphaerophoria novaeangliae</i>	3	Wasp	4.67		Int wasp	No
<i>Sphaerophoria philanthus</i>	7	Wasp	5.51		Int wasp	No
<i>Sphaerophoria sp</i>	11	Wasp	4.67*		Int wasp	No
<i>Spilomyia fusca</i>	2	Wasp (Bald faced hornet)	4.24***		Good wasp	Yes – LW, WW, MS

<i>Spilomyia longicornis</i>	16	Wasp	8.1		Good wasp	Yes – LW, WW, MS
<i>Spilomyia sayi</i>	13	Wasp	7.14	5.76***	Good wasp	Yes – WW, MS
<i>Syritta pipiens</i>	16	Wasp	4.67	2.04	Int wasp	No
<i>Syrphus knabi</i>	1	Wasp			Good wasp	No
<i>Syrphus rectus</i>	4	Wasp	6.14		Good Wasp	No
<i>Syrphus ribesii</i>	26	Wasp	6.8	6.46	Good wasp	No
<i>Syrphus sp</i>	18	Wasp			Good Wasp	No
<i>Syrphus vitripennis</i>	10	Wasp		5.67	Int wasp	No
<i>Temnostoma alternans</i>	7	Wasp	6.4	6.74	Good wasp	Yes – LW, WW, MS
<i>Temnostoma barberi</i>	4	Wasp	5.27		Int wasp	Yes – LW, WW, MS
<i>Temnostoma obscurum</i>	1	Wasp	5.27*		Int wasp	Yes – LW, WW, MS
<i>Toxomerus geminatus</i>	22	Wasp	4.33*		Int wasp	No
<i>Toxomerus magnatus</i>	9	Wasp	4.33		Int wasp	No
<i>Tropidia quadrata</i>	2	Wasp			Int wasp	No
<i>Volucella bombylans</i>	6	Bumble bee	8.3		Good Bee	No
<i>Xylotta sp</i>	2	Wasp			Int wasp	No

\* ranking was for same genus but different species

\*\* Is an average of the species rankings in the genus

\*\*\* this experiment did not include likely models of these species.

**Table A2: Pearson correlation values among the 13 studies used in the abundance analyses. Bold indicates p<0.05.**

	MW	H	KL	Me	Mo	Ou	Ow	R	F	G	T	GO
L	-0.162	0.538	-0.102	<b>0.599</b>	-0.459	<b>0.699</b>	0.165	-0.204	<b>0.526</b>	0.323	0.801	0.382
MW		0.458	-0.274	0.467	<b>0.998</b>	0.150	0.026	<b>0.907</b>	0.142	0.175	0.628	0.202
H			-0.060	<b>0.867</b>	-0.096	<b>0.949</b>	0.422	0.125	<b>0.772</b>	0.385	<b>0.981</b>	0.451
KL				<b>0.534</b>	0.070	0.153	0.262	-0.011	-0.015	0.045	0.933	0.353
Me					0.247	<b>0.849</b>	<b>0.391</b>	0.363	<b>0.667</b>	<b>0.455</b>	<b>0.969</b>	<b>0.459</b>
Mo						-0.086	0.114	<b>0.977</b>	-0.232	0.091	-0.249	-0.016
Ou							<b>0.380</b>	0.010	<b>0.605</b>	<b>0.339</b>	<b>0.980</b>	<b>0.464</b>
Ow								0.083	0.268	<b>0.682</b>	<b>0.960</b>	0.938
R									-0.006	0.154	0.147	0.116
F										<b>0.431</b>	<b>0.900</b>	0.380
G											0.643	<b>0.623</b>
T												0.993

L=Leinon et al. 2006, MW=Marshall & West, 2007, H=Haenke et al., 2009, KL=Kleijn & van Langevelde, 2006, Me=Meyer et al., 2009, Mo=Moron et al., 2009, Ou=Ouin et al., 2006, Ow=Owen, 1981, R=Ricarte et al. 2011, F=Fayt et al., 2006, G=Gilbert et al., 1985, T=Taki et al., 2010, GO= Gilbert & Owen, 1990.

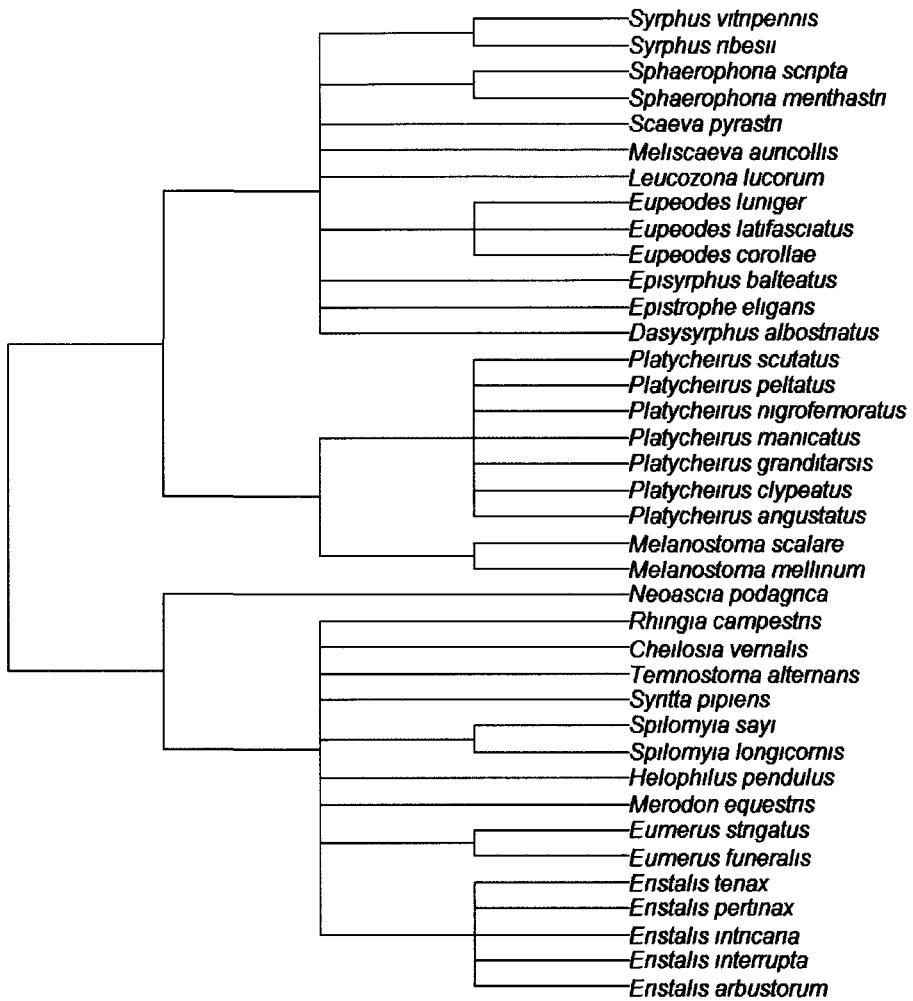


Figure A1: Resulting gene tree based on subfamily, tribe, genus, subgenus, species relationships. All branch lengths were 1, as no genetic information was included to create the phylogeny.