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Mimicry and the hoverflies

By Salma Azmeh, BSc (Hons)

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Abstract

Hoverflies (Diptera: Syrphidae) vary widely in their mimetic associations, comprising wasp-mimetic, bee-mimetic and non-mimetic species. Social wasp mimics are dominated by 'imperfect mimics' which outnumber their supposed models (Hymenoptera: Vespidae) by large factors. The purpose of this thesis is to determine to what degree Batesian mimicry can account for these paradoxes, and to test alternative hypotheses for the evolution of the yellow-and-black patterns.

There is little evidence of an effect of wasp abundance on 'imperfect mimic' abundance across 23 years of trapping data, as predicted if mimics are protected from predators through their resemblance to wasps. The seasonal asynchrony and high abundance of 'imperfect mimics' relative to their models is also notable, as well as the possible significance of wasp predation on hoverflies.

Predictions concerning the function of the colour patterns of 'imperfect mimics' are tested using the association between similarity to the model and flight agility (indirectly measured assuming a trade-off between reproductive potential and flight agility). There is no strong indication that mimetic protection is the primary function of the colour patterns, but the evidence concurs with an aposematic function, signalling to predators the unprofitability of attempting capture. These conclusions are tentatively supported by direct measures of flight agility, though the small differences among species are difficult to pick up. The data on reproductive morphology of hoverflies show considerable variation across species, especially in males. The existence of giant testes in

some species suggests that methods of dealing with sperm competition in hoverflies are diverse and deserve further study.

The high ratio of 'imperfect mimics' to both models and good wasp mimics is also partly explained by habitat disturbance; undisturbed habitats show significantly less 'imperfect mimics' as a proportion of the hoverfly population. Current relative abundance in the UK may therefore be very different to when the colour patterns evolved.

Chapter One

General review of mimicry with reference to hoverflies

1.1 Introduction

Hoverflies (Diptera: Syrphidae) are a common sight in the UK during the spring and summer months. There are around 250 species in Britain, and, while their larvae vary widely in their feeding habits (see Rotheray 1993), adult flies feed on nectar and pollen. Hoverflies are most noted for two aspects of their biology, namely their colour patterns and their flight agility. This thesis focuses on the colour patterns of hoverflies. Though many species are black in appearance, these are rarer than the more conspicuous varieties. In particular, many species are known as mimics of Hymenoptera. For example, *Volucella bombylans* successfully mimics various species of bumblebee (*Bombus*) through different colour morphs, and the common *Eristalis* species are accomplished mimics of honeybees (*Apis* spp). High-fidelity mimics of wasps also exist; for example, *Temnostoma* and *Spilomyia* species are similar in body shape, size and abdominal patterns to *Vespula* social wasps, and use their black front legs to wave in front of their heads to mimic the dark antennae of the hymenopteran (e.g. Waldbauer 1970). There seems little doubt that such species are mimicking wasps. However, the majority of yellow-and-black hoverflies in the UK are not such good mimics; indeed 'perfect mimics' are extremely rarely collected. Common species such as *Episyrphus balteatus*, *Syrphus ribesii*, *Epistrophe* spp, *Melanostoma* spp, *Sphaerophoria* spp and many others, while possessing yellow

or orange bands on the abdomen, could by no means be described as perfect mimics, at least to human eyes. Other, more accomplished mimics of wasps are found in Britain (such as *Chrysotoxum* species, with their darkened and elongated antennae), but are much rarer than the afore-mentioned species. Furthermore, the ‘poor mimics’ outnumber their putative models by far, which makes it difficult to understand how their colour patterns can persist. This thesis aims to examine these paradoxes and attempt to clarify whether hoverflies are mimicking wasps and whether other factors have contributed to the evolution of their colour patterns.

Mimicry is a well-studied and widely-taught field. It is an attractive topic because of its simplicity yet ingenuity, and because it clearly illustrates what can be achieved by natural selection. Furthermore, mimicry has relevance to many and diverse biological fields such as animal behaviour, population genetics, ecological chemistry, polymorphism, origins of biodiversity, adaptive landscapes, community patterns, resource allocation, flight mechanics, the genetics of adaptation, arms races and evolutionary history. Mimicry is also considered a likely route to speciation, as the fixing of local colour morphs may cause reproductive isolation.

Hugh Bates, a naturalist of the 19th century, was the first to publish adaptive explanations of how mimicry could have evolved between species, by the classical type of mimicry which bears his name (Bates 1862). Batesian mimicry was based on Bates’ observations of butterfly species in Amazonia. He noted that the family Heliconidae was very abundant, and showed ‘every sign of

flourishing existence, although of slow flight, feeble structure, unfurnished apparent means of defence, and living in places which are incessantly haunted by swarms of insectivorous birds'. Furthermore, he said 'I never saw the flocks of slow-flying *Heliconidae* in the woods persecuted by birds or Dragonflies, to which they would have been easy prey; nor, when at rest on leaves, did they appear to be molested by lizards or the predacious Flies of the family *Asilidae*, which were very often seen pouncing on Butterflies of other families'. Bates put this 'immunity from persecution' down to unpalatability, since some genera had glands near the anus which protruded when the butterflies were roughly handled, and produced a peculiar smell.

The family Pieridae, in contrast, were 'much persecuted by predators'. Some rare Pierid species, however, mimicked the unpalatable *Heliconidae* (e.g. *Leptalis theonoë* mimicked *Ithomia flora*). These showed a 'minute and palpably intentional likeness which is perfectly staggering', and Bates was 'never able to distinguish the *Leptalides* from the species they imitated, although they belong to a family totally different in structure and metamorphosis from the *Heliconidae*, without examining them closely after capture.' He believed that this was a protective adaptation on the part of the *Leptalides*, a 'most beautiful proof of the truth of the theory of natural selection'. This remains the basis of Batesian mimicry; Bates even also mentioned polymorphism, sympatry and frequency-dependence as aspects of the effectiveness of such mimicry, still considered relevant and much debated today. He also mentioned that unpalatable species sometimes imitated each other; Müller (1879) later expanded on this idea. In

Müllerian mimicry, the advantage is to share the costs of predator education between species.

Mimicry has remained a topic of interest for evolutionary biologists (amongst others) over the years, because it has proved to be one of the most attractive examples of the theory of evolution by natural selection (Darwin 1859). Darwin himself was a supporter of Bates' theories, because they demonstrated natural selection so well. Batesian mimicry showed how two unrelated species could co-evolve a trait; this was a fine example of how selection pressure (here, the risk of being eaten by predators) could directly influence the evolution of a very visible trait. Mimicry further increased its status as a paradigm of evolution by natural selection upon being allocated a chapter in Fisher's (1930) classic text 'The genetical theory of natural selection'. Fisher called mimicry 'the greatest post-Darwinian application of Natural Selection'. The chapter formalised 'classic' mimicry theory, and described many of the factors that influence the success of mimicry.

Since then, a vast literature on mimicry and associated topics has accumulated. Despite this, rather little is known about the effectiveness of mimicry as a protection mechanism in nature. Most work has been limited to theoretical discussions, mathematical models and experiments in artificial conditions. This is not to say that these have not been useful; many of the factors influencing mimicry have been well investigated, and some of this work will be summarised in this introductory chapter. However, experiments in artificial conditions are limited by the uncertainty of their relevance to real life. For

example, typically only one type of predator is used, and prey may be presented under unnatural conditions, though many authors now try to consider these factors. Also, such experiments can typically only alter one or a few factors (e.g. prey abundance, noxiousness) and look at their influence. There is certainly no all-embracing theory that could predict the effectiveness of mimicry in nature given certain conditions.

The lack of field studies is due mostly to the difficulty of observing predator behaviour in the field consistently over time, including the choices predators make about prey. Nevertheless, some field studies have been undertaken. For example, release-recapture methods developed by Brower *et al* (1964) compared predation rates on mimetic and non-mimetic prey. The diurnal moth *Callosamia promethea* was painted to mimic unpalatable butterflies (*Parides* spp). Though there was some indication that mimics were protected, the results, together with further studies (Brower *et al* 1967; Cook *et al* 1969) proved inconclusive, and lacked proper controls (Waldbauer & Sternburg 1976; Waldbauer 1988). In a similar series of experiments, using the same moths (Sternburg *et al* 1977; Jeffords *et al* 1979), they were painted either black (similar to their natural colouration, and that of the toxic pipevine swallowtail butterfly *Battus philenor*), with an orange pattern (like that of the toxic monarch *Danaus plexippus*), or with a yellow pattern (like the palatable tiger swallowtail *Papilio glaucus*). This controlled for a possible increase in predation rate due to conspicuousness alone, since both a palatable and an unpalatable conspicuous species were used. A greater proportion of black and orange moths were

recaptured relative to yellow moths, indicating a protective effect of the mimicry of toxic butterflies, independent of the effects of conspicuousness. Furthermore, daily trapping showed that black and orange individuals survived longer than yellow ones, and examination of wing injuries in recaptured moths showed that yellow-painted moths were attacked the most.

This field study went some way to showing that mimicry can be effective in reducing predation in nature, but many more are needed. It also falls short of exploring the subtle interactions between the many factors that influence the efficacy of mimicry. Though these have been well described theoretically and in the laboratory, there is a lack of concordance on many issues (as described in the rest of this chapter). Novel approaches are now being used to fill these gaps, taking into account real predator and prey behaviour.

This introductory chapter, while inevitably not completely comprehensive, attempts to summarise the major conclusions reached so far in the study of mimicry. These include identifying important factors for mimetic success (for example abundance of models and mimics and the closeness of resemblance of the model and mimic). I also summarise other major topics of debate in the mimicry literature, even when not directly connected to the problem addressed in this thesis, for example the evolution of aposematism and the distinction between Batesian and Müllerian mimicry. I do not include some older 'hot' topics, such as the distinction between crypsis and mimicry.

I will also describe how hoverflies, especially wasp-mimicking hoverflies, do not fit with the expectations of Batesian mimicry. Specifically, they outnumber

their models by far (see 1.3.3). In theory, if mimics are much more common than models, predators will encounter them more often and thus learn that the colours do not signify noxiousness. Furthermore, the colour patterns of wasp-mimicking species common in the UK are far from perfect, unlike those of bee-mimicking hoverflies. If they are wasp mimics, it is unclear why they have not evolved more perfect mimicry.

The introduction is split into parts as follows, with each section including its relevance to the paradoxes of mimicry in hoverflies. 1.2 deals with aposematism, how it evolved, and whether it can exist for traits other than unpalatability. 1.3 concentrates on abundance, specifically model:mimic ratios and sympatry. Part 1.4 deals with mimetic colour patterns, how they might have evolved, and possible explanations for imperfect mimicry. It also includes a section on polymorphism and unexpected diversity in mimetic patterns. 1.5 discusses issues loosely involving levels of unpalatability and unprofitability, such as automimicry, the palatability spectrum and, importantly, the relationship between flight morphology and unprofitability. Finally, section 1.6 briefly recaps on the questions raised by mimicry in hoverflies, and refers to the possible explanations discussed in previous sections.

1.2 Aposematism

1.2.1 The evolution of aposematism

As early as 1871, Charles Darwin proposed that ‘the most gaudy colours’ would result in ‘the most easily recognised individuals’. The idea of aposematism is that prey with these gaudy colours advertise their unprofitable status to predators. Aposematism is a common form of defence against predators, especially in insects, and is widely cited as the reason for bright coloration. It is considered an alternative defence strategy to crypsis, where prey rely on their ability to avoid notice (see 1.5.4 for characters associated with these 2 strategies).

A principle of aposematism is that bright colours make more efficient signals than dull ones (Wallace 1867, 1878; Guilford 1986; Roper & Redston 1987). Much evidence that this is true is anecdotal, and colours can be present for other reasons (Guilford 1986), such as thermoregulation (e.g. Roland 1982) and intersexual recognition (e.g. Silberglied 1984; Lederhouse & Scriber 1996). Nevertheless, birds do associate noxiousness with conspicuous prey more easily than with cryptic prey (Gibson 1980; Gittleman & Harvey 1980; Järvi *et al* 1981; Roper & Redston 1987; Mappes & Alatalo 1997b). Furthermore, most unpalatable butterfly species (the best-studied group) are brightly coloured, or if subdued have bright streaks on their bodies (Mallet & Singer 1987). In addition, their wings have conspicuous undersides, so their advertising patterns are not hidden at rest. This is in contrast to palatable butterflies, whose wings are usually cryptic on their undersides (Chai 1986, 1996). The existence of widespread

mimicry of conspicuous patterns (by both palatable and unpalatable prey) also suggests that predators avoid colourful prey.

Aposematism is often used in a broad sense, but it is comprised of two distinct parts (see Harvey & Paxton 1981): conspicuous coloration and unpalatability (or unprofitability, see 1.2.3). The evolution of the two (Harvey & Paxton 1981; Guilford 1990a) are often confused in the literature, and may evolve quite separately. How ‘conspicuous coloration’ is defined is also not always clear; it involves hue, colour intensity, and the contrast with the background. Contrast is certainly important sometimes (Gittleman *et al* 1980), but some hues also seem more easily recognised than others (Guilford 1990b; Mappes & Alatalo 1997a), notably reds, oranges and yellows (see section 1.4.3.3).

There is a paradox in imagining the evolution of warning signals. Novel conspicuous mutants have increased detectability to predators compared with cryptic prey (Benson 1972; Endler 1988, 1991; Turner & Mallet 1996), but their colours offer no protection as yet (e.g. Fisher 1930; Endler 1991; for mathematical explanation, see Mallet & Singer 1987). The adaptive trough must be crossed between two high fitness peaks of crypsis and aposematism (Sheppard 1962; Wright 1977; Turner 1984b). Somehow, the novel mutants’ frequency must increase to above a critical level where the protection given by the model confers greater fitness than that conferred by the original pattern. Explanations for this have traditionally fallen into two categories; group selection and individual selection. Recently, combinations of the two have come to the fore. The following

arguments are based on unpalatability, but warning colouration may also signal other forms of unprofitability (Baker & Parker 1979, see 1.2.3).

Proponents of group selection believe that population structure can increase a novel mutant's frequency (Uyenoyama & Feldman 1980). Traditional group selectionist explanations for the evolution of aposematism invoke kin selection (Wilson 1975; Uyenoyama & Feldman 1980). The evolution of distastefulness and warning colouration were often not considered separately at this stage. Fisher (1930) noted that some aposematic species had gregarious larvae. He proposed that if related larvae share a novel colour phenotype, predators could learn to associate this phenotype with distastefulness by sampling and killing some of the larvae. The surviving larvae would be avoided, and reproduce with a selective advantage. There does seem to be a relationship between gregariousness (or aggregation) and aposematism (Edmunds 1974; Harvey *et al* 1982, 1983). Where the two do not co-exist, it is possible that kin structures have changed since the evolution of aposematism. Several authors (e.g. Wilson 1975, Pianka 1978, Futuyama 1979) held 'that the occurrence of aposematic animals can only be understood in the light of kin selection, and constitutes evidence for the importance of kin selection *per se*' (Järvi *et al* 1981).

If aposematism does evolve by kin selection, closely related groups of prey must live within a predator's territory (Mallet & Singer 1987). Some caterpillar larvae (e.g. Fisher 1930; Harvey *et al* 1982) and asexual aphids (Malcolm 1986) are examples of prey living gregariously in this way. However, unpalatable species benefit more from aggregation anyway, to facilitate predator

learning (Turner 1984b). Also, many brightly coloured unpalatable butterfly species are highly dispersive (see Mallet & Singer 1987), which disputes the idea. Aggregation could also have led to the evolution of aposematism without invoking kin selection (Guilford 1988; Sillén-Tullberg 1988; Mappes & Alatalo 1997b) (see later for more on ‘green beard’ (Dawkins 1976) or ‘synergistic’ selection).

Other evidence suggests that aposematism can evolve by individual selection under some conditions (Järvi *et al* 1981; Wiklund & Järvi 1982). Predators sometimes leave aposematic prey unharmed after sampling them (Poulton 1890; Edmunds 1974; Järvi *et al* 1981; Wiklund & Järvi 1982; Sillén-Tullberg 1985; Engen *et al* 1986; Chai 1996, but see Pinheiro 1996). If aposematic prey can survive solitarily, it may be possible for aposematism to evolve by individual selection. Furthermore, phylogenetic data suggest that distastefulness and warning colouration evolved before gregariousness in some butterfly species (Sillén-Tullberg 1988).

The individual selection of warning colouration could operate by the evolution of an extreme version of an old wild type pattern (a ‘supernormal sign stimulus’) (Tinbergen 1951), accentuating or enlarging the wild type markings. Alternatively, one can imagine the patterns evolving from crypsis by gradual change, such that initially the colouration was not too conspicuous (Endler 1991; Mallet & Singer 1987; Lindström *et al* 1999). This has been modelled (Yachi & Higashi 1998) as a ‘peak-shift effect’ (Hanson 1959; Leimar & Tuomi 1998). In this model, predators learn to avoid a weak signal, which is subsequently

exaggerated. However, attempts so far to confirm this empirically show that the difference in predation level between a cryptic signal and a weakly conspicuous one are not enough for avoidance learning (Lindström *et al* 1999).

It is possible that warning colouration evolved, by whatever means, before unpalatability. Individual selection for distastefulness could then operate by preadaptation of colours for other reasons (e.g. sexual selection (Turner 1978), or to trick predators (e.g. Poulton 1890; Wickler 1968). If the species then becomes unprofitable to predators (e.g. through a switch of host plant), the predator could use the signals in a different way (Huheey 1961; Mallet & Singer 1987). Alternatively, distastefulness may sometimes evolve before warning colouration. Avoidance learning of the signal by predators would thus be facilitated by the immediate negative reinforcement of unpalatability.

Aggregation of similarly coloured prey may aid the evolution of aposematism. However, it is the sharing of a phenotype, not kin itself, which helps the predator learn that a group of prey is aposematic (Guilford 1988). Related individuals are likely to share a phenotype. However, phenotypes can also be shared between non-related individuals or even species. Therefore, given that it already exists in a population, warning colouration could evolve without being considered novel. Kin selection may have originally favoured warning signals via aggregation of prey, but thereafter predators are no longer 'evolutionarily naïve' about the association of particular colour patterns with distastefulness. Hence even solitary species could form Müllerian mimicry complexes with aposematic prey and thus evolve aposematism themselves (Maynard-Smith 1989; Guilford

1990a,b; Alatalo & Mappes 1996). This is known as ‘synergistic selection’ (an example of ‘green beard’ selection (Dawkins 1976)). The adaptive trough is crossed, because pre-existing avoidance accompanies novel forms that happen to be the same as existing warningly-coloured prey. This is also an advantage to the established aposematic prey, since they will be better protected the more unprofitable prey share the pattern (see 1.3.1). (If a palatable prey evolves the same pattern, as in Batesian mimicry, this is not an advantage to the model.)

Synergistic selection has been modelled mathematically (Alatalo & Mappes 1996). Furthermore, evidence that gregariousness enhances discriminative aversion learning in distasteful prey (Gagliardo & Guilford 1993; Alatalo & Mappes 1996; Mappes & Alatalo 1997b) lends credence to the idea that warning colouration originally evolved by kin selection. Novel prey items using known signals are avoided more than novel signals by great tit predators, using either yellow-and-black patterns or a ‘novel world’ of signals (Alatalo & Mappes 1996; Mappes & Alatalo 1997a,b).

1.2.2 Are hoverflies distasteful?

Hoverflies are generally considered palatable and harmless. However, one explanation for their imperfect mimicry of wasps (see 1.4.2.1) could be that they are distasteful and therefore aposematic. In this case, hoverflies would be Müllerian mimics of each other, rather than Batesian mimics of wasps, and hence their abundance relative to their supposed wasp models would also be explained. However, hoverflies do form a regular and substantial part of the diet of various

avian predators (Grewcock 1992), as shown by examination of their stomach contents and faecal samples (e.g. McAtee 1932; Henry 1977; Kozena 1979; Krištín 1994). In addition, birds and amphibians have consumed hoverflies without apparent harm in experiments (e.g. Brower 1960; Brower & Brower 1962; Evans & Waldbauer 1982; Dlusski 1984). This does not prove that all hoverflies are palatable; there may be variation within species in palatability, for example between areas, as in monarch butterflies (Brower *et al* 1970, 1978; Brower 1984). However, hoverflies are certainly not ubiquitously rejected from the diet of predators, and there is variation between predators in tolerance to distastefulness (see 1.4.3.2).

On occasion, behaviours associated with distastefulness have been noted in predators. For example, Pocock (1911) observed that a thrush displayed bill-wiping behaviour upon rejection of *Volucella bombylans*. However, such behaviours could be interpreted as a reaction to novelty rather than distastefulness. The most convincing evidence to date for unpalatability in hoverflies is for a small yellow-and-black striped species common in South Africa, *Ischiodon aegyptius* (Malcolm 1976). Malcolm found that if the larvae of *I.aegyptius* were reared on aphids that had in turn been reared on milkweeds (*Asclepias* spp), they survived, while larvae of *Metasyrphus (Eupeodes)* hoverflies died. Milkweeds are well known for containing toxic cardiac glycosides, and are the basis for the well-studied aposematism in monarch butterflies (see Brower 1984). Furthermore, adult *I.aegyptius* fed on these aphids contained four types of cardiac glycoside-like chemicals, and extracts of their

bodies had an adverse effect on the heart activity of two vertebrate species (*Xenopus* and *Chamaeleo* spp.). Since *I.aegyptius* voids its stomach contents at pupation, it appeared to be sequestering these chemicals from the milkweeds, via aphids, for its own defence, and thus seemed to be aposematic. However, doubt is cast on this conclusion by the fact that *I.aegyptius* raised on aphids which did not feed on milkweeds contained the same cardiac glycosides. Furthermore, the results could not be reproduced by the same author (Malcolm 1981, 1992), and he declared the hypothesis falsified. Nevertheless, it is possible that localised populations of *I.aegyptius* are somehow synthesising their own toxic chemicals. As yet, no further evidence of this has been produced.

Milkweeds do not grow in the UK and thus could not form the basis for aposematism in hoverflies here. Grewcock (1992) suggests that umbellifers are a possible candidate for the role in Britain, since they are commonly infested by aphids and hoverflies, and contain alkaloids and furanocoumarins, two types of toxic compound. Furthermore, furanocoumarins are found at higher levels in umbellifers of open ground, where aphidophagous hoverfly species tend to feed, compared with in woodland (Berenbaum 1981). It therefore seems possible that 'poor' mimics, which are often aphidophagous, are in fact aposematic, while good mimics, which are often woodland dwelling, are true mimics. Grewcock (1992) points out, however, that some furanocoumarins inhibit the growth of insects, and, while some hoverflies may be able to overcome this, it is likely to be a specialised, rather than a ubiquitous, skill. There is also some doubt over whether

the furanocoumarins are found in the phloem of the umbellifers, from where aphids usually feed (Camm *et al* 1976).

Umbellifers and furanocoumarins are not the only possible candidates for a pathway to hoverfly distastefulness, especially if they can somehow synthesise toxic chemicals themselves. Further biochemical analyses of hoverflies would be enlightening. However, at present there is little evidence that hoverflies are unpalatable, and this does not seem the most likely explanation for their colour patterns.

1.2.3 Aposematism for other types of unprofitability

1.2.3.1 Examples of aposematism not for distastefulness

Warning colouration is generally associated with unpalatability, but there are other types of unprofitability (Van Someren & Jackson 1959; Baker & Parker 1979; Gibson 1974, 1980; Mallet & Singer 1987; Pinheiro 1996). One common example is the yellow-and-black patterns of wasps, which advertise a noxious sting. There seems little doubt that their conspicuousness is associated with their noxiousness. Other types of unprofitability that may be advertised are urticating hairs, sticky exudates, hard or spiny integuments, impenetrable cases and escaping ability (Rettenmeyer 1970). In the case of prey with good escaping ability, the signal would indicate to the predator that it would be a waste of resources to spend time and energy trying to capture them.

There are several cases which have been interpreted as prey advertising that they are hard to catch (see below). Furthermore, in some cases there is mimicry of these unprofitable prey ('evasive mimicry' or 'locomotor mimicry' (Gibson 1974, 1980; Srygley 1994,1999) see 1.5.4.3). For example, some butterflies (e.g. in the *Adelpha-Doxocopa* complex (Nymphalidae) have warning colouration, but are palatable (Aiello 1984; Chai 1986; Pinheiro 1996). Some of these butterflies are particularly agile flyers (Aiello 1984; Pinheiro 1996). Furthermore, different palatable butterflies in the group have converged closely in their flight patterns, suggesting that this is a Müllerian mimicry group for escaping ability alone (Srygley 1994,1999; Pinheiro 1996, but see Brower 1995).

Flea-beetles (Alticinae: Chrysomelidae) (Lindroth 1971) and aposematic forms of the meadow spittlebug *Philaemus spumarius* (Thompson 1973) also have an effective escape mechanism, jumping, and are palatable to bird predators. Palatable *Lebia* ground beetles (Coleoptera: Caribidae) appear to mimic flea-beetles' colouration, with no ability of their own to jump. Lindroth (1971) suggested that an efficient escape mechanism could be just as effective as distastefulness in affording protection from predators. Escape could give protection by frustrating predators' efforts, wasting their time and energy, in a form of 'frustration learning' which can be as effective as pain learning (such as distastefulness) (Sutherland & Macintosh 1971; Gibson 1974,1980). Frustration learning has been shown to work in practice, as both seed-eating and insectivorous birds can be taught to avoid artificial prey that suddenly disappear before they can be eaten (Gibson 1974,1980).

Brower (1995) raises several objections to the idea that there can be mimicry in palatable but unprofitable prey (but see Srygley 1999), and also doubts the existence of aposematism for escaping ability, pointing out that many of the examples cited here have not been properly tested for unpalatability. However, the best-described example of advertising escape ability is in *Morpho* butterflies; here, there seems little doubt that this strategy is used. While some species are cryptic in colouration (e.g. *M.granadensis polybaptus* and *M.peleides limpida*), sympatric *Morpho* species are bright blue (e.g. *M.amathante*, *M.crypsis*) (Young 1971). *Morpho* species are palatable (Chai 1986, 1996), but *M.amathante* and *M.crypsis* use a conspicuous display of their colouration through their flight pattern, like unpalatable butterflies (Young 1971) (see 1.5.4). They are also hard to catch, with a high recapture rate and few signs of injury compared to cryptic species in release-recapture studies (Young 1971). Two other bright *Morpho* species (*M.achilles* and *M.menelaus*) were almost uncatchable by tyrant-flycatchers in a caged situation (Pineiro 1996), and were among few species to ever be sight-rejected by the birds. This indicates that birds can indeed learn to avoid species that advertise their escaping ability.

1.2.3.2 Are hoverflies advertising their unprofitability?

If hoverflies were advertising their unprofitability, as described in the previous section, this could help explain their appearance. They would have no particular reason to mimic wasps accurately if the function of their colour patterns was not mimicry. Hoverflies are noted for their agile flight, so it seems

conceivable that this is something they advertise. Predators would be warned that hoverflies were of very low profitability, and the resources necessary to chase such an agile flyer could be better spent elsewhere. The quick, darting flight of poor wasp mimics is very different from wasps' slow, meandering flight pattern, and thus behaviourally they are certainly not mimicking wasps. 'Perfect' wasp mimics, such as *Temnostoma* spp (which are absent from the UK) do seem to fly more slowly, 'lazily', and nearer the ground, in a manner similar to wasps (personal observation). It is possible that there are elements of both mimicry and advertisement in the colour patterns of poor mimics; there seems no reason why the two must be mutually exclusive.

There are few measurements of hoverflies' flight agility (but see Collett & Land 1978; Ellington 1984), though it is widely accepted that they are agile. Typically, hoverflies hover in one spot and then dart away with very high acceleration. As in other Diptera, the halteres, short stumps adapted from the hindwings, act as gyroscopes to stabilise flight, enabling sudden changes of direction, turning at right angles and even flight backwards (Chapman 1982). Their large multi-faceted eyes give them the acute vision necessary for fast flying, and their heads remain still relative to the thorax during flight (Gilbert 1986). The thorax is packed with flight muscle which provides power for the fast wingbeat, and the wings are corrugated with tiny hairs, also improving flight performance.

While hoverfly flight has been studied technically in the laboratory (Ellington 1984), there are few data comparing different species, or looking at the capability of predators to capture them. Dlusski (1984) measured the flight speed

of *Eristalis* species relative to hoverfly-eating bird species (the Pied Wagtail *Motacilla alba*, Redstart *Phoenicurus phoenicurus*, Spotted Flycatcher *Muscicapa striata* and Pied Flycatcher *Muscicapa hypoleuca*). *Eristalis* had a maximum flight speed of 1.63 ms^{-1} , whereas the diving speed of the birds ranged from 3.5 ms^{-1} to 6.6 ms^{-1} (but see Collett & Land 1978). Given the reaction times of *Eristalis* feeding on flowers when confronted with lifelike model birds, this implies that birds could catch them easily. However, aspects of flight behaviour in the field mean that hoverflies are nevertheless difficult to catch. In particular, birds may have to slow down in the last part of their dive towards the insect, and when hoverflies do react, they tend to fly in a direction at right angles to that the bird is approaching from (Dlusski 1984). Thus for a successful capture, the bird would need to turn and in doing so reduce its flight speed. It should also be noted that *Eristalis* is a good bee mimic; the poor wasp mimics may have higher flight speeds.

1.3 Abundance of models and mimics

1.3.1 Frequency-dependence in mimicry

As mentioned above, any new species joining a Müllerian mimicry ring will benefit not only itself, but also other mimics already in the ring (see 1.5.3 for possible exceptions). Müllerian mimics are best protected when common (Sheppard 1959; Turner *et al* 1984; Joron & Mallet 1998); the more often a predator encounters similar unprofitable prey, the more it will associate the

unprofitability with the pattern. It is therefore expected that Müllerian mimics will evolve into just one, local mimicry ring via purifying frequency-dependent selection (i.e. monomorphism, see 1.4.4.1). Any polymorphism would only serve to dilute the message.

In Batesian mimicry, on the other hand, mimicry will benefit the mimic, but disadvantage the model. Traditionally in Batesian mimicry, 'imitation is only advantageous to mimics if highly outnumbered by their models' (Bates, 1862, see also Fisher 1930; Cott 1940; Sheppard 1959). The abundance of the unprofitable model maintains the pattern's validity as a deterrent. The mimic weakens the deterrent by teaching predators that the pattern is a profitable one to try. Theoretically, if the mimic's abundance relative to the model increases, the variability in mimics' colour patterns will also increase because of a decreased selective advantage of close mimicry, so-called 'mimetic breakdown' (Ford 1936; Sheppard 1959).

Though Batesian mimicry is density dependent, mimics do not need to be outnumbered by their models (Rettenmeyer 1970; Huheey 1984; Turner *et al* 1984). Empirical work, mainly in the laboratory (Brower 1960; O'Donald & Pilecki 1970; Huheey 1980; Avery 1985; Nonacs 1985) but also in the field (Jeffords *et al* 1979) has shown that Batesian mimics do not necessarily need to be rarer than the model to evolve close mimicry. For example, Brower's (1960) classic experiment used starlings as predators and mealworms as artificial models and mimics. She showed that mimics are just as protected when comprising 60%

of the population as when comprising 30%. At 90% mimics, the level of protection was much lower, though still present.

The experiments cited above are mostly ‘reciprocal frequency experiments’. In these, a constant number of prey is offered to the predator, while the proportions of models and mimics are varied. While their results have provided some useful insights, they have tended to use inadequate replication and not enough palatabilities or frequencies (Turner & Speed 1996). In addition, these experiments are a poor reflection of the natural situation; sometimes no alternative prey are present, and there is simultaneous rather than sequential presentation of prey (Lindström *et al* 1997). Furthermore, each experiment uses one type of predator, and predators vary in their behaviour (Dlusski 1984; Hetz & Slobodchikoff 1988). These factors, along with the fact that most use artificial or dead prey, mean that the results could be quite different to how Batesian systems function in the dynamic context of the natural environment.

In the natural situation, the abundance of alternative prey is important. Its presence has been shown to increase the effectiveness of Batesian mimicry (Cook *et al* 1969; Dill 1975; Nonacs 1985; Slobodchikoff 1987; Hetz & Slobodchikoff 1988), presumably by reducing predation on the entire model-mimic complex (see 1.4.2.2 for more on the importance of resource availability to the evolution of mimicry).

Mathematical models can also attempt to show how relative frequencies affect Batesian systems. These usually predict the predation rate given certain parameters. For example, Huheey (1964) created a simple model where the

predator had a set 'forgetting time' (n). The predation rate, P , (probability an individual will be eaten) was predicted just in terms of n , p (frequency of mimic) and q (frequency of model), such that:

$$P = 1/(p+nq)$$

This fits reasonably well with the predation rates seen in some of the reciprocal frequency experiments mentioned (Brower 1960; Huheey 1980; Avery 1985, see Huheey 1988). (However, other mathematical models also fit well (Turner & Speed 1996, see 1.5.3.2). Many more complex mathematical models have been based on this 'n-parameter model' (Holling 1965; Brower *et al* 1970; Pough *et al* 1973), adding in such parameters as time and alternative prey availability. Generally, it is found that mimicry can evolve and persist in the presence of more mimics than models (e.g. Holling (1965) found that mimics were protected down to 30% models).

There is much debate on the relevance of such mathematical models to the natural situation, because of *a priori* assumptions they make about predator behaviour, specifically learning and forgetting (Huheey 1988; Turner & Speed 1996; Speed 1999). Small differences in behaviour can lead to fundamental differences in the predictions of the model (see 1.5.3.2). To adequately assess how frequency affects Batesian mimicry in nature, properly controlled field experiments (e.g. Jeffords *et al* 1979; Lindström *et al* 1997) and mathematical models which make realistic assumptions about predator behaviour (see e.g. Speed 1999) are needed.

1.3.2 Synchrony in space and time

Another traditional tenet of mimicry is that mimics and their models must be found in the same place at the same time (Fisher 1930; Sheppard 1959; Wickler 1968). There is evidence from clines that mimics are most similar to their models where distributions overlap; when a mimic ranges beyond its model, the colour patterns tend to regress towards a non-mimetic form (Rettenmeyer 1970). The best-known example of this is with the butterfly model *Battus philenor* and its mimics in the United States (Brower 1958b; Brower & Brower 1962). While mimetic forms of *Papilio glaucus* coincide with areas of abundant *B. philenor*, the non-mimetic yellow form is abundant wherever the model is rare. This appears to be independent of geographical factors. *Papilio troilus* is another mimic of *B. philenor*; where the model is abundant it mimics it very closely, but where it is rare, the mimicry is less accurate. However, the butterfly *Hypolimnas bolina* ranges from Asia to Australia and retains a mimetic pattern far outside the range of any model (Clarke & Sheppard 1975).

Temporal sympatry, however, is not as strict a condition as previously imagined (Huheey 1980, 1984, 1988; Slobodchikoff 1987). Temporal separation of model and mimic was first reported (Rothschild 1963) between the white ermine moth *Spilosoma lubricipeda*, which is mimicked by the buff ermine *S. luteum*. The mimic emerges later in the season than the model. This may afford the mimic extra protection, if predators encounter the model first, and learn to avoid the colour pattern before the mimics emerge. This protection seems to continue even when the model has ceased to reinforce the learning, since *S. luteum* is still

abundant after its model has disappeared. Relatively late emergence of the mimic has also been observed in other cases. For example, the beetle *Eleodes obscura* occurs in spring through to autumn, while its mimic *Stenomorpha marginata* is only abundant in autumn (Hetz & Slobodchikoff 1988).

Another well-described example is in wasp- and bee-mimicking hoverflies, which are seasonably abundant in spring and late summer, but not in midsummer (Waldbauer & Sheldon 1971; Waldbauer *et al* 1977; Waldbauer & LaBerge 1985; Owen 1991). Their models, however, are not present until midsummer. Waldbauer *et al* (1977) reasoned that the mimics are nevertheless protected, because in the early spring most birds have not yet fledged their young. Therefore, the mimics are exposed mostly to adult birds that remember the unprofitability of the colour patterns from experiences they had with wasps and bees the previous summer. By the time the hoverflies re-emerge in the late summer, fledging birds will have had experiences with wasps and bees and learned about the colour patterns.

This theory depends on the assumption that predators' responses to colour patterns are learned, not innate (see 1.4.3.3), and that avoidance learning can be retained over a period of several months. Red-winged Blackbirds and Grackles trapped early in the season, before hoverflies were abundant, still rejected bumblebee mimics on sight (Evans & Waldbauer 1982), while naïve hand-reared birds tried to eat both models and mimics. Other evidence also suggests that avoidance memory is retained in birds for some considerable time (Mostler 1935; Rothschild 1964; Pilecki & O'Donald 1971). This could explain how wasp-

mimicking hoverflies can be abundant at times when wasps are absent (see also 1.3.3). However, the work of Waldbauer and colleagues was on perfect mimics; there is no evidence that the same avoidance is retained for poor mimics.

1.3.3 Frequency patterns in hoverflies and their models

Batesian mimics are best protected when rare (see 1.3.1) and their frequency relative to their models is limited, though they may outnumber them. In hoverflies, however, poor wasp mimics are very frequent compared with wasps. This is in contrast to bee mimics, whose ratios to bees are more in line with the expectations of Batesian mimicry. Data from malaise trapping over 20 years in Leicester show that honeybees are approximately equal in number to their mimics, and bumblebees outnumber their hoverfly mimics by on average 7.3:1 (Owen 1991). In contrast, wasp mimics outnumber wasps (all species of *Vespula* combined) by on average 4:1 for the years 1972-1992. In June, at the peak of hoverfly abundance, and when wasps have not yet emerged in large numbers, wasp mimics outnumber their models by on average 7:1 (1973-1987). Even in August and September, when wasps are at their peak, wasp-mimicking hoverflies outnumber them by 6:1 and 2:1 respectively (J. Owen, unpublished data). (J.Owen's data are discussed in detail in chapter 2). High mimic: model ratios have been found using census walks, so these ratios are not simply the result of selective trapping (Grewcock 1992; Howarth 1998).

Dlusski (1984) looked at abundance of bee-mimicking hoverflies and their models in the environs of Moscow over several years. He does not provide the

actual data to compare bee mimic numbers with their models. However, using data from census walks along transects in various areas, there is some correlation between proportions of bees and bee mimics. For example, the transect with the most bees also had the most bee mimics. There was also some correlation in abundance over the five years of the study; when bee numbers were severely depleted one year, bee mimics were dramatically reduced compared to areas where bee numbers stayed high. Again, this supports the notion that these hoverflies really are bee mimics.

Dlusski (1984) also counted wasps and their mimics. As in the UK, there were many fewer wasps (of all types) than their mimics, the majority of which were imperfect mimics similar to those found in the UK (*e.g. Syrphus, Helophilus, Sphaerophoria, Sericomyia, Myathropa*). This was true for six transects on 46 of 50 days spread over two seasons. On average, there were 8.3 times fewer wasps than their mimics. If only perfect mimics were considered (*Sphecomyia, Spilomyia, Temnostoma, Chrysotoxum, Conops* and *Physocephala*), they were much less common than their mimics. Again, this implies that the colour patterns of common imperfect mimics may be fulfilling a different function than mimicry. It should be noted, however, that the abundance from the predator's point of view is important when considering relative abundances. When a bird approaches a group of hoverflies and hymenoptera feeding on flowers, observations indicate that while the hoverflies scatter, their models continue feeding undisturbed (Dlusski 1984). Therefore birds may encounter hymenoptera relative to hoverflies more often than indicated by abundance data.

Nevertheless, birds will not only encounter insects when feeding in groups at flowers, and it is questionable whether such large ratios of mimics to models could be supported even given this behaviour.

As mentioned in 1.3.2, the abundance over the season also varies and could account for some large numbers of hoverflies. If birds can remember from the previous year about wasps' noxiousness, then hoverflies could be protected the next spring despite few wasps being present (Waldbauer & Sheldon 1971; Waldbauer *et al* 1977; Waldbauer & LaBerge 1985). However, though this could protect the perfect mimics considered in these studies, imperfect mimics outnumber their models even when wasps are at their most abundant, and when fledging birds are learning about wasp patterns.

Another explanation for the high abundance of poor wasp mimics concerns their larval ecology. It is possible that the artificial effects of habitat disturbance by humans have caused a shift in the natural relative abundance of species, unrelated to the effects of mimicry. If numbers of poor mimics have been artificially inflated in this way, it could be that in the past they were not so common, and mimicry has simply not been lost yet. There is evidence of the effect of human disturbance on mimicry dynamics in another context; habitat change has altered the dominant model species for *Heliconius cydno* in Columbia, and the colour patterns of the mimic appear to have changed accordingly (Linares 1997).

In the context of mimicry in hoverflies in the UK, the change in land use from ancient woodland to urban-agricultural use has probably dramatically

reduced the availability of larval habitats (tree holes and rotting wood) for perfect mimics like *Temnostoma* species (see Rotheray 1993 for larval habitats). In contrast, large areas of disturbed ground have been created which are much more suitable for the more imperfect mimics. Many of these species (e.g. *Syrphus* spp., *Dasysyrphus* spp., *Parasyrphus* spp.) are aphidophagous, and aphids thrive in open or edge habitats (Dixon 1973).

The colour patterns of hoverflies probably evolved in the ancient forests which previously covered the Palaearctic, since most Palaearctic hoverflies are naturally associated with open glades in forest habitats (Speight *et al* 1975; Speight 1983). Therefore it seems conceivable that poor wasp mimics, if they were in more natural conditions, would be at a much lower frequency relative to their mimics than the paradoxical abundance we observe now (Grewcock 1992). At low frequencies, the existence of imperfect mimicry is easier to explain (see 1.4.2.4). The actions of predators, the primary force behind mimicry, might have had little influence as yet, since the land disturbance has only occurred in recent ecological time, and the super-abundance of poor mimics is so great.

There is some support for this theory. In the relatively undisturbed Polish Bialowieza forest, while ubiquitous species like *Syrphus ribesii* and *Dasysyrphus venustus* are common, so are perfect mimics such as *Temnostoma vespiforme* (Bankowska 1995). Limited data on model: mimic ratios, comparing British woodlands with a relatively undisturbed site in south-eastern France, indicated that the wasp mimic: wasp ratio was much more balanced (1.94: 1) in the less disturbed site (Grewcock 1992). However, Bankowska (1980) showed in Poland

that, while human activity does change hoverfly abundance, it tends to exaggerate patterns which are already present. In Bankowska's study, she found that overall diversity decreased, and the relative abundance of already-dominant species increased. If this is true in the UK, the super-abundance of poor wasp mimics could just be an exaggeration of already common species. Either way, the existence of poor mimicry at all still needs to be explained.

1.4 Colour patterns in mimicry

1.4.1 Evolution and genetics of mimetic patterns

1.4.1.1 The evolution of mimicry

The evolution of mimicry presents a problem similar to that described for aposematism in section 1.2.1, crossing an adaptive landscape (Wright 1977) in which fitness valleys are probably common (Mallet & Singer 1987). If mimicry evolved from crypsis there may be a significant fitness disadvantage if this crypsis is lost and the individual is not noxious (Endler 1991), especially if the mimicry is initially imperfect. Some early authors (Punnett 1915; Goldschmidt 1945, 1952) therefore thought mimicry must have evolved by a single systemic macromutation (or 'saltation'). Fisher (1927; 1930), however (as part of his general theory that individual differences, however small can be detected by natural selection) took the opposite view that all mimicry evolved by gradual tiny evolutionary steps. This seemed particularly apt for Müllerian mimicry, where the mimic is noxious, and therefore would still be afforded some protection by virtue of its noxiousness

despite small changes in colour pattern. However, others (Poulton 1912; Nicholson 1927; Ford 1964; Turner *et al* 1984; Turner 1987, 1988; Mappes & Alatalo 1997a) suggested that mimicry would be more likely to evolve by a two-step process; an initial large mutation to imperfect mimicry, followed by its modification to perfection by smaller mutations over time. Many experiments have shown that imperfect mimicry can provide some protection from predators (see 1.4.2.4, e.g. Goodale & Sneddon 1977; Dittrich *et al* 1993; Lindström *et al* 1997). Furthermore, the existence of supergenes controlling wing pattern mimicry in butterflies (Clarke & Sheppard 1960a,b, see 1.4.1.3) supports the idea of closely linked modifier genes gradually perfecting the resemblance. Even if this is so for Batesian mimicry, Müllerian mimicry may have evolved only gradually by convergence (Ford 1964), but genetic work on butterflies supports the idea that both types evolved by a 2-step process (Clarke & Sheppard 1960a,b; Turner 1987, but see Charlesworth & Charlesworth 1975; Turner 1984b).

An alternative to 2-step evolution is that Batesian mimicry evolved via Müllerian mimicry (Huheey 1976, 1984; Endler 1991); pre-existing mimics could have lost their noxiousness (with the advantage of being able to expand their host-plant range). There would be no need to cross a valley of low fitness intermediates. While this is possible in some species, in others that have no noxious ancestors (e.g. hoverflies) this seems unlikely (Mappes & Alatalo 1997a).

1.4.1.2 The two-step system

In the 2-step system described above, the initial mutation from crypsis to mimicry would have to be a large one to produce a conspicuous phenotype that immediately provides a substantial resemblance (Turner 1987; Mappes & Alatalo 1997a). If not, insufficient protection would be gained for the initial mutation to be selected. Mappes & Alatalo (1997a) looked at how accurate the initial signal must be for Batesian mimicry to evolve. Using a 'novel world' of black shapes (which rule out the possible confounding effects of innate aversions to certain colours), most imperfect mimics were protected from great tit predators more than cryptic prey (though less than perfect mimics). Importantly, though, the imperfect mimic closest in appearance to crypsis suffered increased predation. They concluded that Batesian mimicry can evolve by a 2-step process, but the initial mutation must be dramatic.

In the second stage, 'modifier' genes directionally select the mimic towards a closer resemblance to the model (Sheppard 1959; Scriber *et al* 1996). In this stage, it has been suggested that there is a major difference between Müllerian and Batesian systems. In Müllerian mimicry, the process is advantageous to the model, whereas in Batesian mimicry it is not (but see 1.5.3). Hence in Müllerian mimicry, the two mimics converge in pattern, since it is to the advantage of both to do so. In Batesian mimicry, however, convergence is not to the model's advantage, so in theory it may escape by evolving a new colour pattern of its own; in this case this second stage has been termed 'advergence' (Turner 1987). (For

more on the resulting coevolutionary chase, including the reasons why it may not play a major part in the evolution of mimetic diversity, see 1.4.2.3).

1.4.1.3 Supergenes and linkage

It is traditionally thought that Batesian mimicry is controlled by mimetic supergenes, while in Müllerian mimicry there is little purposeful linkage between genes (Turner 1977, 1987, but see Joron & Mallet 1998). There is genetic evidence that ‘supergenes’ exist which control Batesian mimetic patterns in *Papilio* butterflies (Clarke & Sheppard 1960a,b). This has not happened by chance; modifier genes which are linked to the original major mutation are more likely to be selected for. Mimicry will improve more quickly with closely linked genes, because they are unlikely to be separated again by recombination. In this way, in butterflies, whole blocks of genes build up, each controlling a minor aspect of wing coloration. Crossing experiments show that these do tend to be inherited together (Clarke & Sheppard 1955, Sheppard 1961). In Batesian polymorphisms, this tendency is particularly strong (Charlesworth & Charlesworth 1975) because any minor mutation that is advantageous to one morph will be disadvantageous to another; linkage provides them with the means to evolve independently. Furthermore, the genes must be tightly linked from the onset of the evolution of the polymorphism, or tighter linkage will not evolve, as recombination will destroy the adaptive polymorphism before it is stabilised (Charlesworth & Charlesworth 1975; Joron & Mallet 1998). This distinctive genetic architecture in Batesian mimicry may make it very difficult for novel

mutants to escape to a different colour pattern. This is what Turner (1984b) calls the 'evolutionary sieve'. It may explain why models do not always escape from mimics (see 1.4.2.3) and why monomorphisms sometimes persist in Batesian mimicry (see 1.4.4.1) (Joron & Mallet 1998). It should be noted, however, that some genes in Batesian mimicry are not linked to the supergene, contrary to expectations (Clarke & Sheppard 1960a,b).

In Müllerian mimicry, monomorphism, not polymorphism, is expected because of frequency-dependent purifying selection. For this reason, little purposeful linkage is expected between mimicry genes (Turner 1987). However, in some Müllerian mimics (e.g. some *Heliconius* races, *Zygaena ephialtes* (Sbordoni *et al* 1979)) tight linkage is found. Rothschild (1980) suggests that the tight linkage already existed before mimicry evolved, in pre-existing polymorphisms for other characters, and that mimicry gradually evolved from these. This still leaves the evolution of the original polymorphisms to be explained. Alternatively, the linked genes may have arisen from a single ancestral gene by tandem duplication, explaining why they are close together (Sheppard 1975; Turner 1987). Some closely linked Müllerian mimicry genes do seem to share very similar functions (e.g. Turner 1972 on *Heliconius melpomene*).

1.4.2 *Perfect and imperfect mimicry*

1.4.2.1 Why perfect mimicry?

In the second stage of the 2-step process, mimicry moves from an imperfect to a perfect state. In Batesian mimicry, since the mimic is deceiving the predator, the closer the resemblance to the model, the more likely it is to deceive (Fisher 1930; Cott 1940; Sheppard 1959; Huheey 1984, 1988). Therefore, it should always be advantageous to improve the perfection of Batesian mimicry, as long as the mortality of the mimic is greater than the mortality of the model (Fisher 1930; Nur 1970). Cott (1954) also suggested that mimicry must be perfect to deceive a range of predators, each with good discrimination capabilities for different aspects of a colour pattern. There is evidence that prey are protected more by perfect mimicry than imperfect (e.g. Hetz & Slobodchikoff 1988; Mappes & Alatalo 1997a). In Müllerian systems, mimicry may not need to be as perfect, since the mimic only needs to remind predators of its unprofitability by suggesting a resemblance between it and other unprofitable prey (Sheppard 1959; Huheey 1988, but see Srygley 1994).

Most experiments and theories on mimicry assume perfect mimicry. However, imperfect mimicry is observed in nature more often than might be thought. One example, in the hoverflies, has already been mentioned. While some species (e.g. *Temnostoma* spp., *Spilomyia* spp.) are very accomplished mimics, the common wasp mimics in the UK are imperfect. In genera such as *Syrphus*, *Eupeodes*, *Megasyrphus* and *Episyrphus*, the black abdomen has orange or yellow stripes, but in detail these are not very similar to wasps' abdominal patterns.

Humans can quickly learn to distinguish between such hoverflies and wasps (see 1.4.3.1 for predators' perception).

1.4.2.2 Perfect mimicry via imperfect mimicry

In Batesian mimicry, cases of imperfect mimicry that are observed in butterflies, hoverflies, beetles and other species, have often been explained by the mimic being in transition towards perfect mimicry (Sheppard 1959; Duncan & Sheppard 1965; Alcock 1971). If this is the case, predators must generalise between patterns to some extent, or they would never mistake imperfect for perfect mimics, and imperfect mimicry would not be selected for (Morrell & Turner 1970; Alcock 1971). On the other hand, for imperfect mimicry to evolve to perfection, predators must also be able to discriminate between imperfect and perfect mimicry, or perfect mimicry could not be selected for. Alcock (1971) suggested that it was variation in generalisation and discrimination capabilities that led to the eventual evolution of perfect mimicry. For example, hunger levels affect which prey birds are willing to try (Chai 1996; Srygley & Kingsolver 1998). Srygley & Kingsolver (1998) found that birds were willing to sample more unpalatable butterflies during fledging times when resources were low, and surmised that such times could lead to the necessity for perfect mimicry. In particular, they suggested that when resources were plentiful, predators used inexpensive general colour cues to select prey, and imperfect mimics were protected. However, in times of limited resources, birds sample distasteful prey

and their mimics; it is during this time that directional selection towards perfect mimicry can occur.

As well as this within-individual variation in predator discrimination, Alcock (1971) suggested that intra- and inter-species variation could play a part in the balance between generalisation and discrimination that drives the evolution of perfect mimicry. Firstly, individual predators within a species differ in discrimination capabilities, for example in Jacamars (*Galbula ruficauda*) (Chai 1996) and Darwin's Finches (*Pinaroloxias inornata*) (Werner & Sherry 1987). Secondly, there is variation between species (e.g. Alcock 1971; Dlusski 1984; Srygley & Kingsolver 1998). Those individuals and species which are most discriminating will select for the perfection of mimicry. Hence the evolution of perfect mimicry is likely to be more of a dynamic system than a steady process.

Poor wasp mimics could be in the process of evolving towards perfect mimicry; there is no particular reason to suppose that they have reached a stable endpoint in the evolution of the colour patterns. However, this seems unlikely to be the explanation for such widespread imperfect mimicry across many areas of syrphid phylogeny. It is improbable that so many genera are all at approximately the same stage of evolution towards perfect mimicry, and that this is true of species in both Europe and America. Moreover, it is difficult to understand how they could persist from year to year in such large numbers compared to their models if their only protection from predators is imperfect mimicry, even if they are in a transition phase.

1.4.2.3 The coevolutionary chase

One explanation for so many species being in transition towards perfect mimicry, and thus the abundance of imperfect mimicry, is the coevolutionary chase. When a Batesian mimic converges on to the pattern of its model, this is to the detriment of the model, since any profitable prey sharing its pattern will dilute its warning message to predators. Therefore it seems logical that the model should 'escape' from the mimic by changing its colour pattern. Several authors (Nur 1970; Rettenmeyer 1970; Turner 1987; Huheey 1988; Joron & Mallet 1998) have discussed the idea of a 'coevolutionary chase' in Batesian mimicry (similar to the arms race concept in host-parasite interactions), where the model is constantly evolving away from the mimic, while the mimic strives to catch up. Potentially, this could explain the existence of imperfect mimics, if they converged onto the colour pattern of a model which has since changed its appearance (Rettenmeyer 1970). Furthermore, it could explain race and morph differentiation and the existence of sympatric mimicry rings (see 1.4.4) (Pough *et al* 1973; Huheey 1988).

However, though it may be advantageous to the model to evolve away from the mimic, it can only operate within the realms of what is genetically possible (Turner 1987). Mimetic polymorphisms are tightly linked from the start of their evolution (see 1.4.1.3). Therefore it requires a particular type of genetic architecture to be able to escape the mimic, probably only available to the model if it is already polymorphic (Joron & Mallet 1998). Only a few species of model will be able to pass through this evolutionary sieve (Turner 1984b). Escape is also

hampered by the constraint of strong purifying selection on warning colouration in the model (Nur 1970; Gilbert 1983; Turner 1984b). While the mimic always benefits from becoming more similar to the model, the model may lose out by changing its colour pattern, because predators will no longer recognise it as unprofitable. Selection on the mimic to converge on the model is therefore stronger than selection for the model to escape. Mathematical modelling (Gavrilets & Hastings 1998) shows that cyclical coevolution is only possible if interspecific interactions (e.g. the relative benefits and costs of mimicry to the model and mimic) are stronger than intraspecific interactions (like aposematism and palatability). This may indeed sometimes be the case. However, if models are more common than mimics (as is theoretically the case with Batesian mimics) the intraspecific effect of purifying selection is likely to be stronger than any interspecific interactions.

The constraints on the escape of the model may explain how perfect Batesian mimicry can exist at all in the context of the coevolutionary chase (Fisher 1930; Sheppard 1959; Nur 1970). They also put cyclical coevolution into doubt as an explanation for imperfect mimicry and polymorphism. In the particular case of hoverflies and their wasp models, it is possible that the large number of mimics has increased the costs to wasps of bearing them, and thus promoted the coevolutionary chase. On the other hand, the high noxiousness of wasps should make them capable of bearing this cost, and as models they would have to escape the evolutionary sieve described above.

1.4.2.4 Evidence of protection by imperfect mimicry

Experiments have shown that a variety of predators do generalise and discriminate, which is necessary for the evolution of perfect mimicry via imperfect mimicry. In particular, many authors have been concerned with the former and shown that there is some protection to be gained from imperfect mimicry. This has been demonstrated on numerous occasions, under the conditions of particular experiments (e.g. Morgan 1900; Mühlmann 1934; Mostler 1935; Brower 1958c; Schmidt 1958; Brower *et al* 1963; Duncan & Sheppard 1965; Morrell & Turner 1970; Pilecki & O'Donald 1971; Goodale & Sneddon 1977; Hetz & Slobodchikoff 1988; Lindström *et al* 1997; Mappes & Alatalo 1997a).

Early work showed that birds can learn to associate colours or patterns with nastiness, and thereafter also reject modifications of these patterns (Morgan 1900; Mühlmann 1934; Mostler 1935). Schmidt (1958) found more evidence of generalisation; chicks only needed a very small part of a pattern of a distasteful 'model' to be copied for them to avoid it. Further to this, jays were found to generalise among two species of *Danaus* butterfly, and two sub-species of *Limenitis archippus* (Brower 1958c; Brower *et al* 1963).

There is great variation between experiments carried out on imperfect mimicry. This is also true of reciprocal frequency experiments generally, and is worthy of some comment. Some are carried out in natural or semi-natural settings, such as gardens or woodlands (Morrell & Turner 1970; Pilecki & O'Donald 1971; Goodale & Sneddon 1977; Hetz & Slobodchikoff 1988), while use captive

predators (Duncan & Sheppard 1965; Lindström *et al* 1997; Mappes & Alatalo 1997a). Some studies have used predators in unnatural choice situations (Duncan & Sheppard 1965; Morrell & Turner 1970; Pilecki & O'Donald 1971; Goodale & Sneddon 1977); in the wild, it is unlikely that a bird would be faced with the simultaneous choice between several prey (Lindström *et al* 1997). The type of 'model' also varies. Most experiments use some form of unpalatable chemical (e.g. quinine) to simulate noxiousness, though Duncan & Sheppard (1965) used electric shocks of different degrees of intensity; pain is a very different type of reinforcement to an unpleasant taste (see Goodale & Sneddon 1977). Most studies used dyed or painted pastries or other fake prey (Morrell & Turner 1970; Pilecki & O'Donald 1971; Goodale & Sneddon 1977; Mappes & Alatalo 1997a), with one using painted mealworms (Lindström *et al* 1997) and only one that I know of used real imperfect prey (Hetz & Slobodchikoff 1998, with Coleoptera *Eleodes obscura* and *Stenomorpha marginata*). The type of imperfection used also differs; some used intensity of hue as the imperfection (Duncan & Sheppard 1965; Pilecki & O'Donald 1971; Goodale & Sneddon 1977). Others have used the presence or absence of a mark (against the background of a certain 'mimic' colour) (Morrell & Turner 1970), or the position of a mark on the prey (Lindström *et al* 1997). One study used black-and-white shapes and intermediates between them (Mappes & Alatalo 1997a). It is debatable whether all of these are perceived as equivalent to imperfect mimicry by the predator.

Nonetheless, there is general agreement that imperfect mimics are increasingly protected as models become more frequent (Pilecki & O'Donald

1971; Lindström *et al* 1997) and more distasteful or unprofitable (Duncan & Sheppard 1965; Goodale & Sneddon 1977; Lindström *et al* 1997). The patterns of poor wasp mimics could therefore provide protection, despite their imperfection, as wasps are likely to be particularly unprofitable models. One imagines that the sting of a wasp would be a great deterrent for avian predators, and Leipelt (1963) observed that a wasp sting rendered a captive shrike inactive for several hours. The tissues of wasps are also highly unpalatable (Mostler 1935). In this context, there may be no advantage to poor wasp mimics increasing their similarity further. However, in this case, why do perfect wasp mimics exist at all? Also, imperfect mimics are best protected if models are frequent; this is certainly not the case relative to poor wasp mimics (see 1.3.3). If even perfect wasp mimics need to be as rare relative to wasps as they are, it seems likely that poor wasp mimics would need to be even more infrequent to avoid predation.

Predators can discriminate as well as generalise; perfect models are protected more than imperfect ones (Morrell & Turner 1970; Hetz & Slobodchikoff 1988; Mappes & Alatalo 1997a). There is evidence that predators both generalise and discriminate between wasps and their hoverfly mimics. Pigeons trained to peck at images of wasps do not treat images of hoverflies the same way, so birds seem capable of discriminating between them (Dittrich *et al* 1993). This is also the case when pinned specimens are used rather than images (Green *et al* 1999). Furthermore, images of twelve different hoverfly species were rated variably in terms of their similarity to wasps, mostly in the same order as they are rated by humans (Dittrich *et al* 1993, but see 1.4.3.1). Therefore not only

can birds distinguish perfect from imperfect mimicry, but they also rate some imperfect mimics as better than others. This variation can be assessed objectively by using a computer-calculated similarity score, measured by overlaying the two images and comparing them pixel by pixel, and measuring the Euclidian distance apart of each pair of corresponding pixels in red-green-blue colour space (Grewcock 1992; Dittrich *et al* 1993). The similarity scores produced by the program again largely agree with the ratings of pigeons (Dittrich *et al* 1993) and therefore they will be considered as objective similarity scores for the remainder of this thesis. This similarity program will be described in more detail in chapter 4).

Another possible contributory factor to the colour patterns of hoverflies is thermoregulation. If patterns are constrained by thermoregulation, this could explain why mimicry is sometimes imperfect. In *Eristalis tenax*, a honeybee mimic, there is a black band overlying the dorsal blood vessel that might need to be retained in order to maximise the absorption of light to heat the blood (Heal 1979, 1982). However, many mimetic hoverflies do not have a black band in this area, and there is variation in aspects of abdominal patterns which have no obvious connection with thermoregulation. Therefore, while thermoregulation could play a role in some species, it seems unlikely to be the main force behind the evolution of colour patterns in hoverflies.

1.4.3 *Predator perception*

1.4.3.1 Predator perception and imperfect mimicry

Another interpretation of imperfect mimicry is that, to predators' eyes, imperfect mimicry is in fact more perfect, since predators' perceptions of the colour patterns are different from humans'. We do appear to share some aspects of our perceptual systems with predators, as we can at least recognise visual mimicry in insects. However, unexplained imperfect mimicry could be accounted for if predator generalisation from a model species is influenced strongly by one particular feature of the model, and much less by any other features. Resemblance in that feature alone could then be sufficient for mimetic protection (Dittrich *et al* 1993). Unfortunately, knowledge is lacking in this area. Dittrich *et al* (1993) showed that generally, pigeons rated the perfection of wasp-mimicking hoverflies' similarly to humans. However, two common species which are poor mimics to human eyes were rated as very wasp-like by pigeons, indicating some unknown constraints or biases in their perceptual systems. Some differences between avian and human colour vision are known (Cuthill & Bennett 1993), notably that birds can see well in UV, whereas humans can not, and birds have five classes of cones, and thus see in 5-dimensional rather than 3-dimensional colour space. However, pigeons pecking at pinned hoverfly specimens under natural light, and therefore with UV cues available, still rated them as intermediate between wasps and flies (Green *et al* 1999).

The nature of colour is not fixed; the interpretation of signals rests with the predator (or receiver) and depends on its previous experience (Guilford &

Dawkins 1991). The context the colour is seen in may also be important. For example, the same signal can both warn and attract depending on the context (e.g. the colour red warns a robin to avoid unpalatable prey, but attracts it to females to mate with, or rosehips to eat (Rothschild 1984)). A familiar signal in an unusual context may be confusing to a predator, and could help explain imperfect colour patterns ('satyric mimicry', Howse & Allen 1994). Presenting two equally probable messages simultaneously could lead to a lengthening of the predator's perceptual process and thus give the prey time to escape. For example, a hoverfly that is a poor wasp mimic has colour patterns which signal unprofitability, but a body type (a fly's) which signals profitability. Howse & Allen suggested that the principle behind this was similar to the 'startle' tactics of some cryptic insects with, for example, brightly coloured underwings which they can flash at predators (e.g. *Catocala* moths, Sargent 1990). While this theory deserves further exploration, repeated exposure to such 'ambiguous' prey will decrease the startle effect, as predators habituate or learn that the prey is profitable. It is also unclear why satyric mimics should not still evolve towards perfect mimicry.

An alternative view of imperfect colour patterns is as 'aide-memoire mimicry' (Rothschild 1984). Her theory was that mimics need not always be actually mistaken for noxious or dangerous prey, but that merely reminding the predator of these attributes will suffice. As in satyric mimicry, a slight hesitation on the part of the predator could provide enough time to enable escape. Rothschild was chiefly referring to phenomena such as the 'pseudo-stings' and wasp-like abdomens of various tough or noxious lepidopterans which could not

be mistaken for wasps. She suggested that this type of mimicry was used by insects which use a standard form of protection for their family, with this 'aide-memoire' as 'an extra string to their bow'.

Despite differences between avian predators' perceptions and our own, birds still consider 'poor' wasp mimics to be imperfect. When presented with a random series of *Vespula* and *Syrphus* spp (a common imperfect wasp mimic), Pekin Robins (*Leothrix lutea lutea*) immediately swallowed *Syrphus*, while wasps were only eaten after a long handling time to remove their sting (Grewcock 1992). *Syrphus* was also often taken in choice tests using Redstarts (*Phoenicurus phoenicurus*) and Pied Flycatchers (*Muscicapa hypoleuca*), when paired with *Eristalis* or honeybees tethered to a feeding platform (Dlusski 1984) (though one can never be sure whether the choices made in truly natural conditions would be the same). Individual birds sometimes initially avoided *Syrphus*, but once they had tried it once, they ate any further individuals without hesitation, showing the importance of previous experience and learning (see section 1.4.3.3).

1.4.3.2 Variation among predators

As well as differences between humans and hoverfly predators in colour perception, there are also differences among predators. Firstly, birds are not the only predators which eat brightly coloured insects. Experiments using other predators are relatively rare, though some have used amphibians (Brower 1960; Huheey 1980), mammals (Hetz & Slobodchikoff 1988) or reptiles (Boyden 1976). However, birds are probably the selective force behind mimicry, because they are

common, and hunt visually. For butterflies at least, bird predation is considered the prime selective agent (Bowers *et al* 1985).

This is also likely to be true for hoverflies. Other recorded predators of hoverflies include many predatory insects, such as digger wasps, hornets, dragonflies and spiders (see Torp 1994). Though these may hunt visually, the bold patterns of hoverflies seem more likely to have evolved for the good colour vision of avian predators. Common bird species which are known to take hoverflies include swallows, swifts, robins and great tits (Torp 1994).

There are also differences between bird species in perception of colour patterns. Specialised insectivorous birds, for example, may be able to discriminate better among insects' colour patterns than generalised birds such as the pigeons used in Dittrich *et al* (1993). Cott (1954) suggested that the variation in perceptual systems of predators was the reason why Batesian mimics should evolve perfect mimicry; if each predator is influenced strongly by a different part of the pattern, all parts may need to be perfect to fool all predators. There is certainly also variation between predator species' levels of sight-rejections of prey, their tolerance to unpalatability, and their foraging strategies (e.g. Alcock 1971; Dlusski 1984; Chai 1996; Pinheiro 1996).

1.4.3.3 Do predators avoid innately or learn to avoid?

However predators perceive colour patterns, they can certainly associate unprofitability with them (see 1.2.1). Avoidance of warning colours is likely to have some genetic basis, through an evolutionary history of avoiding certain

colours. Some colours, or combinations of colours, such as red, yellow-and-black, and white spots on a black background are found across phylogenetic classifications as warning colours (e.g. in many insect orders, amphibians, snakes, birds, fish and plants) (Wickler 1968; Rothschild 1984). These colours seem to be more effective signals than others (Guilford 1990b), and predators can learn avoidance behaviour associated with them more quickly than with other colours (Bisping *et al* 1974; Smith 1975, 1977; Schuler 1982). Naïve chicks have also been found to have some innate aversion to black-and-yellow patterns (Schuler & Hesse 1985; Roper & Cook 1989).

However, learning is also crucial to the avoidance of warning colouration (Mostler 1935; Brower & Brower 1965; Alcock 1970; Schuler 1974, Alatalo & Mappes 1996; Chai 1996). For example, naïve, hand-reared jacamar chicks showed no initial preference towards any particular butterflies (Chai 1996), but rapidly learnt to associate visual characteristics and acceptability. Other studies also show exploratory behaviour in young (Alcock 1973; Barrows *et al* 1980). With reference to hoverflies, hand-reared naïve adult grackles and red-wing blackbirds ate bumblebee mimics without hesitation until stung by a bumblebee, following which all mimics were avoided (Evans & Waldbauer 1982). Also, *Sericomyia*, a good (though not perfect) wasp mimic, was not approached in choice tests using flycatchers and wagtails (Dlusski 1984) until one individual was taken. Following this, incident, *Sericomyia* was always taken. Therefore there seems little doubt that, despite some innate tendencies, learning can take over as the force behind choice of prey.

A related question is whether conspicuousness or novelty *per se* (not of any particular colour) is avoided (so-called ‘neophobia’ or ‘oddity effect’). Some evidence has been found for this (Coppinger 1970; Smith 1975, 1977; Schuler 1982; Greenberg 1984), but as noted above many others have seen exploratory behaviour in young inexperienced birds (Alcock 1973; Barrows *et al* 1980; Smith 1983; Alatalo & Mappes 1996; Chai 1996). Furthermore, experiments with zebra finches show that it is colour, not conspicuousness *per se*, that acts as a signal for innate avoidance (Sillén-Tullberg 1985).

1.4.4 Polymorphism and diversity in mimicry

1.4.4.1 Polymorphism in Batesian and Müllerian mimicry

Batesian mimics are expected to be relatively rare compared with their models, to maintain the validity of the warning colouration’s deterrent (see 1.3.1). Consequently, stable polymorphisms are also expected in Batesian mimics (Sheppard 1959; Turner 1984b, 1987), since polymorphism will help maintain the rarity of each colour morph of a species (sometimes including cryptic morphs) (Huheey 1988).

A well-known example of a Batesian polymorphism is in *Pseudacraea* butterflies (Owen 1971), where several morphs mimic various species of *Bematistes*. In hoverflies, some mimics of bumblebees (e.g. *Volucella bombylans*) have several different colour morphs, each resembling a different species of *Bombus*. The common morph changes geographically with the dominant

bumblebee species (Gabritchevsky 1926), thus retaining their rarity relative to each model. However, such examples are surprisingly rare. This could partly be explained by the fact that the tightly linked nature of the genes controlling Batesian mimicry (Clarke & Sheppard 1960a,b; Turner 1984b) makes it difficult to evolve new colour patterns (Joron & Mallet 1998, and see 1.4.1.3, 1.4.2.3). In fact, the best-studied Batesian polymorphisms are not among different morphs, but between sexes (Clarke *et al* 1968; Turner 1984a; Krebs & West 1988; Joron & Mallet 1998).

Conversely, Müllerian mimics are least protected when rare (see 1.3.1), and are expected to be monomorphic (Sheppard 1959; Mallet & Singer 1987; Turner 1987; Owen *et al* 1994). Selection should always favour a single mimicry ring, at least within a local area. Nevertheless, there are numerous examples of polymorphic Müllerian mimics. The classic example is *Danaus chrysippus* in sub-Saharan Africa, which has four different colour morphs (Smith 1975; Gordon 1984), all of which feed on unpalatable milkweeds (Rothschild *et al* 1975). Another commonly cited example is *Heliconius numata*, an unpalatable butterfly which has eleven sympatric morphs in South America (each mimicking a separate species of the ithomiine *Melinaea*) and 38 morphs in total (Brown & Benson 1974). In Europe, it is best known in bumblebees, where several Müllerian mimicry rings exist sympatrically (Plowright & Owen 1980). Unexpected diversity in Müllerian mimics has been the topic of much debate in the literature. The next two sections briefly discuss the main points (see Joron & Mallet 1998 for review).

1.4.4.2 Geographical races in Müllerian mimicry

As well as local polymorphism in Mullerian mimics, there is also geographical variation within species into separate ‘races’ in different areas. Furthermore, as Bates noted in 1862, two species can both show this geographical variation, with local morphs mimicking each other. For example, races of *Heliconius erato* and *H. melpomene* mimic each other locally all over South America (Turner 1987; Brower 1996). This ‘parallel race formation’ has been attributed to coevolutionary mutualism, in other words evolution by the same route from the same ancestral pattern (e.g. Turner 1987), especially since the genetic control of the patterns is the same in both species (Turner 1984b). However, mitochondrial DNA evidence (Brower 1996) shows that the patterns could not have coevolved since the mDNA of the two species does not share a common biogeographical history. The similar genetic control of the two species can be explained by their common phylogenetic history (Turner 1984b). Therefore alternative explanations are needed for the evolution of racial divergence in Müllerian mimics.

There are two main theories of how this diversity in Müllerian mimicry rings has come about, biotic drift and the shifting balance (Turner & Mallet 1996; Mallet & Turner 1997). Biotic drift (Brown *et al* 1974; Turner 1984b) is random change in overall biota composition (relative abundances and extinctions) caused by genetic drift. Random changes in abundance within mimicry rings will vary between local areas. Therefore a particular species may be ‘captured’ by different

rings in different areas, switching between rings many times in its evolutionary history. This could lead to the racial divergence observed, as mimics use the protection of locally abundant models. The process of biotic drift is accelerated by island refuges, because these increase the rate of extinction and density variation. Such refuges may have periodically appeared during evolutionary time as the rainforest expanded and contracted over the Pleistocene. The patterns seen now could be a relict of the isolation that once existed. However, it is difficult to see why this geographical variation does not collapse back into a single mimicry ring once the areas are connected again (Joron & Mallet 1998).

An alternative is the theory based on Wright's (1977) 'shifting balance' between adaptive fitness peaks (Mallet 1993; Mallet & Turner 1997). This also relies on genetic drift, and has much in common with the biotic drift theory (Turner & Mallet 1996). However, in this case a species does not 'switch' between mimicry rings as a result of geographic isolation; instead, random mutation and drift provide variation for selection to act upon, and therefore local variation in novel colour patterns happens by chance. Any advantageous patterns could stabilise locally, and then spread to wider areas through the movement of clines. This seems to make more sense given that Müllerian mimics are subject to purifying selection (Turner & Mallet 1996; Joron & Mallet 1998). However, both theories rely on genetic drift, and other explanations may still be forthcoming for the evolution of geographical races. Once races have evolved, each race undergoes a form of geographical isolation as any recombination of the patterns

will probably be a disadvantage (Joron & Mallet 1998). This seems a likely route for the formation of new species.

1.4.4.3 Polymorphism in Müllerian mimics

Though there may be reasons for geographic races, this does not explain why we see polymorphism in Müllerian mimics within local areas (see examples in 1.4.4.1). This could be explained by genetics; for species to converge, they will again need to undergo a peculiar type of genetic change (see 1.4.1.3, 1.4.2.3, 1.4.4.1) (Turner 1987). Another part of the explanation could be that many systems considered Müllerian may not be truly Müllerian, in the sense that both mimics benefit from the relationship (Huheey 1976, 1988; Speed 1993a, but see Sheppard & Turner 1977; Benson 1977). If two distasteful species differ in their degree of distastefulness, while the more palatable one benefits, this may be to the detriment of the more distasteful one. This is known as quasi-Batesian mimicry, because the relationships are similar to those in Batesian mimicry, though both species are unpalatable (for more on quasi-Batesian mimicry, see 1.5.3.1). If true Müllerian mimicry is rare (Turner & Speed 1996), it is not surprising that quasi-Batesian mimics are acting in a Batesian way and evolving polymorphism. However, different assumptions about predator behaviour have a large influence on whether quasi-Batesian mimicry is common in nature, and it may not have a significant role to play (Joron & Mallet, see 1.5.3.2).

Polymorphism in Müllerian systems may also be partly explained by the fact that relative abundances of species are constantly changing. Mathematical

models of mimicry are usually based on constant percentages of models and mimics in the population, while in reality there are constant variations in relative frequencies and palatabilities (Ritland 1994, see 1.3.2, 1.5.2). This could mean that the role of a species within a mimicry ring is switching between model and mimic (Speed 1993a,b; Brown & Benson 1974), with the accompanying switch between purifying and diversifying selection. This could potentially lead to stable polymorphism (Joron & Mallet 1998). However, there is no empirical evidence for this.

Local polymorphism in Müllerian mimics could also be explained if different Müllerian mimicry rings were operating sympatrically. There is some evidence for this (Papageorgis 1975; Mallet & Gilbert 1995; Beccaloni 1997), especially in butterflies that use different levels of host-plants in the forest canopy. However, it seems unlikely that predators will only forage within one level, and observations show that there is some spatial overlap in the mimicry rings (Burd 1994; Mallet & Gilbert 1995).

The diversity in Müllerian mimics still remains largely unexplained, and the answer probably lies in a combination of some of the explanations presented here. It is difficult to look for general patterns leading to stable balanced polymorphisms because of the complex nature of the system; diversity in mimicry may be best seen as 'the result of a dynamic balance between geographical divergence, speciation and mimetic evolution, rather than because it is a stable community optimum' (Joron & Mallet 1998).

1.5 *Distastefulness and unprofitability*

1.5.1 *Relationships between unpalatability and avoidance*

Theoretically, the model in a Batesian system can be protected by any form of unprofitability (e.g. stings or escaping ability). However, it is usually characterised as being distasteful or unpalatable to the predator. Unpalatability is not aimed at killing the predator (though some models (e.g. *Danaus plexippus*) can contain highly toxic chemicals (Parsons 1965)). The survival of the predator is of benefit to the model, as it will learn to avoid the prey in the future.

Sometimes, there are no obvious effects (e.g. vomiting) on a predator from eating a prey item, but it will still be subsequently avoided (Rothschild 1961; Chai 1996). Birds' stomach contents also indicate that many species considered Batesian models or Müllerian mimics can be eaten without lethal effects (McAtee 1932; Krištín 1994). Many studies have compared relative palatabilities using a range of predators (e.g. Swynnerton 1915; Brower 1958a; Chai 1986, 1996; Srygley & Kingsolver 1998). A few cases of unpalatability have also been investigated directly via bioassay (e.g. Brower 1969; Bowers 1980).

Distasteful chemicals are obtained from food plants (Brower & Brower 1964; Rothschild 1972; Brower 1984). Most work on insects' use of plant secondary chemicals has been on butterflies; the five main groups that serve as models (Papilioninae-Troidini, Ithomiinae, Nymphalinae-Heliconiini, Acraeinae, and Danainae) (Rettenmeyer 1970) are restricted to a narrow group of food plants. These plants (e.g. species of Passifloraceae and Asclepiadaceae (milkweeds)) chemically defend themselves with distasteful chemicals, but some insects have

overcome this by detoxifying or sequestering the chemicals. This is best-documented in the monarch butterfly (*Danaus plexippus*), which sequesters and stores toxic, bitter cardenolides from at least some of its larval food plants (Cohen 1985; Malcolm *et al* 1989).

However, though insects are often described as either palatable or unpalatable, there are degrees of distastefulness (see 1.5.2, 1.5.3.1). Also, predators vary in their classification of distastefulness (see 1.4.3.2, 1.5.4). The degree of distastefulness of the model also affects the dynamics of mimicry. Batesian mimicry is more likely to evolve in the presence of a highly noxious model (Endler 1991), but even mildly noxious species may be models if highly abundant (modelled by Pough *et al* 1973).

Experimental data shows that highly unpalatable models can support higher frequencies of mimics than more palatable ones (Brower 1960; O'Donald & Pilecki 1970). The degree of unpalatability could also affect the fidelity of imitation; imperfect mimics survive better if the model is highly distasteful (Duncan & Sheppard 1965; Goodale & Sneddon 1977; Lindström *et al* 1997, see 1.4.2.4). In terms of wasp-mimicking hoverflies, the model is not only unpalatable (Mostler 1935), but also noxious. It seems likely that the high unprofitability of the sting (see 1.4.2.4) could allow imperfection in the mimics in the same way as high unpalatability does.

1.5.2 Automimicry

The degree of unprofitability of the model is important to the dynamics of mimicry. More than this, it determines the whole nature of the mimetic relationship. In Batesian mimicry, the unpalatable species is the model and the palatable one is the mimic. If their palatabilities are equal, it is Müllerian mimicry. But sometimes palatability varies within a species ('automimicry') (Brower *et al* 1967, 1970, 1978; Pough *et al* 1973; Ritland 1995). In this case, palatable individuals of the species are identical in appearance to unpalatable individuals (automodels) and are in effect intraspecific Batesian mimics (automimics).

Automimicry (in those cases studied) arises through mimics feeding on host plants with variable toxic chemical contents (Brower *et al* 1967; Ritland & Brower 1991; Ritland 1994). The best-studied case is the Monarch (*Danaus plexippus*) – Queen (*Danaus gilippus*) – Viceroy (*Limentis archippus*) complex. The monarch and the almost identical queen have traditionally been considered Batesian models for the viceroy (Walsh & Riley 1869; Brower 1958a,c) (though the relationship was also considered Müllerian by some at an early stage (Poulton 1909)). Brower's (1958a,c) studies upheld the view that the system was Batesian, since monarchs were less edible than viceroys to jays, and the same birds generalised between queens and monarchs.

However, monarchs and queens sometimes possess lower chemical defences than expected (see Ritland & Brower 1991). Also, other studies with birds show differences from Brower (1958a,c). For example Scrub Oak Jays,

Pinon Jays, and Chickadees will eat some monarchs (Peterson 1964). Moreover, red-winged blackbirds (*Agelaius phoeniceus*) found viceroy abdomens as unpalatable as monarchs', and more unpalatable than queens' (wings were removed to eliminate colour cues) (Ritland & Brower 1991). This implies that the relationships between the species are Müllerian, not Batesian. This variation in relative palatability can be explained by automimicry; in each case a different set of butterflies was used, and their relative palatabilities depended on which host-plant they had fed on. For example, queens fed on four milkweed species varied in acceptability to red-winged blackbirds (Ritland 1994). The variability is so great that their relationship with viceroys could be as Batesian models, Müllerian co-mimics, or Batesian mimics, depending on which plant they were from. Furthermore, queens feed on all four species in nature (Ritland 1994), and 280 queens caught in one area were extremely variable in palatability (Moranz & Brower 1998). To add to the variation even further, monarchs have been found to vary in palatability according to their age (Alonso-Meja & Brower 1994).

The reason female butterflies sometimes lay on non-toxic plants is unclear. Unpalatability is advantageous, since it reinforces predators' associative learning, yet populations of some butterflies can contain up to 80% automimics (Brower *et al* 1975). Though low levels of models can protect mimics (see 1.3.1), this implies a cost to laying on toxic host plants, for example a decrease in larval growth rate (Brower *et al* 1972; Feeny *et al* 1985, but see Smith 1978; Feeny *et al* 1985) or increase in parasitoid attack rate (Gibson 1984). There could also be a seasonal effect, similar to that seen between species (see 1.3.2) where automodels

emerge before automimics. If individuals become more palatable as they get older (Alonso-Meja & Brower 1994), or toxicities decrease over the season (Srygley & Kingsolver 1998), predators could learn to associate warning colouration with unpalatability early in the season with automodels, and later-emerging automimics would be protected.

Hence there can be variation in palatability between and within individuals of a species. On top of this, there is variation in acceptability to predators according to their level of hunger and variation between predators in their tolerance to distastefulness and discrimination capabilities (Alcock 1971; Chai 1996; Dlusski 1984). This variation must lead to an extremely dynamic system, which would be almost impossible to model, with a mosaic of relationships differing in benefits over time and space.

If hoverflies are unpalatable (see 1.2.2) it is possible that they too are automimics. If so, their colour patterns could be true warnings in some cases, advertising their unpalatability. Unpalatable individuals would be Müllerian mimics of each other, and palatable ones would be Batesian automimics. If this were the case, there would be no reason to expect perfect mimicry of wasps. Though there are reasons to doubt whether hoverflies are unpalatable at all (see 1.2.2), this is an idea worthy of further investigation.

1.5.3 The palatability spectrum and its implications

1.5.3.1 The distinction between Müllerian and Batesian mimicry

Acceptability to predators also varies across a wide range between prey species (Brower *et al* 1963, 1968; Brower & Brower 1964; Marples *et al* 1989; Sargent 1995). This is known as the palatability spectrum. In many cases, prey cannot be simply categorised as ‘palatable’ or ‘unpalatable’, but are found to be of an intermediate palatability, or weakly distasteful (Huheey 1976, 1980, 1988; Benson 1977; Sheppard & Turner 1977; Turner 1987, 1995; Malcolm 1991; Speed 1993a,b; Gavrilets & Hastings 1998; MacDougall & Dawkins 1998). The palatability spectrum has caused great debate because it complicates the traditional definitions of Batesian and Müllerian mimicry. If ‘Müllerian’ species are not equally unpalatable, the mutualistic nature of Mullerian mimicry is put into question, because the more unpalatable mimic may suffer from the presence of the more palatable (Huheey 1976; 1988; Speed 1993a,b). This type of mimicry is somewhat Batesian in nature, and is hence called ‘quasi-Batesian mimicry’ (Speed 1993a). Monte-Carlo simulations show that mimics can benefit and models lose out up to quite a high level of mimic palatability (Speed 1993a). This implies that mimicry is often of this type, since mimics are rarely completely palatable (Pinheiro 1996), and it seems unlikely that a model and mimic will have exactly equal palatabilities. The concept of quasi-Batesian mimicry is also useful in explaining polymorphism in supposedly Müllerian mimicry rings (see 1.4.4.3).

Alternatively, while the weakly unpalatable mimic must benefit more than the strongly unpalatable mimic does, the latter could still benefit to some extent (Sheppard & Turner 1977; Benson 1977; Turner *et al* 1984; Turner 1984a,b.) If so, the mutualistic nature of Müllerian mimicry is maintained, and there is a clear difference between the evolutionary dynamics of Batesian and Müllerian mimicry. Alternative mathematical models to those of Huheey (1976) and Speed (1993a) show discontinuity between Müllerian and Batesian mimicry (Turner *et al* 1984; Owen & Owen 1984).

1.5.3.2 Predator behaviour in mathematical models

The debate hinges on *a priori* assumptions made about predator behaviour by the mathematical models (Joron & Mallet 1998; MacDougall & Dawkins 1998; Speed 1999). Mathematical models use varying algorithms of learning and forgetting, which make big differences to their predictions (Turner & Speed 1996; Speed 1999), so the results of each mathematical model must be treated with caution.

The nature of predators' memory has been a subject for particular debate. Huheey (1964) devised a simple 'n-parameter' model, with a set forgetting variable, n , upon which many other more complex models have been based (Huheey 1976,1980,1988; Brower *et al* 1970; Pough *et al* 1973; Estabrook & Jespersen 1974; Bobisud & Potratz 1976; Luedeman *et al* 1981; Owen & Owen 1984). However, it is debatable whether there is a real relationship between n and biological time (Benson 1977; Turner 1984a,b). Other mathematical models have

used a fluctuating probability of the predator eating the prey in place of n (Turner *et al* 1984; Turner 1987; Speed 1993a; Turner & Speed 1996). This attack probability increases if the prey experienced is palatable, decreases if it is unpalatable, and thereafter returns asymptotically to 50% over time if the prey is not encountered again. Running Monte-Carlo simulations with such a system allows many different algorithms of forgetting to be tested, including the assumptions of the n -parameter models (Turner & Speed 1996).

Exactly how a predator's attack probability decreases in nature is uncertain; for example it may be cumulative or instantaneous, constant or variable according to the strength of the stimulus, and dependent on time or on the occurrence of external events (Turner & Speed 1996). There is a lack of knowledge on this topic (Speed 1993a,b; Charlesworth & Charlesworth 1975; Turner 1995; Turner & Speed 1996), and mathematical models have often ignored models of learning developed by psychologists (see Turner & Speed 1996). However, an important step was to use psychologically (Pavlovian) based rules for learning, memory and motivation (Speed 1993a). The rules included that the speed and asymptotic level of learning were dependent on the palatability of prey, were not constant, and there was time-based forgetting. For a particular mimic-model pair, the predator has an average asymptotic attack probability (aaap). Speed found that a small difference between the model and mimic in palatability could cause a big enough increase in the aaap for the model to outweigh the benefits of sharing predator education; hence his premise that quasi-Batesian mimicry is the norm.

Furthermore, Turner & Speed (1996) ran Monte-Carlo simulations of 30 different combinations of 5 learning rules and 7 forgetting rules, and found that most produced a spectrum of Batesian-quasiBatesian-Müllerian mimicry 'zones', supporting this notion. However, in nature intermediate aaap's may be rare, since predators have sharp boundaries between their likes and dislikes (Turner *et al* 1984; Malcolm 1990; Chai 1996). If intermediate aaap's are rare, then the quasi-Batesian zone may be only theoretical (Joron & Mallet 1998), and quasi-Batesian mimicry would rarely be seen in practice.

Also, Turner & Speed (1996) did not include any consideration of predator recognition errors in their analysis, but assumed the predator identified the prey correctly 100% of the time. This factor could sometimes outweigh the costs of an increased attack probability for the Müllerian 'model'. This is because the presence of even a more weakly unpalatable mimic could decrease the predator's chances of misidentifying the prey if it has a limited number of patterns it can learn (MacDougall & Dawkins 1998). Whether the costs (an increased aaap) or the benefits (a decrease in predator discrimination errors) are more important will depend largely on the processing capacity of a particular predator. If it has a large processing capacity, there will be no advantage in decreasing the number of patterns and quasi-Batesian mimicry may dominate. However, if it has a more limited processing capacity, the advantages of having a mimic could outweigh the costs and thus the relationship could be truly Müllerian (mutualistic).

The limited amount of information on forgetting, learning, real levels of aaap's, the costs of increases in aaap's and discrimination errors make it very

difficult to decide which of these factors are most important (Joron & Mallet 1998; MacDougall & Dawkins 1998; Speed 1999). In addition, parameters such as hunger levels, alternative prey and imperfect mimicry will also impact on the dynamics of mimicry. Therefore, while mathematical models can indubitably provide insights, it is difficult to see how progress can be made in this area without real empirical data using real predators.

1.5.4 Relationships between mimicry, unprofitability and flight morphology

Previous sections have shown in some detail how warning colouration and mimicry can provide effective defence mechanisms against predation in the complex and dynamic environment of variable profitability, relative abundance and predator behaviour. However, the relationship between unprofitability and colour pattern is only part of the picture.

Different prey have different strategies to cope with predation; some are cryptic, and others deliberately advertise themselves with conspicuous colouration, either honestly (if aposematic) or dishonestly (if Batesian mimics). Generally, two alternative defence strategies can be identified: 'aposematism' and 'escape'. Kammer & Heinrich (1978) predicted that this divergence should be associated with morphological, metabolic and thermoregulatory divergence. Most work on this has been across butterfly families (e.g. Chai 1986; Srygley & Chai 1990a,b; Chai & Srygley 1990; Marden & Chai 1991; Srygley & Dudley 1993; Srygley 1994; Chai 1996; Pinheiro 1996; Srygley & Kingsolver 1998). I shall describe these relationships in some detail, since a later part of this thesis will

attempt to use some of the relationships described here to determine what type of defence strategy hoverflies are using. Table 1.1 (adapted from table 1 in Srygley (1994)) shows some of the characters associated with the two strategies of aposematism and escape.

These divergent patterns are geographically robust between Panamanian (Chai & Srygley 1990; Srygley & Chai 1990a; Srygley 1994), Costa Rican (Marden & Chai 1991; Srygley 1994; Chai 1996), and Brazilian (Pinheiro 1996) butterflies. There is also some indication from a small number of species that they also exist in temperate regions (Srygley & Kingsolver 1998), though maybe less so than in the tropics because of the relatively small proportion of specialised predators (Chai 1996).

Most palatability and escaping ability information is based on the preferences of rufous-tailed jacamars (*Galbula ruficauda*) (Chai 1996; Chai & Srygley 1990). These are specialised avian insectivores, and usually attack flying insects (see Chai 1996). However, the relative palatabilities and escaping abilities of butterflies were found to be similar using a generalist kingbird (*Tyrannus melancholicus*) (Pinheiro 1996), though their tolerance to unpalatability was much higher. Palatabilities of three temperate butterfly species with Red-winged Blackbirds (*Agelaius phoeniceus*) have also been broadly in agreement (Srygley & Kingsolver 1998).

Character	Defence Strategy	
	'Aposematism'	'Escape'
	e.g. Heliconiines, danaines, ithomiines and their mimics	e.g. Pierids and nymphalines
Palatability ^{1,2,3}	Relatively low	Relatively high
Thoracic temperature ^{1,4}	Relatively low	Relatively high
Difference between thoracic temperature and ambient temperature ¹	Small	Large
Flight activity ⁴	Many times and places	Only in warm micro-habitats with access to sunlight
Flight muscle (thoracic allocation) ⁵	Relatively small	Relatively massive
Gut/ ovary (abdominal allocation) ⁵	Relatively large	Relatively small
Abdomen shape ^{1,6,9}	Long, slender	Short, stout
Centre-of-body-mass position ^{3,7,8}	Posterior to wing base	Nearer wing base
Flight speed ^{1,6,10}	Slow	Fast
Flight pattern ¹	Regular, in straight lines	Bobbing, erratic
Probability of attack ^{1,9}	Low	High
Probability of escape if attacked ^{1,2,3}	Low	High
Damage when captured ⁹	Little damage	More damage
Centre-of-wing-mass position ⁸	Relatively far from wing base	Near wing base
Conspicuousness at rest ^{9,10}	Conspicuous (wing undersides bright)	Cryptic (wing undersides cryptic)

¹ Chai & Srygley 1990

² Pinheiro 1996

³ Srygley & Kingsolver 1998

⁴ Srygley & Chai 1990b

⁵ Marden & Chai 1991

⁶ Srygley & Chai 1990a

⁷ Srygley & Dudley 1993

⁸ Srygley 1994

⁹ Chai 1996

¹² Mallet & Singer 1987

Table 1.1. Adaptive suites in butterflies with relation to defence strategies. Data was obtained with live butterflies by a variety of methods (see references above).

1.5.4.1 Temperature and flight muscle

An association is expected between body temperature and evasive flight ability (Marden & Chai 1991), as temperature affects both whether insects can fly at all, and their wingbeat frequency. Therefore it is not surprising that those (mostly unpalatable) species which are relatively poor flyers have lower thoracic temperatures than palatable, able flyers (Chai & Srygley 1990; Srygley & Chai 1990b). Furthermore, good flyers' thoracic temperature is higher relative to the ambient temperature, which is important for escape from a stationary position (Chai & Srygley 1990) (though birds have also been observed capturing flying butterflies (see Chai & Srygley 1990)). The maintenance of this high temperature means that palatable butterflies tend to be active only in warm, sunny microhabitats, whereas unpalatable species are able to perform in a wider range of locations and conditions (Chai & Srygley 1990; Srygley & Chai 1990b).

To improve flight performance even further, palatable species tend to have much more massive flight muscles (measured as FMR, flight-muscle mass/ total body mass) relative to unpalatable species (Marden & Chai 1991). This additional flight muscle mass in the thorax increases the power available for flight (Ellington 1991), which increases potential acceleration and flight speed (Chai & Srygley 1990). FMR is directly proportional to aerial acceleration (Marden 1987; Marden & Chai 1991), and influences manoeuvrability (Marden & Chai 1991). Thus, there is a clear divergence here between unpalatable butterflies, which do not retain the ability to accelerate away from predators, and palatable butterflies, which have been selected to do so.

The thorax is largely composed of flight muscle (85-95% in dragonflies, Marden 1989). Thus when the FMR is decreased (as in unpalatable butterflies), we might expect that resources could be reallocated to other areas, notably reproductive effort (e.g. Denno *et al* 1989; Groeters & Dingle 1989). A trade-off is indeed observed, both between migratory and sedentary morphs of butterflies (i.e. a trade-off with flight activity) and within sedentary morphs, with an inverse relationship between ovarian mass and evasive flight capacity (i.e. a trade-off with flight ability) (Srygley & Chai 1990a; Marden & Chai 1991).

1.5.4.2 Body shape and its implications

As noted above, unpalatable butterflies tend to have a relatively small flight muscle, which trades-off with a relatively large abdominal mass (Srygley & Chai 1990a; Marden & Chai 1991). This larger abdomen in unpalatable butterflies is also associated with a long, slender shape (Chai & Srygley 1990; Srygley & Chai 1990a; Chai 1996). Conversely, palatable butterflies tend to have short, stout abdomens. The shape is again connected with flight agility and thus escape ability; palatable butterflies not only have greater acceleration from their large flight muscle mass, but are also more manoeuvrable in flight. This is because the short, stout shape of palatable butterflies positions the centre-of-body-mass closer to the wing base than in the long, slender, unpalatable butterflies (Srygley & Dudley 1993; Srygley 1994; Srygley & Kingsolver 1998). Positioning the centre-of-body-mass nearer the wing base reduces the body's radial moment of inertia, which increases the body's responsiveness to pitching motions generated by the

wings (Ellington 1984). This maximises angular acceleration and manoeuvrability, which effectively means that rapid changes in speed and direction are facilitated (Ellington 1984; Srygley & Dudley 1993; Srygley 1994).

The position of the centre-of-body-mass produces obvious differences in flight pattern between palatable and unpalatable butterflies (e.g. Bates 1862; Carpenter 1939; De Vries 1987; Chai & Srygley 1990). Palatable butterflies generally have a faster, more 'bobbing' flight, while unpalatable butterflies' flight pattern is more regular and smooth. This smooth flight is due to the positioning of the centre-of-body-mass more distally on the abdomen (further from the wing base) (Srygley & Chai 1990a; Srygley 1994 for details). This is an advantage to unpalatable butterflies as it saves them the energetic costs of an irregular flight path (Dudley 1991), and also increases the conspicuous effect of their colouration, thus decreasing the chance of mistaken attack (Turner 1984b; Guilford 1986; Chai & Srygley 1990). The energetic costs of bobbing flight in palatable species are outweighed by the advantages of having a flight path that is hard to predict, making them hard to catch (Chai & Srygley 1990). It may also act as a signal to predators in itself, discouraging them from attacking unprofitable prey (Edmunds 1974; Gibson 1974; 1980) (see 1.2.3, 1.5.4.3).

As well as affecting flight pattern and flight performance, body shape itself may serve anti-predator functions. The short bodies of palatable butterflies are less easily grasped by predators than long, thin bodies. This increases palatable species' probability of escape if attacked (Chai & Srygley 1990; Pinheiro 1996; Srygley & Kingsolver 1998), since capture by the wing is less

harmful (Chai & Srygley 1990). While unpalatable species are more easily captured, they are more likely to escape undamaged (Chai 1996), sometimes due to their emitting a pungent scent when captured.

The general pattern of divergence between the two anti-predator strategies is also seen in wing loading (Chai & Srygley 1990; Srygley 1994); palatable species' centre-of-wing-mass, like their centre-of-body-mass, is positioned nearer the wing base than in unpalatable butterflies. The position of the centre-of-wing-mass affects the acceleration of the wing stroke, and the wingbeat frequency (through changes in radial acceleration and inertia of the wings during acceleration and deceleration during the wing stroke) (Ellington 1984; Srygley 1994). Positioning it nearer the wing base in palatable butterflies increases potential flight speed by favouring rapid wing acceleration during the wing stroke (Betts & Wootton 1988; Srygley 1994), again improving flight performance.

1.5.4.3 Mimicry and flight morphology

As described above, the body shape, flight pattern, centre-of-body-mass, and wing loading of palatable butterflies all contribute to improving their flight performance, while in unpalatable species, performance is compromised, with energetic gains. However, as well as affecting flight performance, all these characters may also act as signals to the predator. This is particularly well established in unpalatable butterflies, where the flight pattern serves to increase their often conspicuous colouration, and their long body shape is another obvious signal to predators. Long-bodied butterflies are rejected on sight more by

jacamars than short-bodied ones (Chai 1996). As well as the 'long body' signal, unpalatable butterflies are usually conspicuous at rest, with bright aposematic or mimetic uppersides and bright undersides to their wings, whereas palatable butterflies usually have non-aposematic uppersides and cryptic undersides (Mallet & Singer 1987; Chai 1996).

Batesian (palatable) mimics of unpalatable species will therefore improve their mimicry if they mimic both wing colouration and body shape. Therefore we would expect their characteristics to be similar to those in the 'unpalatable' adaptive suite. If mimicry is effective, the need for agile flight should be reduced anyway since predation pressure will be reduced, again giving a flight morphology similar to that of unpalatable species. However, selection may also favour retaining features that contribute to evasive flight, since Batesian mimics will not be released if captured by predators (unlike unpalatable species). This makes it difficult for a good Batesian mimic with the flight pattern of the model to evolve (Srygley & Chai 1990a; Srygley 1994; Chai 1996). Indeed, there seem to be a very low number of 'cheaters' which have evolved a long abdomen without unpalatability; most long thin butterflies, when tasted by jacamars, are not eaten (Chai 1996).

Examples of Batesian mimics indicate that they do not fully mimic their unpalatable models. For example, *Dismorphia amphiona* has a relatively large thoracic mass relative to its models (Chai 1996), suggesting that it has retained flight speed and acceleration in case of detection. *Consul fabius*, another palatable mimic, positions its centre-of-body-mass near the wing base like other palatable

species, retaining manoeuvrability, but positions its centre-of-wing-mass near to that of its models (further from the wing base) (Srygley 1994). Again, this suggests that it has retained aspects of evasive flight over its models (though a change in centre-of-body-mass position could follow later in its evolution) (Srygley 1994).

Müllerian mimics, on the other hand, do not have the same problem; their colour patterns, long abdomens and unpalatability all reinforce each other. There is evidence that the positions of centres-of-body-mass and centres-of-wing-mass converge strongly within Müllerian mimicry complexes, independent of phylogenetic effects (Srygley 1994, 1999; Pinheiro 1996), leading to close mimicry of flight patterns as well as colour patterns. This is in contrast to the traditional view that Batesian mimics will evolve to appear more similar to their models than Müllerian mimics do.

This strong association of positions of centres-of-body-mass and centres-of-wing-mass within mimicry groups is not only found among unpalatable species (Srygley 1994, 1999; Pinheiro 1996). Two mimicry groups, the *Adelpha-Doxocopa* complex (Aiello 1984) and a green-and-black pattern group, are usually considered to contain Batesian mimics, but no evidence was found of any unpalatable models (Pinheiro 1996). However, some species in both complexes exhibit a good ability to escape predators. If predators avoid these unprofitable species (as they do unpalatable species), their mimicry of each other could be purely for escape ability (what Srygley (1994) calls 'locomotor' mimicry), see also 1.2.3).

Additionally, some very bright palatable species may be aposematic purely for flight agility (see 1.2.3). Specifically, two bright *Morpho* species were the only palatable species (apart from Batesian mimics) ever rejected on sight by kingbirds (Pinheiro 1996). (see 1.2.3 for more details).

1.5.4.4 Flight morphology in hoverflies

There are therefore a number of patterns we might expect if hoverflies are mimics of wasps or if they are advertising their own flight agility (see 1.2.3.2). If they are Batesian mimics of wasps, they will experience reduced predation pressure, and thus be able to reduce their flight agility. Their subsequent flight morphology would also be an advantage because it would mimic that of their unprofitable models, which have no need for agile flight. On the other hand, as discussed above, some mimics have retained some features of palatable species to retain some flight agility in case of detection by predators. Since hoverflies vary in their similarity to wasps, we might expect that those species which most resemble wasps would have least need of retaining these features. Therefore, the greater the similarity, the more 'unpalatable' features are likely to be retained. Hence with increasing similarity to wasps, we might expect decreasing flight agility (and thus a centre-of-body-mass further from the wing base), and a subsequent increase in reproductive potential as seen in butterflies (Marden & Chai 1991).

If, on the other hand, hoverflies are aposematic, different flight morphologies would be expected. Since hoverflies would not be mimicking

wasps, there would be no particular pattern of decreasing flight agility with an increase in similarity to wasps. If hoverflies are unpalatable, and are advertising this in the same way as butterflies, a pattern similar to that seen in table 1.1 would be expected. Hence, ‘mimics’ (hoverflies with yellow-and-black stripes) would have lower flight agility than ‘non-mimics’ (black or cryptic species), with the flight morphologies to match. If hoverflies are aposematic for unprofitability via escaping ability, the opposite would be true; those species with black-and-yellow patterns would be those with the best flight ability. Therefore we would expect ‘mimics’ to have better flight agility than ‘non-mimics’, and hence centres-of-body-mass nearer the wing base and a lower reproductive potential. There would again be no correlation between degree of similarity and flight agility.

Whichever kind of unprofitability they were advertising, hoverfly species would be Müllerian mimics of each other, and there should be strong convergence within mimicry groups for centre-of-body-mass position and other features of flight morphology, as in neotropical butterflies (Srygley 1994, 1999).

No comparative study of flight morphology and reproductive features with regard to colour patterns has yet been carried out for hoverflies. This could help elucidate which, if any, of these scenarios is correct. One of the aims of this thesis is to examine some of these hypotheses.

1.6 Mimicry in hoverflies

In this introductory chapter, I have tried to summarise the literature on mimicry, emphasising which factors may impact on the efficacy of mimicry. This

section briefly recaps, referring back to previous sections, the reasons why mimicry in hoverflies is a particularly intriguing problem and what some possible explanations are for the paradoxes we observe.

In hoverflies which mimic honeybees and bumblebees, we see many of the features associated with classic Batesian mimicry; high fidelity of imitation (see 1.4.2.1), low numbers relative to their models (see 1.3.1), polymorphism within species for different models (see 1.4.4.1), and correlations in numbers of mimics and models (see 1.3.3).

Some hoverflies are highly accomplished wasp mimics. The function of high fidelity imitation of the abdominal patterns of *Vespula* in genera like *Temnostoma* and *Spilomyia* is almost indubitably Batesian mimicry, especially when seen in combination with behavioural mimicry (see section 1.1.1). These high fidelity mimics, rarely seen in Britain, are relatively rare compared with their models (Dlusski 1984). This is also true of the best mimics in this country, such as *Chrysotoxum* spp (J. Owen, unpublished data).

However, the majority of wasp mimics, certainly in the UK, are ‘poor’ mimics, easily distinguished from wasps, at least by humans. Mimicry theory predicts that Batesian mimics should evolve to have perfect mimicry, and it is unclear why so many hoverfly species have not done this (see 1.1.1, 1.4.2.1). These imperfect mimics often outnumber their supposed models by factors not allowable by any theoretical model or experiment on Batesian mimicry (see 1.3.1, 1.3.3). If mimics outnumber models, predators should learn that their colour patterns do not signal noxiousness because they will encounter mimics more often

than models; in this case, there seems no reason why the mimetic patterns in hoverflies should persist.

Alternative explanations to wasp mimicry need to be sought to account for these paradoxes. Table 1.2 summarises possible explanations for poor wasp mimicry in hoverflies.

<i>Explanation</i>	<i>Explains imperfection or abundance?</i>	<i>Brief description</i>	<i>Colour patterns mimetic?</i>	<i>Refer to section</i>
High noxiousness of wasps	Both	High unprofitability of model means more mimics, and less faithful mimics, can be supported	Yes, Batesian	1.4.2.4, 1.5.1
Disturbed habitat hypothesis	Abundance	Human-caused habitat disturbance has led to an increase in larval food source (aphids) for poor mimics, artificially boosting their numbers	Not clear	1.3.3
Thermoregulation	Both	Black areas in pattern must coincide with blood vessels which need to be heated for flight capability, thus constraining the patterns	No	1.4.2.4

Table 1.2. Hypotheses explaining the existence and abundance of imperfect wasp mimics (continued over page).

<i>Explanation</i>	<i>Explains imperfection or abundance?</i>	<i>Brief description</i>	<i>Colour patterns mimetic?</i>	<i>Refer to section</i>
Encounter rate	Abundance	Predators actually encounter mimics less often than models, despite their abundance relative to models	Yes, Batesian	1.3.3
Satyric mimicry	Both	A combination of ambiguous signals leads to confusion in the predator, allowing time to escape	Not clear	1.4.3.1
Aposematism for unpalatability	Both	Hoverflies are unpalatable, and are advertising their unpalatability	Yes, Müllerian	1.2.2, 1.5.2, 1.5.4.4
Transition to perfect mimicry	Imperfection	Poor wasp mimics are in a transitory phase towards the evolution of perfect mimicry	Yes, Batesian	1.4.2.2
Aposematism for flight agility	Both	Warning colouration signals to predators that it will not be profitable to chase such agile prey	Yes, Müllerian	1.2.3.2, 1.5.4.4
Predator perception	Imperfection	To predators, the colour patterns are not imperfect, as their vision differs from humans'	Yes, Batesian	1.4.3.1
Phenology	Abundance	Seasonal fluctuations in abundance mean naïve predators learn to avoid wasps before they encounter large numbers of hoverflies	Yes, Batesian	1.3.2, 1.3.3

Table 1.2(continued). Hypotheses explaining the existence and abundance of imperfect wasp mimics

Not all of these explanations are mutually exclusive; the colour patterns of hoverflies could have evolved for a combination of reasons. It is not possible to examine all possible options within the remit of this thesis, but some of the more likely and testable hypotheses are presented in subsequent chapters.

The remainder of the thesis is in the form of articles for scientific journals (with the exception of chapter four, which explores the image analysis technique). For this reason, I have covered a great deal of the information presented in subsequent chapters in this general introduction, to put them into context. This layout inevitably involves some repetition, particularly in the introduction and methods sections.

I have used a variety of novel approaches to investigating mimicry, rather than the ubiquitous mathematical models and reciprocal frequency experiments. The data used are derived from a variety of sources, including long-term population data from Malaise trapping by J.Owen, many other hoverfly population studies from the literature, and a large morphological dataset mostly assembled by F.Gilbert.

The next three chapters (2-4), as well as drawing their own conclusions, test assumptions and explore data used in the subsequent three (5-7). Firstly, Chapter Two will use a long-term dataset from a suburban UK garden to closely examine asynchrony in wasp mimics and ratios of mimics to models in this particular ecosystem. This dataset also gives an opportunity to examine the influence of model numbers on mimic abundance among years, as well as

comparing wasp mimics and bee mimics. It is also used later to compare with less disturbed habitats.

Chapter Three is not directly concerned with mimicry, but will explore an extensive dataset on morphological characters across a wide range of hoverfly species, which is later used to test predictions about hoverflies' colour patterns. The relationship of the evolution of reproductive potential with that of body size will be investigated, and the main selection pressures on these characters discussed. Independent contrasts methods are used when comparing across species, in this and subsequent chapters.

Chapter Four will make some important tests of the image analysis technique used to rate similarity of hoverflies and wasps. The large-scale use of the techniques in this thesis merit the close examination of these methods. I will check whether any adjustments need to be made, and whether assumptions made in the use of images are valid.

Chapter Five will then draw on both the population dataset from Leicester and the image analysis technique to compare this highly human-influenced habitat with undisturbed habitats through fieldwork and literature data, to test hypotheses about the high abundance of poor mimics in the UK.

Following this, Chapter Six will attempt to clarify the reasons why wasp-mimic patterns have not evolved to perfection in most hoverflies, by testing predictions from different evolutionary scenarios using morphological reproductive data across hoverfly taxa. Chapter Seven continues on this theme, but using a direct measure of flight agility.

Chapter Two

Abundance of Batesian mimics and their models in a suburban garden

2.1 Introduction

One of the key factors in Batesian mimicry is the relative abundance of models and mimics. Protection is afforded to Batesian mimics through predators mistaking them for their unprofitable models (Bates 1862). The more abundant the model relative to the mimic, the more the signal will be reinforced. Therefore abundance of the model should have a large effect on the effectiveness of Batesian mimics to survive and reproduce. This influence could be evident in a number of ways.

Abundance of mimics is limited compared to abundance of models, since if mimics are common relative to models, predators are more likely to encounter mimics, thus undermining the effectiveness of the signal (Fisher 1930; Sheppard 1959; Edmunds 1974). Theoretical (e.g. Huheey 1964; Pough *et al* 1973; Turner & Speed 1996), empirical (e.g. Brower 1960; Huheey 1980; Nonacs 1985) and field (Jeffords *et al* 1979) studies have shown that Batesian mimics are indeed better protected from predators when model abundance is high (though mimics do not necessarily have to be less common than models to be protected (Brower 1960; Turner 1984a)).

Model abundance can also affect the timing of mimic abundance. However, strict temporal synchrony is not essential for protection of mimics, as once thought (e.g. Sheppard 1959; Wickler 1968). Some mimics emerge after their models in the year, and persist even after their models have disappeared (Rothschild 1963; Hetz & Slobodchikoff 1988). Thus predators learn to associate unprofitability with the pattern before mimics emerge, and still remember this message even if the model is no longer present. This may even include the following season, if predators' memories are long enough (Evans & Waldbauer 1982).

The hoverflies (Diptera: Syrphidae) comprise around 250 species in the UK, many of which appear to mimic wasps or bees (Wickler 1968; Stubbs & Falk 1983; Torp 1994). However, many wasp mimics only poorly resemble wasps, compared with the high-fidelity mimicry of bees by hoverflies, or the mimicry between butterfly species. The abundance of many hoverfly 'wasp mimics' is also high relative to their putative models (Grewcock 1992; Dlusski 1984). These facts put the status of hoverflies as Batesian mimics of wasps into some doubt, though their mimicry of honeybees (*Apis* spp.) and bumblebees (*Bombus* spp.) is less controversial.

A 23-year Malaise trap dataset of hoverfly and Hymenoptera numbers gives a unique opportunity to examine relative abundance of putative models and mimics across years, and helps clarify the hoverflies' status as mimics.

The abundance of wasp mimics relative to models should be relatively low if this is Batesian mimicry. However, other studies show that relative mimic

abundance is high in hoverflies (Dlusski 1984; Grewcock 1992; Howarth 1998). This does not rule out their status as mimics, since mathematical models (Turner 1984) show that mimics can still persist up to a maximum of 10 mimics per model, and practical studies (e.g. Brower 1960; Holling 1965; Avery 1985; Nonacs 1985) have also shown that mimics can still be protected even when they outnumber models. Nevertheless, numbers should still be limited by model abundance, even if this limit is high. Since the abundance of mimics is limited by model abundance, correlations between wasp numbers and wasp mimic numbers are predicted among years. Mimics should lose protection and hence suffer increased predation as mimetic frequency increases (e.g. Lindström 1997). For example, a season of high wasp abundance could support more wasp mimics, because predators will encounter models more often. This might not be evident in the season itself, because numbers will be restricted by the number of reproducing adults already present, and most hoverfly species only have 1-2 generations per year (Owen 1991). However, mimic abundance in subsequent years is predicted to be affected because of the high survival rate and hence increased numbers of individuals available to reproduce the next season. There could also be an effect via predator learning; high abundance of models one year should lead to greater reinforcement of the pattern's signal, and more avoidance the following year (providing predators can retain their memory of patterns over the winter (Evans & Waldbauer 1982; Waldbauer & Laberge 1985)). Mimic numbers are not expected to influence subsequent model abundance via predation effects in a similar way, because models have the genuine protection of noxiousness.

This study compares wasp and wasp mimic abundance across years to see if they are correlated in the same year, or in adjacent years. If there are correlations which are not seen between non-mimics and models, these could be due to mimicry. These patterns are compared to bees and their hoverfly mimics, which are expected to show some correlation between models and mimics across years. There is some evidence of the influence of honeybee abundance on their mimics; a sharp decrease in honeybee abundance in a Russian forest coincided with a decrease in honeybee mimics in the same and subsequent years (Dlusski 1984).

Temporal synchrony is not seen between wasps and wasp mimics in previous studies in the UK (Howarth 1998), US (Waldbauer *et al* 1977; Waldbauer & Laberge 1985) or Russia (Dlusski 1994). Wasp mimics tend to be present early in the season relative to wasps. This could still be explicable in terms of mimicry if experienced birds remember the signal from the previous year (Evans & Waldbauer 1982). The Leicester dataset is examined for similar patterns, again compared to the equivalent in bees and bee mimics.

The abundance of alternative prey could also be important (Nonacs 1985; Hetz & Slobodchikoff 1988), as its presence can reduce predation pressure on the entire model: mimic complex. A high proportion of alternative prey in this case might be part of the explanation for the persistence of mimics at times when models are absent. Data on alternative prey are available from this dataset in the form of counts of non-mimetic hoverflies. These are not the only alternative food

source to mimetic hoverflies for their predators, but they are likely to be a major source of alternative prey to predators which catch flying insects.

2.2 Methods

2.2.1 Hoverfly data

Abundance data for hoverflies and Hymenoptera are from a long-term Malaise trap study (partly published in Owen (1991)) of a suburban garden in Leicester, U.K. (52°38' N, 1°05' W). The garden is well-stocked with flowers suitable for hoverfly adult feeding, and includes a variety of areas, comprising sun, shade, trees, lawn, paving, flowerbeds and so on. The Malaise trap is described in detail by Owen (1991, p.54). Essentially, it is a tent-like structure made of meshed fabric; flying insects in its 2 metre-wide path hit a vertical 'baffle' of fabric and climb up it towards the light. They are then directed via an obliquely pitched roof into a collecting jar of killing agent. The bottom of the trap is coloured black, and the top white, to encourage the upward movement of insects.

A Malaise trap, in theory, samples the population of flying insects in its path without selectivity. It is therefore a better index of absolute populations than traps which use attractants (Southwood 1978; Muirhead-Thomson 1991). Some trap selectivity is inevitable; for example, larger beetles hit the baffle, drop to the ground and walk away (Owen 1991). However, Malaise traps have been found to be particularly suitable for highly active flying insects, such as the larger Diptera

and Hymenoptera (Juillet 1963). The trap is dependent on insects climbing upwards after hitting the baffle, and hoverflies do always climb upwards when captured in a jar (pers. obs.). Flight behaviour may also affect trap selectivity. For example, Owen (1991) reports that *Eristalis tenax*, *E.pertinax* and *Myathropa florea* may be under-represented in the Malaise trap catch, based on her observations of numbers in the garden. She suggests that the strong flight of these species makes them more likely to fly out of the trap when they hit the baffle. Despite any possible effects of trap selectivity, relative numbers can certainly be compared across years, since these effects should be the same each year. The trap was placed in the same position in the garden (see Owen 1991) in all years (except 1978), and this should also give consistency in catches across years.

All hoverfly, bee and wasp individuals were identified to species level. The years used, and the period over which specimens were totalled, varied among wasps, bees and hoverflies (Table 2.1). Years with no bee counts do not indicate that no bees were present.

The weekly hoverfly counts were also converted to monthly data for some analyses. Collections were made weekly on Sundays, and the weeks were numbered from 1 each year, hence the actual dates of these weeks vary among years. Where a week did not fall in the same month every year, the data were allocated to whichever month the majority of its days fell into in the relevant year. For convenience of reference to some figures, week numbers and months are compared in Table 2.2.

	<i>Hoverflies</i>	<i>Wasps</i>	<i>Bumblebees</i>	<i>Honeybees</i>
1972	Weekly	Annual	Annual	No data
1973	Weekly	Monthly	Annual	No data
1974	Weekly	Monthly	Annual	No data
1975	Weekly	Monthly	Annual	No data
1976	Weekly	Monthly	Annual	No data
1977	Weekly	Monthly	Annual	No data
1978	Weekly	Monthly	No data	No data
1979	Weekly	Monthly	No data	No data
1980	Weekly	Monthly	No data	No data
1981	Weekly	Monthly	No data	No data
1982	Weekly	Monthly	Annual	No data
1983	Weekly	Monthly	Annual	No data
1984	Weekly	Monthly	Annual	Annual
1985	Weekly	Monthly	Annual	Annual
1986	Weekly	Monthly	Annual	No data
1987	Weekly	Monthly	Annual	Annual
1988	Weekly	Annual	Annual	Annual
1989	Weekly	Annual	Annual	Annual
1990	Weekly	Annual	Annual	No data
1991	Weekly	Annual	Annual	Annual
1992	Weekly	Annual	Annual	Annual
1993	Weekly	Annual	Annual	Annual
1994	Weekly	Annual	Annual	Annual

Table 2.1. Frequency of data collection for hoverflies, wasps, bumblebees and honeybees for the years 1972-1994.

Month	Weeks
April	14, 15, 16, 17, (18)
May	(18), 19, 20, 21, (22)
June	(22), 23, 24, 25, (26)
July	(26), 27, 28, 29, 30, (31)
August	(31), 32, 33, 34, (35)
September	(35), 36, 37, 38, 39, (40)
October	(40), 41, 42, 43, (44)
November	(44), 45, 46

Table 2.2. Weeks which fall into each month (for reference to graphs). Weeks in brackets fall into different months depending on the year.

For the purposes of the analysis, hoverflies were categorised as bumblebee mimics, honeybee mimics, wasp mimics or non mimics (Table 2.3). This was a subjective judgement, but generally agreed with the judgements of others (e.g. Stubbs & Falk 1983; Grewcock 1992; Torp 1994). Species with bright yellow or orange stripes or lunules were classified as wasp mimics, while black species and those with small faint markings (such as *Platycheirus* spp., *Melanostoma* spp. and *Syritta pipiens*) were considered non-mimics. Bumblebee and honeybee mimics were also judged subjectively by their similarity to *Bombus* and *Apis* spp., but were easier to classify as their species do not vary in quality as much as wasp mimics.

Bumblebee mimics		
<i>Criorhina berberina</i>	<i>Eristalis intricarius</i>	
<i>Merodon equestris</i>	<i>Volucella bombylans</i>	
Honeybee mimics		
<i>Cheilosia illustrata</i>	<i>Criorhina floccosa</i>	<i>Eristalis abusivus</i>
<i>Eristalis arbustorum</i>	<i>Eristalis horticola</i>	<i>Eristalis nemorum</i>
<i>Eristalis pertinax</i>	<i>Eristalis tenax</i>	
Wasp mimics		
<i>Dasyrphus albostrigatus*</i>	<i>Syrphus ribesii*</i>	<i>Melangyna umbellatarum</i>
<i>Dasyrphus lunulatus*</i>	<i>Syrphus torvus*</i>	<i>Meliscaeva auricollis</i>
<i>Dasyrphus tricinctus*</i>	<i>Syrphus vitripennis*</i>	<i>Meliscaeva cinctella</i>
<i>Dasyrphus venustus*</i>	<i>Chrysotoxum bicinctum</i>	<i>Myathropa florea</i>
<i>Epistrophe grossulariae*</i>	<i>Chrysotoxum festivum</i>	<i>Scaeva pyrastris</i>
<i>Epistrophe nitidicolus*</i>	<i>Chrysotoxum verralli</i>	<i>Scaeva seleniticus</i>
<i>Epistrophe eligans</i>	<i>Episyrrhus balteatus</i>	<i>Sericomyia silentis</i>
<i>Eupeodes corollae*</i>	<i>Helophilus hybridus</i>	<i>Sphaerophoria menthastris</i>
<i>Eupeodes latifasciatus*</i>	<i>Helophilus pendulus</i>	<i>Sphaerophoria ruelletii</i>
<i>Eupeodes latilunulatus*</i>	<i>Helophilus trivittatus</i>	<i>Sphaerophoria scripta</i>
<i>Eupeodes luniger*</i>	<i>Melangyna cincta</i>	<i>Xanthogramma pedissequum</i>
<i>Parasyrphus malinellus*</i>	<i>Melangyna lasiophthalma</i>	
<i>Parasyrphus punctulatus*</i>	<i>Melangyna triangulifera</i>	
Non mimics		
<i>Baccha obscuripennis</i>	<i>Lejogaster metallina</i>	<i>Platycheirus ambiguus</i>
<i>Cheilosia albitarsis</i>	<i>Neoscia podagrica</i>	<i>Platycheirus angustatus</i>
<i>Cheilosia bergenstammi</i>	<i>Neocnemodon vitripennis</i>	<i>Platycheirus clypeatus</i>
<i>Cheilosia paganus</i>	<i>Orthonevra splendens</i>	<i>Platycheirus immarginatus</i>
<i>Cheilosia proxima</i>	<i>Paragus haemorrhous</i>	<i>Platycheirus manicatus</i>
<i>Cheilosia vernalis</i>	<i>Paragus tibialis</i>	<i>Platycheirus peltatus</i>
<i>Chrysogaster hirtella</i>	<i>Pipiza austriaca</i>	<i>Platycheirus scambus</i>
<i>Eumerus strigatus</i>	<i>Pipiza bimaculata</i>	<i>Platycheirus scutatus</i>
<i>Eumerus tuberculatus</i>	<i>Pipiza fenestrata</i>	<i>Rhingia campestris</i>
<i>Ferdinandea cuprea</i>	<i>Pipiza luteitarsis</i>	<i>Syrpita pipiens</i>
<i>Ferdinandea ruficornis</i>	<i>Pipiza noctiluca</i>	<i>Triglyphus primus</i>
<i>Heringia heringii</i>	<i>Platycheirus albimanus</i>	

Table 2.3. Allocation of species caught to mimicry status groups. * indicates species is in

‘*Syrphus* group’. Allocation to groups was subjective, but generally agreed with the judgements of others (e.g. Stubbs & Falk 1983; Grewcock 1992; Torp 1994).

2.2.2 Data analysis

Cross-correlations were carried out to compare model and mimic numbers among years. In a cross-correlation, observations of one time series are correlated with observations of another, at various lags and leads. In this case, the two series are annual model totals and annual mimic totals over a number of years. A lag of -2 to +2 years was used, effectively carrying out five correlations (Table 2.4).

Numbers of non-mimics and mimics were separately cross-correlated with model numbers, and compared, to differentiate between fluctuations caused by general factors affecting all hoverflies (e.g. weather conditions) and those which could be due to mimicry.

Lag	
-2	Mimic total correlated with model total 2 years later
-1	Mimic total correlated with model total 1 year later
0	Model total correlated with mimic total in the same year
+1	Model total correlated with mimic total 1 year later
+2	Model total correlated with mimic total 2 years later

Table 2.4. Explanation of correlations carried out by cross-correlation of lag -2 to +2.

2.3 Results

54032 individual hoverflies were collected and identified to 94 species (by J.Owen) over the 23 years 1972-1994. Annual totals of putative models were also obtained (Figure 2.1). Yearly totals of *Vespula* spp. were obtained for all years,

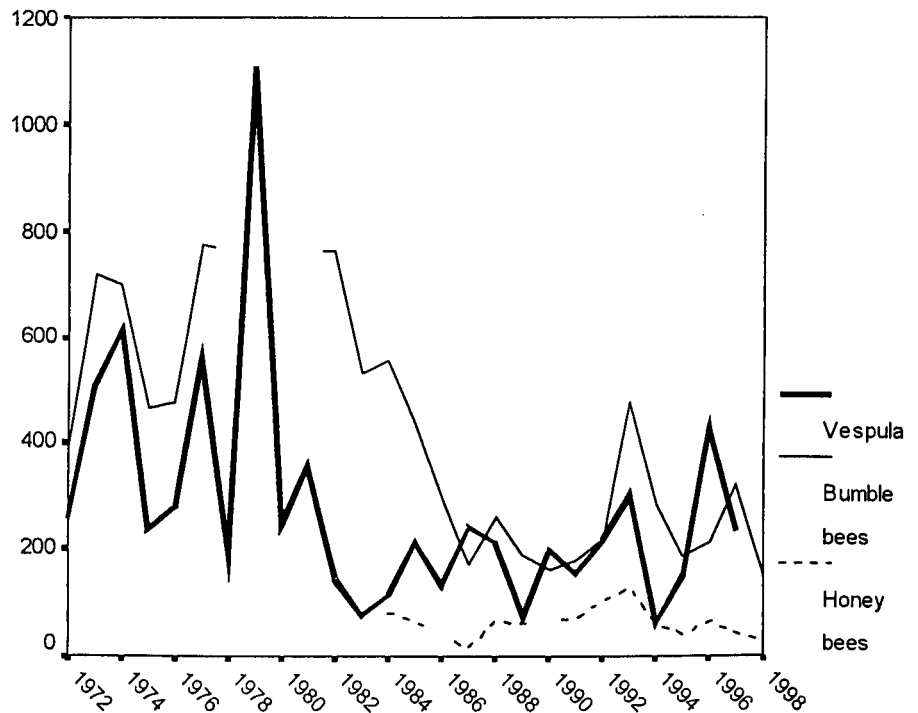


Figure 2.1. Annual catches of putative models.

and monthly data on *Vesputa* were available for 15 years (from M. Archer, College of Ripon & St. John, York) (Table 2.1). *V. vulgaris* was the commonest wasp, followed by *V. germanica*. Other *Vesputa* and *Dolichovesputa* species were rarely caught.

The most common bumblebee was *Bombus pascuorum* (54% of bumblebees caught), followed by *B. pratorum* (13%), *B. hortorum* (12%), *B. terrestris* (8%), *B. lucorum* (6%), and *B. lapidarius*, *B. ruderarius*, *B. ruderatus* and *Psithyrus* spp. with less than 5% each.

2.3.1 Within year data

Of the model data, only that for *Vespula* was segregated within years into monthly totals. Thus three aspects of within-year patterns could be examined:

- (a) relative proportions of different types of hoverfly over the season
- (b) abundance of hoverflies relative to wasps over the season
- (c) relative timing of emergence of hoverflies and wasps

2.3.1.1 Relative proportions of hoverfly types within years

For the early part of the season (May/ June), non-mimics usually outnumber wasp mimics (Figure 2.2), but from July-September they are more

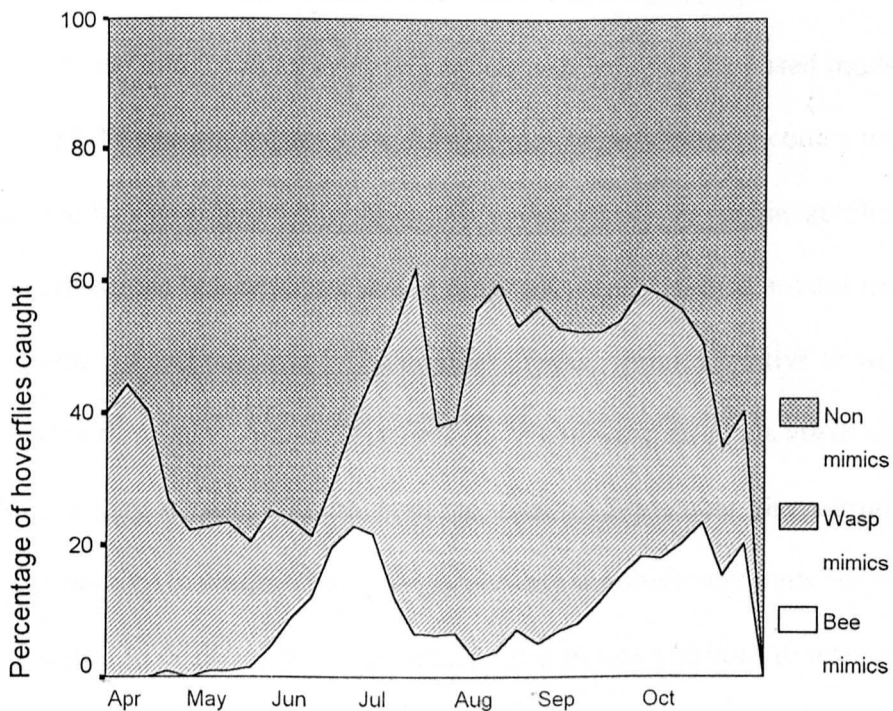


Figure 2.2. Relative catches of non-mimetic hoverflies, wasp-mimetic hoverflies and bee-mimetic hoverflies (comprising honeybee and bumblebee mimics). Percentages are calculated weekly. Months are marked for reference.

equal in number. Wasp mimics form a particularly low proportion of the hoverflies caught at the end of June.

Bee mimics (in Figure 2.2 including both honeybee and bumblebee mimics) form a much smaller percentage of the hoverflies caught than non-mimics and wasp mimics. They are proportionally very few in August, despite this being a time when honeybee numbers are at their peak (see Figure 2.8a, 2.8b).

Good wasp mimics (*Xanthogramma* and *Chrysotoxum* spp.) are relatively rarely caught. They generally only appear in July and August when total hoverfly numbers are very high, and then only comprise 0.1-0.3% of the hoverflies present.

2.3.1.2 Abundance of hoverflies relative to wasps within years

Wasp mimics in an average year outnumber their supposed models for nearly all the season (Figure 2.3a, 2.3b). (The *Vespula* weekly counts were estimated by dividing the monthly totals by 4/5 weeks; hence the graph shows sharp gradations between numbers in different months, which are not necessarily a reflection of real numbers.) The number of wasp mimics relative to wasps rises from May through to August (Figure 2.4). When wasp numbers are at their peak in August they are also outnumbered the most. In September, the number of wasp mimics relative to wasps drops sharply as wasp numbers stay high, but wasp mimics start to decline. The mean annual ratio of wasp mimics to wasps is 4.64 to 1 (± 0.81) over the whole season.

Non-mimics show less extreme variation over the season (Figure 2.3a), though they have the same general pattern of a small peak in May/ June and a

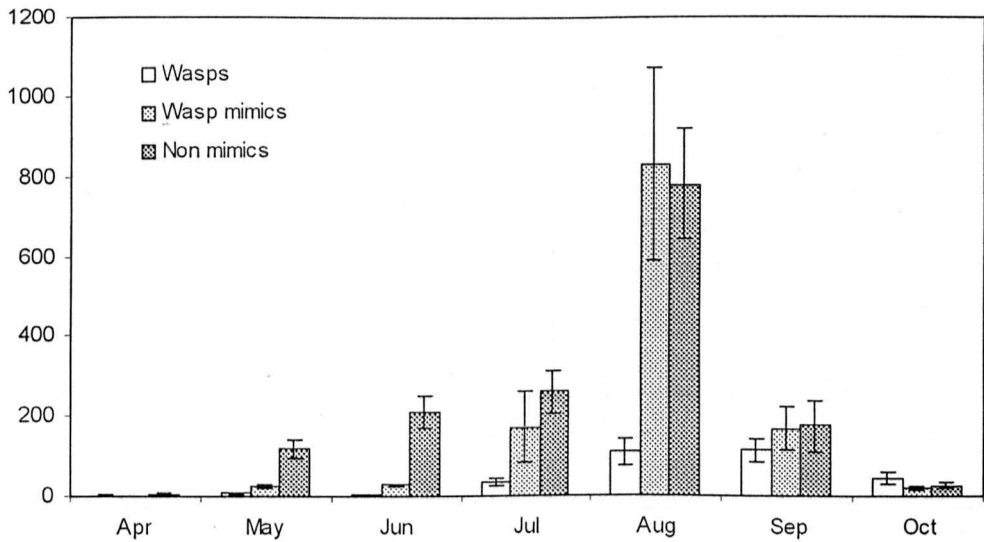
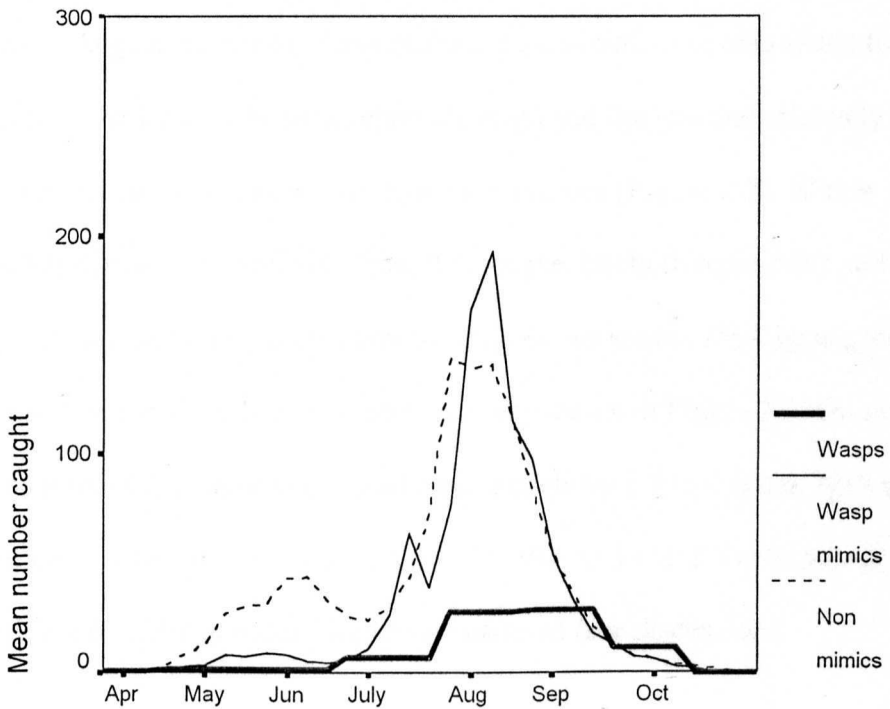


Figure 2.3 (a). Relative timing of weekly catches of wasps (*Vespula* spp.), wasp-mimetic hoverflies and non-mimetic hoverflies. Wasp numbers are means for 1973-1987, hoverfly numbers are means for 1972-1994. Weekly wasp data is approximated from monthly totals by dividing by 4/5 weeks. **(b)** Mean monthly catches of wasps, wasp mimics and non-mimics (1973-1987 only). Bars show standard errors.

large one in August. However, these peaks are more similar in magnitude than in wasp mimics, with the early peak relatively large and the late one relatively small. Bee mimics are much less common than wasp mimics (Figure 2.2). Within year bee (model) data are not available from this source, but both honeybees and bumblebees, unlike wasps, are present throughout the season from spring through to autumn. The mean totals caught each year are shown in Figure 2.5. On average, honeybee mimics caught outnumbered their models by 1.7 to 1 (± 0.6 , $N=9$ years), and bumblebees outnumbered their mimics by 10.6 to 1 (± 2.2 , $N=19$ years), though this will differ between bumblebee patterns (see discussion).

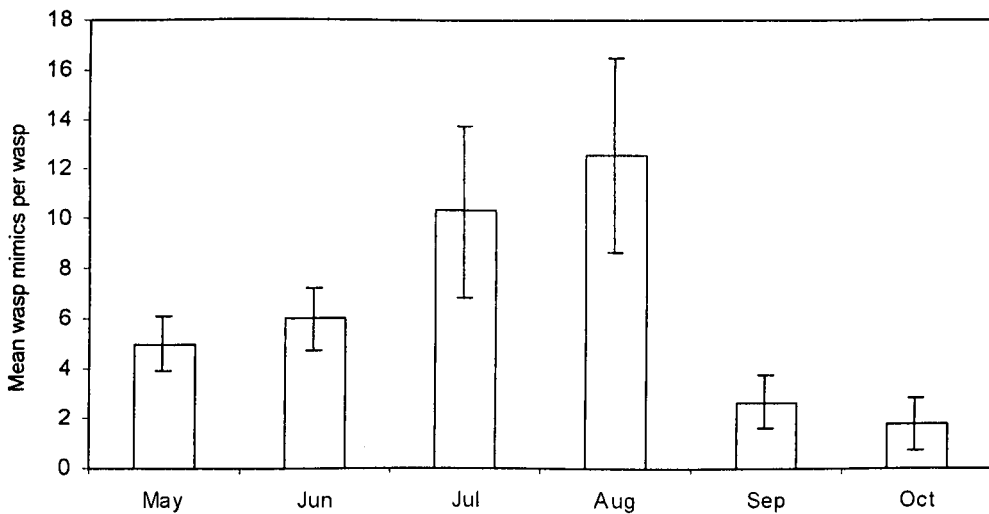


Figure 2.4. Mean and standard error of monthly wasp mimic catch/ monthly wasp catch (1973-1987).

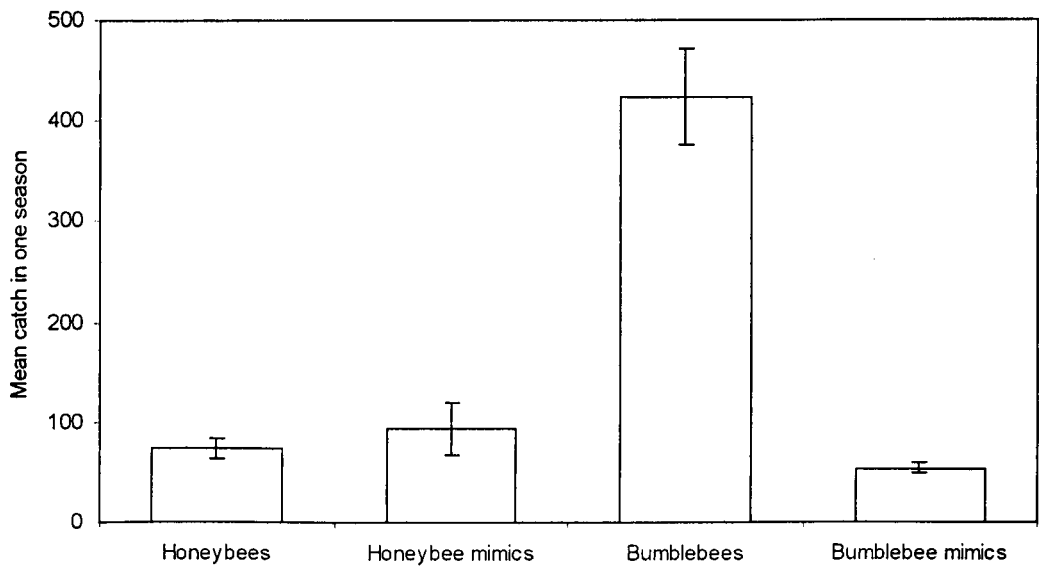


Figure 2.5. Mean annual catch of honeybees and their mimics (1984-1985, 1987-1989, 1991-1994, and bumblebees and their mimics (1972-1977, 1982-1994). Bars show standard errors.

2.3.1.3 Relative timing of hoverflies and wasps within years

The main peak in overall hoverfly abundance is in early/ mid August, at the start of the peak time for wasps (Figure 2.3a). Hoverfly numbers then drop quickly, while wasp abundance stays fairly constant well into September. As well as this large peak in hoverfly numbers, there is also a smaller one at around week 22 (end May/ beginning June), building up from the first hoverflies emerging around the beginning of May. There is then a dip in numbers at the beginning of July. Wasp queens start emerging at the same time as hoverflies, but numbers stay very low until workers start to emerge during July. By far the most wasps appear in August and September. There are often still many present in October, when hoverflies have greatly declined.

The timing of wasp mimics (Figure 2.3a) is similar to hoverflies in general, but the early peak is much smaller as many hoverflies present at this time are non-mimics. The main peak in wasp mimic numbers is again during weeks 32-34 (mid-August), just after wasps have started being common, but their numbers quickly tail off while wasps continue to be abundant. Non-mimics (Figure 2.3a) show a larger early peak in May/ June than the wasp mimics. The second peak is again at the beginning of the main wasp season, and numbers tail off more quickly than wasps'.

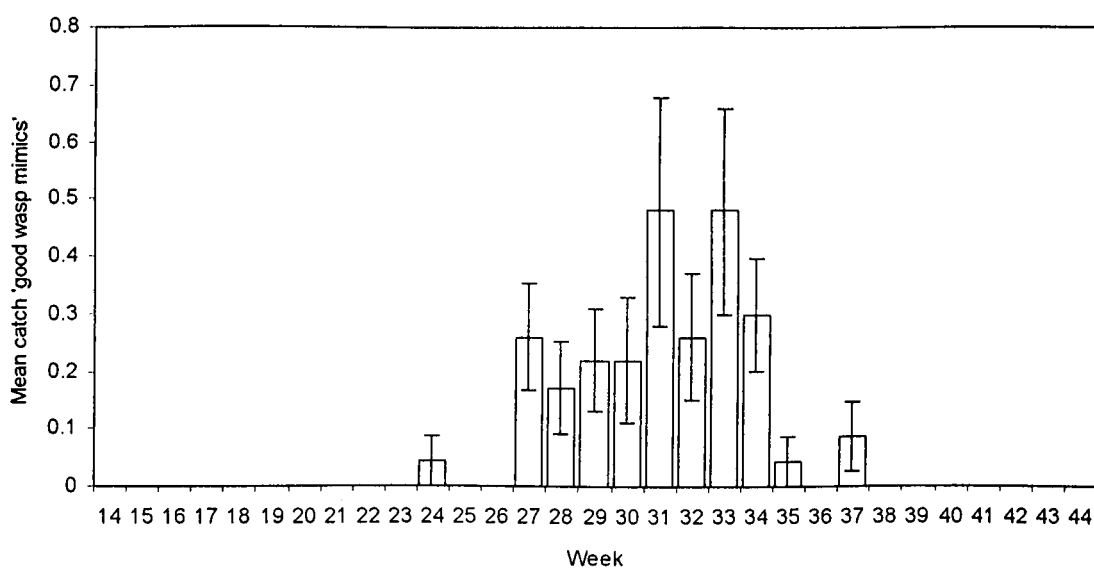


Figure 2.6. Mean and standard error of weekly catch of 'good wasp mimics' (*Chrysotoxum* and *Xanthogramma* spp.) (1972-1994).

The 'wasp mimic' category includes a wide variety of hoverfly species. These were split further to examine when different colour pattern types are abundant. 'Good wasp mimics' (Figure 2.6), i.e. species with a high degree of resemblance to wasps (*Chrysotoxum* and *Xanthogramma* species), only start

emerging at the beginning of July, well after many wasp mimics. Their peak in numbers (though very low throughout) coincides with that of other syrphids, and again numbers decrease quickly after this.

Other species were categorised as the '*Syrphus* group' (see Table 2.3). These are the 'typical' hoverfly species, comprising a variety of species, but all medium-sized, rounded in abdomen shape, with yellow stripes or lunules. Figure 2.7 shows their mean weekly catches. The '*Syrphus* group' follows the general pattern of hoverflies closely, with low early numbers, a trough at the end of June, and the main peak in early August. Hence they form a fairly constant proportion of the hoverfly population, despite the variation in numbers. Their proportion is highest in July/ August (26-27% of hoverflies).

Episyrphus balteatus (Figure 2.7) emerges late, hardly appearing at all before week 26 (beginning of July), and staying at lower or similar numbers to wasps until the beginning of August, when numbers increase rapidly at about the same time as wasps, overtaking them by some way. They form 17% of all hoverflies in August and 22% in September. *Helophilus*, a more convincing wasp mimic (quite large, with bright yellow markings) does not become common until later than any of the previously mentioned groups; most do not appear until after the beginning of August (Figure 2.7). There is no large peak as with many other species, but they stay fairly constant in number throughout August and September.

The timing of bee mimics is quite different (Figure 2.8a, 2.8b), with very defined periods of activity. Bumblebee mimics peak much earlier, around week

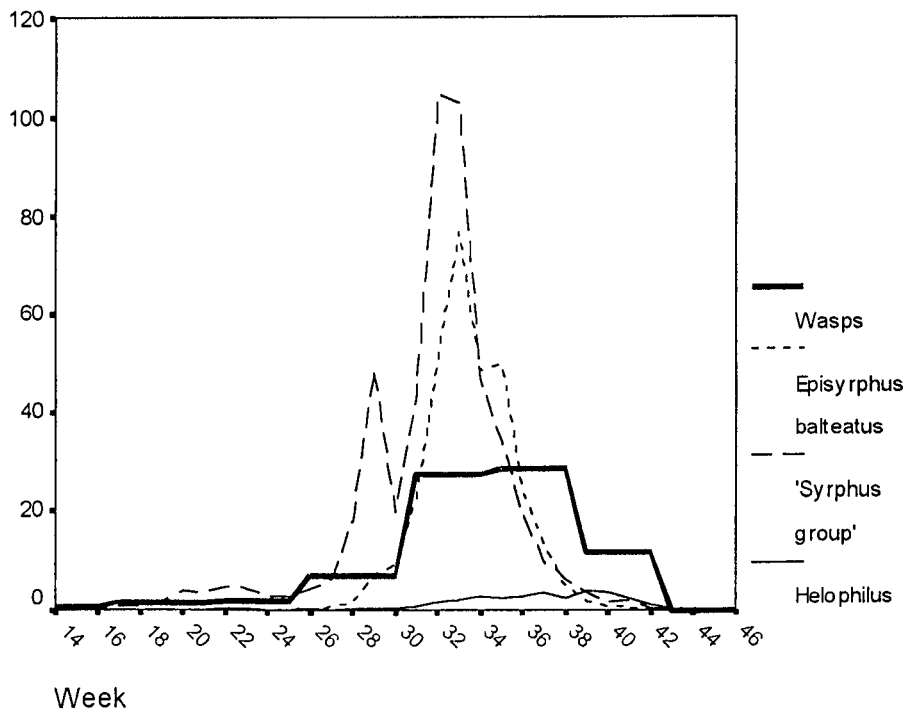


Figure 2.7 Mean weekly catches of wasps, 'Syrphus group' (Table 2.3), *Episyrphus balteatus* and *Helophilus* spp 1972-1994. Weekly wasp catches are estimated from monthly totals for the period 1973-1987; hoverfly numbers are available for the period 1972-1994.

25 (end of June), and have all but finished by August when other hoverflies are becoming most abundant. The majority of the bumblebee mimics are various morphs of *Merodon equestris*, some of which are better mimics than others. If *Merodon* is excluded, the other (good) bumblebee mimics are later, though still early relative to other hoverflies (Figure 2.8a).

Honeybee mimics (most were *Eristalis* spp.) are more similar in timing to late-emerging wasp mimics like *E. balteatus* (Figure 2.8a, Figure 2.7). They start being caught at the beginning of July and peak around mid-August. Numbers then decline sharply, though they often persist through October. Despite large numbers

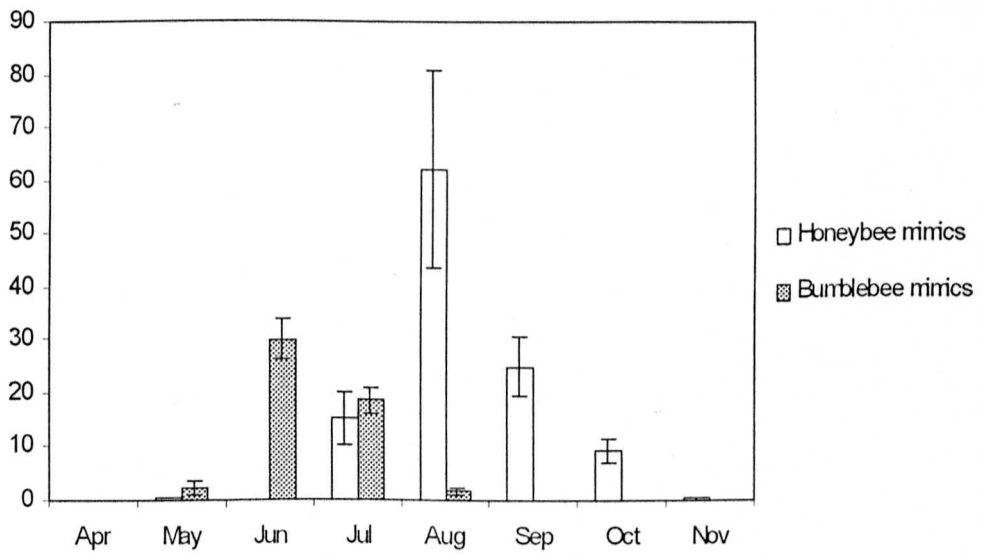
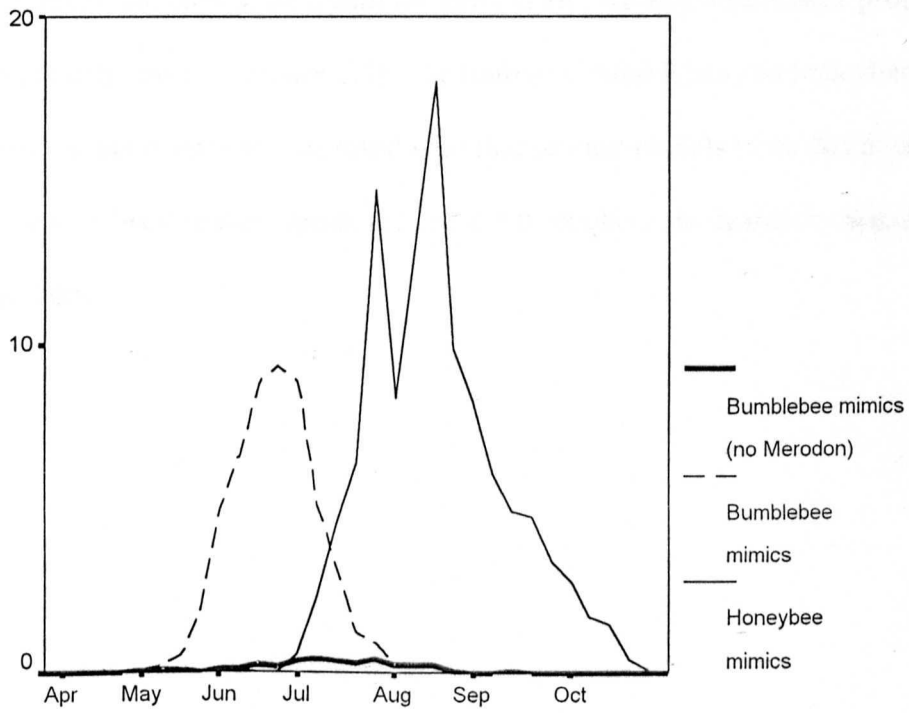


Figure 2.8(a). Mean weekly catches of bumblebee and honeybee mimics (1972-1994).
(b) Mean and standard error of monthly catches of bumblebee and honeybee mimics (1972-1994).

in August, the coincidence with the peak in all syrphids means their proportion stays fairly low (see Figure 2.2). The timing of bumblebee and honeybee mimics within years cannot be compared with that of their models from this dataset. However, bees, unlike wasps, are present throughout the season in reasonable numbers.

2.3.2 Among-year data

2.3.2.1 Wasps and wasp mimics

Yearly totals of *Vespula* spp. and hoverflies were compared for the 23 years 1972-1994. Figure 2.9 shows the yearly totals of wasp mimics, non-mimics and wasps. Cross-correlation coefficients are indicated in Table 2.5.

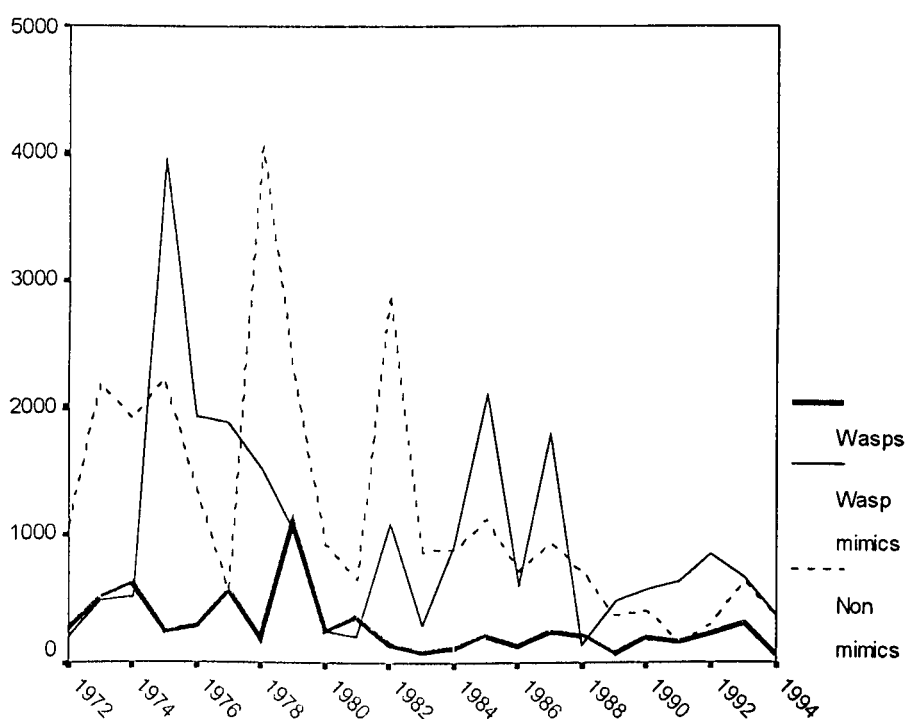


Figure 2.9. Total annual catches of wasp, wasp-mimetic hoverflies and non-mimetic hoverflies.

When non-mimic numbers were compared with wasps, there was a significant positive correlation (+0.60) between hoverfly numbers and wasp numbers the following year (Figure 2.10). There were also positive correlations between wasp numbers and non-mimics in the same and subsequent years. Wasps

and wasp mimics (Figure 2.11) shows no significant correlations between years with a lag of -2 to +2. There were positive correlations between wasp numbers and wasp mimic numbers in the same and subsequent years, but these were

	Lag in years between wasp and fly data					
<i>Hoverfly group</i>	-2	-1	0	+1	+2	Figure number
<i>Non-mimics</i>	0.01	0.60*	0.30	0.36	0.17	2.10
<i>Wasp mimics</i>	0.34	0.13	0.07	0.10	0.10	2.11
<i>Good wasp mimics</i>	-0.05	-0.01	0.06	0.12	0.29	2.12a
<i>Syrphus group</i>	0.24	0.11	0.08	0.19	0.26	2.12b
<i>Episyrphus balteatus</i>	0.44*	0.02	0.11	-0.06	-0.11	2.12c
<i>Helophilus</i>	-0.06	0.10	-0.21	-0.04	-0.18	2.12d

Table 2.5. Cross correlation coefficients between wasps, non-mimics and wasp mimics.

Data consist of 23 yearly totals caught in the Malaise trap. * indicates the coefficient was within 95% confidence limits.

smaller than for non-mimics. In contrast to non-mimics, the largest correlation (+0.34) was a positive one between mimic numbers and model numbers two years later. Breaking the wasp mimics down into smaller groups (as for the within-year analysis), there were no significant correlations between the small number of 'good wasp mimics' and wasp numbers (Figure 2.12a) with a lag of -2 to +2 years.

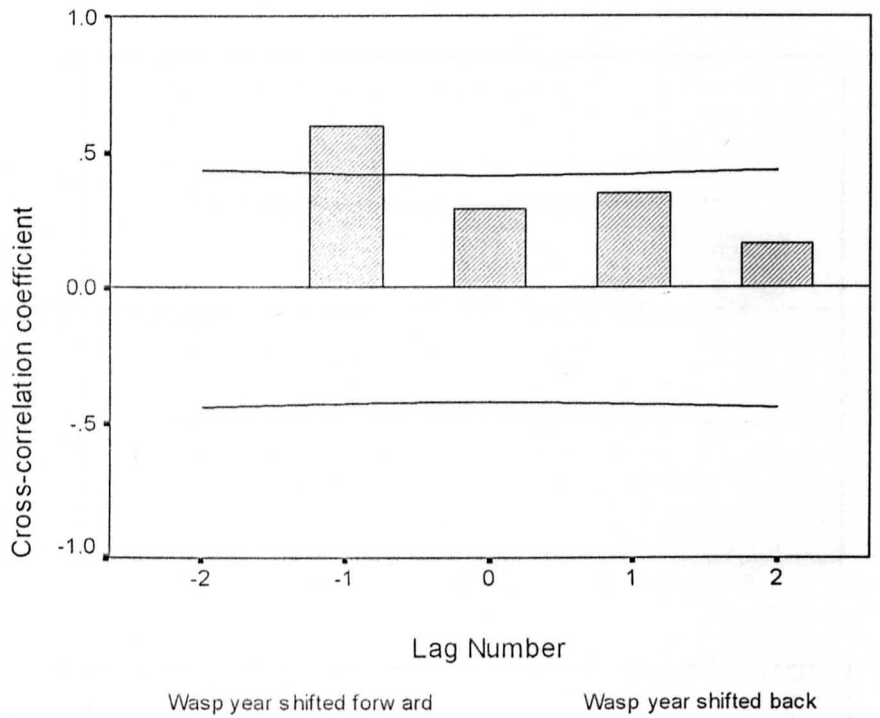


Figure 2.10. Cross-correlation between annual wasp catch and annual non-mimetic hoverfly catch (1972-1994). Blocks show size of correlation coefficient. Lines are confidence limits at the 95% level. Lag number explained in Table 2.4.

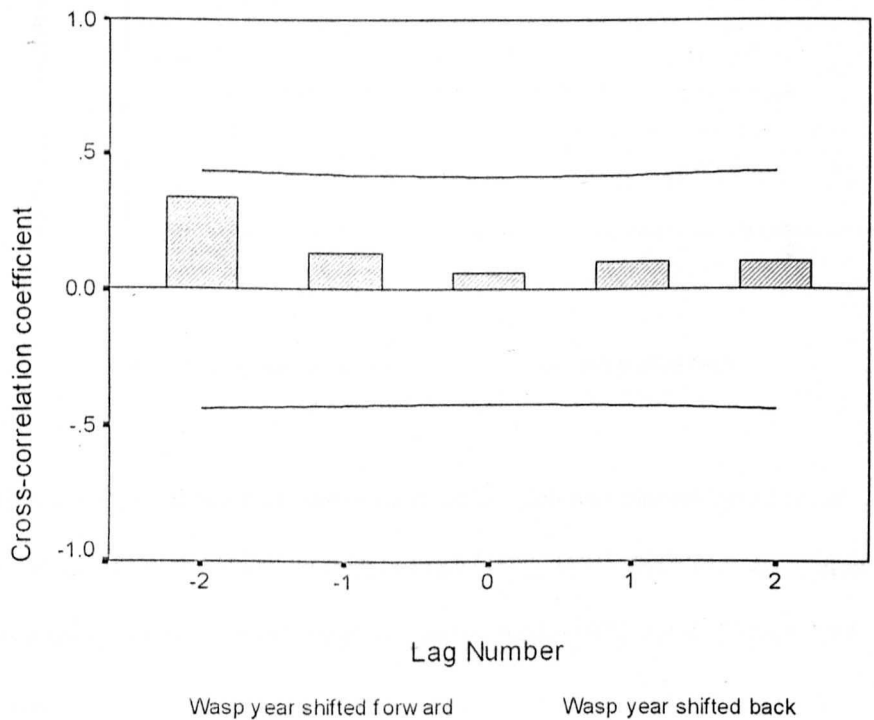


Figure 2.11. Cross-correlation between annual wasp catch and annual wasp-mimetic hoverfly catch (1972-1994).

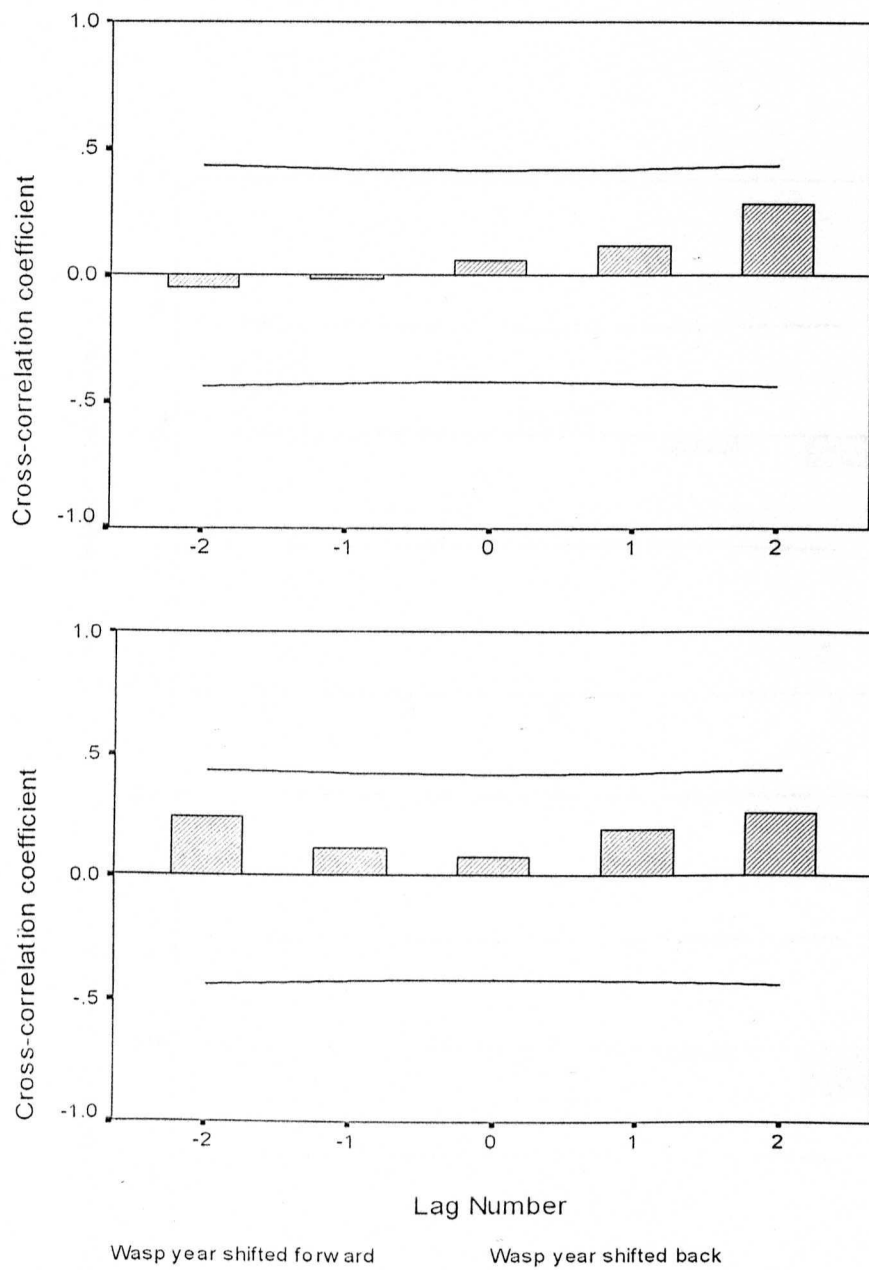


Figure 2.12 (a). Cross-correlation between annual wasp catch and annual 'good wasp mimics' catch (*Chrysotoxum* and *Xanthogramma* spp.) (1972-1994) (b) Cross-correlation between annual wasp catch and annual 'Syrphus group' catch (1972-1994) (figure 2.12 continues over page).

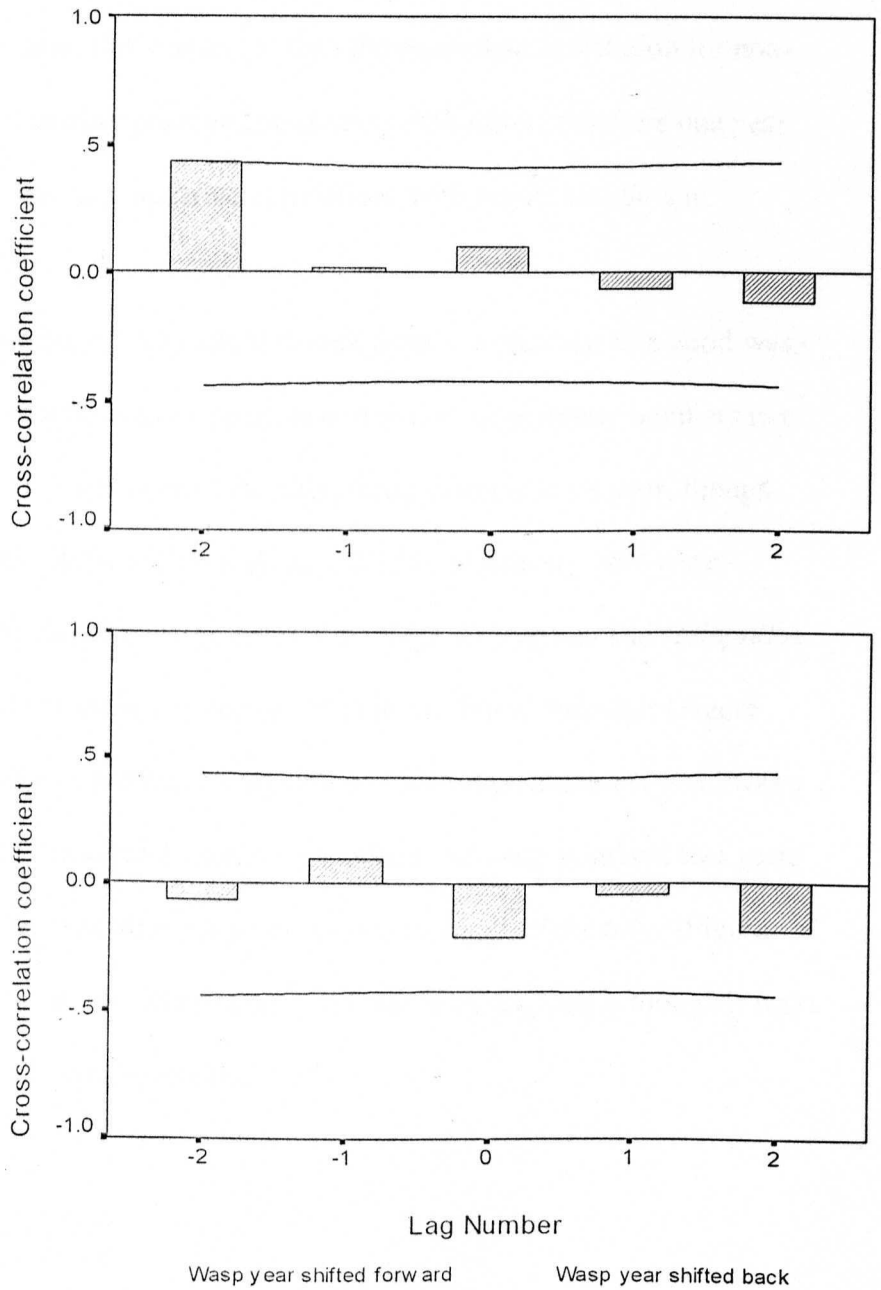


Figure 2.12 (c) Cross-correlations between annual wasp catch and annual *Episyrphus balteatus* catch (1972-1994). **(d)** Cross-correlations between annual wasp catch and annual *Helophilus* catch (1972-1994).

The pattern was different from that for non-mimics (Figure 2.10). The largest correlation (+0.29) was a positive one between wasp numbers and mimic numbers two years later; this was larger than the equivalent correlation for non-mimics. There were smaller positive correlations with mimic numbers one year later and the same year, and negative correlations with mimic numbers in previous years.

The '*Syrphus* group' was also different from non-mimics; like good wasp mimics, they showed a decreasing positive correlation from mimic numbers two years after models, through to one year after, through to the same year, though none were significant at the 5% level (Figure 2.12b). However, there were positive correlations almost as large for positive lags. *Episyrphus* and *Helophilus* (Figure 2.12c,d) did not show any consistent patterns. For *L. balteatus* (Figure 2.12c), the only shift that produced a significant correlation at the 5% level was a positive one (+0.439) between *L. balteatus* numbers and wasp numbers two years later. Correlations between all other years were very small. *Helophilus* (Figure 2.12d) showed no significant correlations with wasps among years, though it was different from non-mimetic hoverflies.

2.3.2.2 Bees and bee mimics

The test for bumblebees and honeybees was less powerful because model data were available for fewer adjacent years.

Bumblebee catches were counted in 1972-1977, and 1982-1994. Six successive years' model data are missing, so analysis was only carried out for the

thirteen successive years 1982-1994 (Figure 2.13). Cross-correlations (Table 2.6) between bumblebees and non-mimics show by far the biggest correlation was a significant positive one (+0.79) between mimic and model numbers in the same year (Figure 2.14a). All other lags also showed positive correlations. Bumblebee and bumblebee mimic numbers

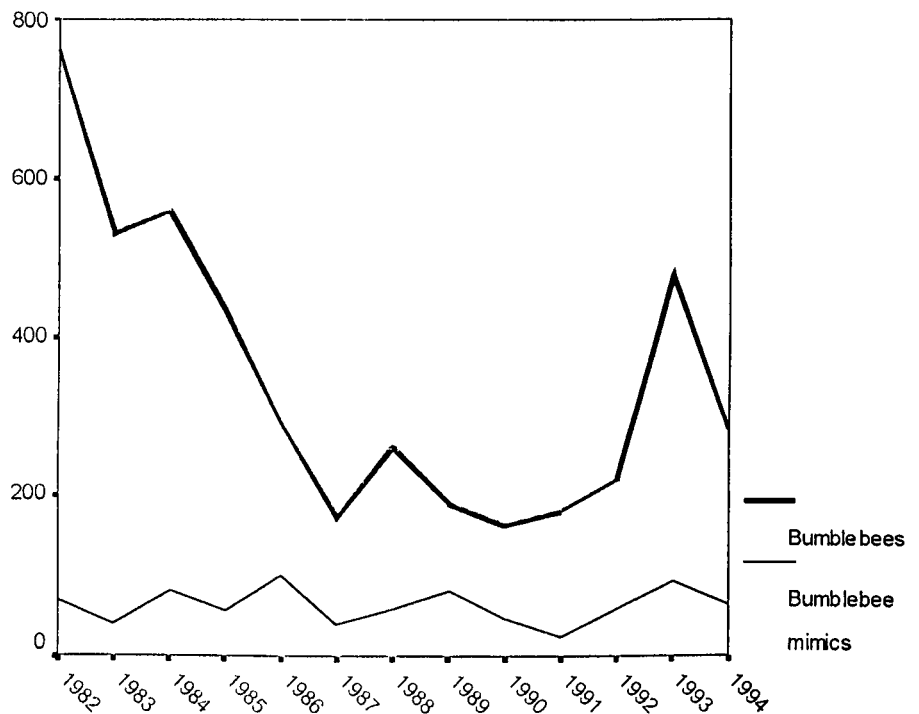


Figure 2.13. Annual catches of bumblebees and bumblebee mimics.

also showed their largest correlation (+0.30) in the same year (Figure 2.14b), though this was smaller than the correlation for non-mimics and not significant. There was also a (non-significant) positive correlation between model numbers and mimic numbers 2 years later (+0.24). Other time lags did not show the positive correlations seen between bumblebees and non-mimics. Bumblebee mimics included the species *Criorhina berberina*, *Eristalis intricarius*, *Merodon equestris* and *Volucella bombylans*, but numbers were dominated by *M.equestris*,

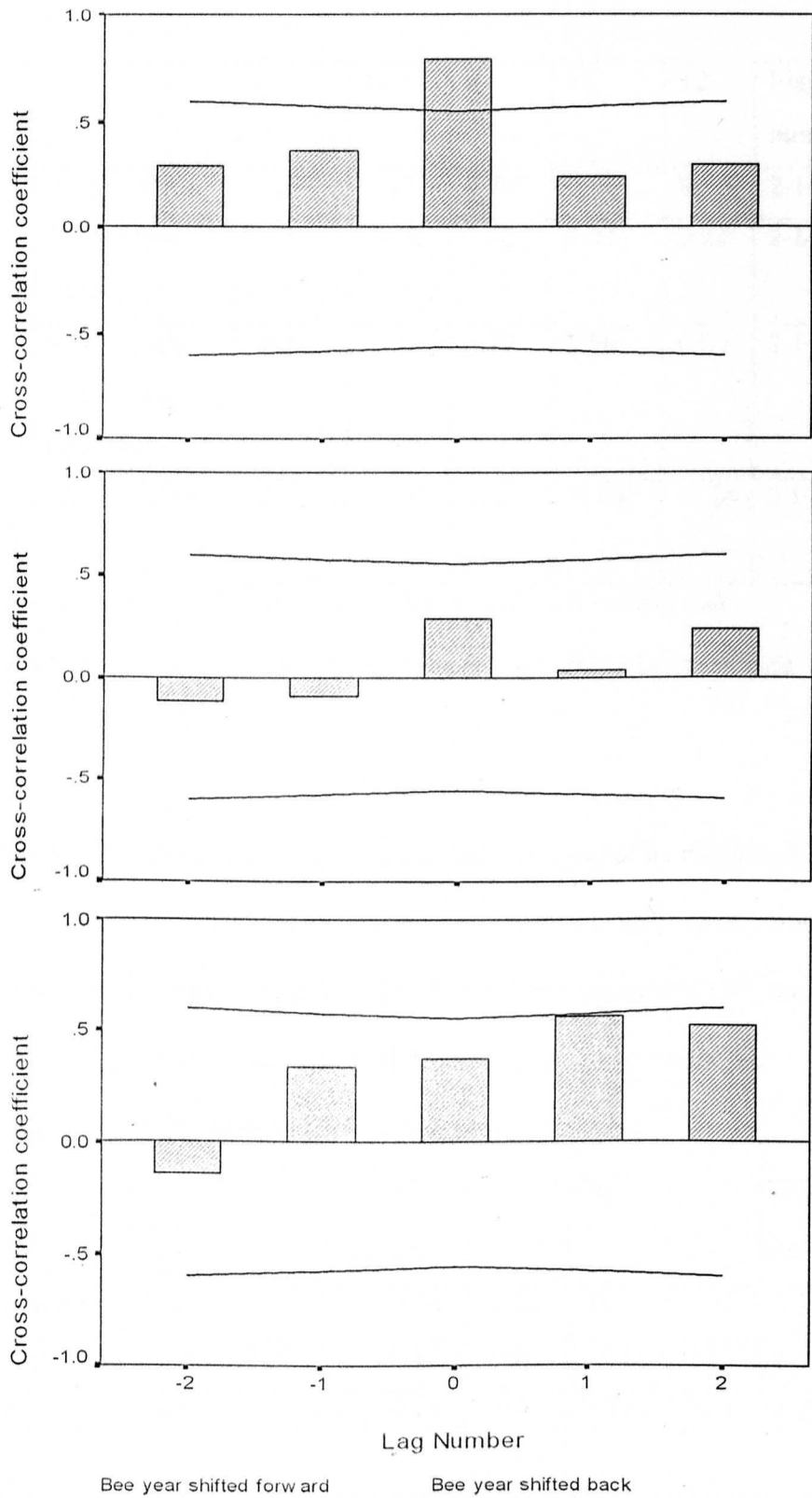


Figure 2.14 Cross-correlations between annual bumblebee catch and (a) annual non-mimetic hoverfly catch (b) annual bumblebee-mimetic hoverfly catch (c) annual bumblebee-mimetic hoverfly catch excluding *Merodon equestris*. (All 1982-1994).

		-2	-1	0	+1	+2	Figure number
Bumblebees	Non mimics	0.29	0.37	0.79*	0.24	0.30	2.14a
Bumblebees	Bumblebee mimics	-0.11	-0.09	0.30	0.04	0.24	2.14b
Bumblebees	Bumblebee mimics excl. <i>Merodon</i>	-0.14	0.34	0.37	0.56	0.52	2.14c
Bumblebee mimics	Non mimics	-0.19	-0.16	-0.05	-0.49*	-0.16	2.17

Table 2.6. Cross correlation coefficients between bumblebees, non-mimics and bumblebee mimics 1982-1994. * indicates the coefficient was within 95% confidence limits.

debatably a less faithful mimic than the others, at least in some of its morphs. If it was excluded (Figure 2.14c), the largest positive correlations were between model numbers and mimic numbers one year later (+0.56) and two years later (+0.52).

This is in contrast to the pattern between models and non-mimics, where the largest correlation was in the same year (Figure 2.14a).

		-2	-1	0	+1	+2	Figure number
Honeybees	Non mimics	-0.73*	-0.50	-0.26	-0.12	0.13	2.15a
Honeybees	Honeybee mimics	-0.55	-0.14	0.04	-0.09	0.01	2.15b
Honeybee mimics	Non mimics	0.08	-0.11	0.69*	0.21	0.09	2.16

Table 2.7. Cross correlation coefficients between honeybees, non-mimics and honeybee mimics 1984-1994. * indicates the coefficient was within 95% confidence limits.

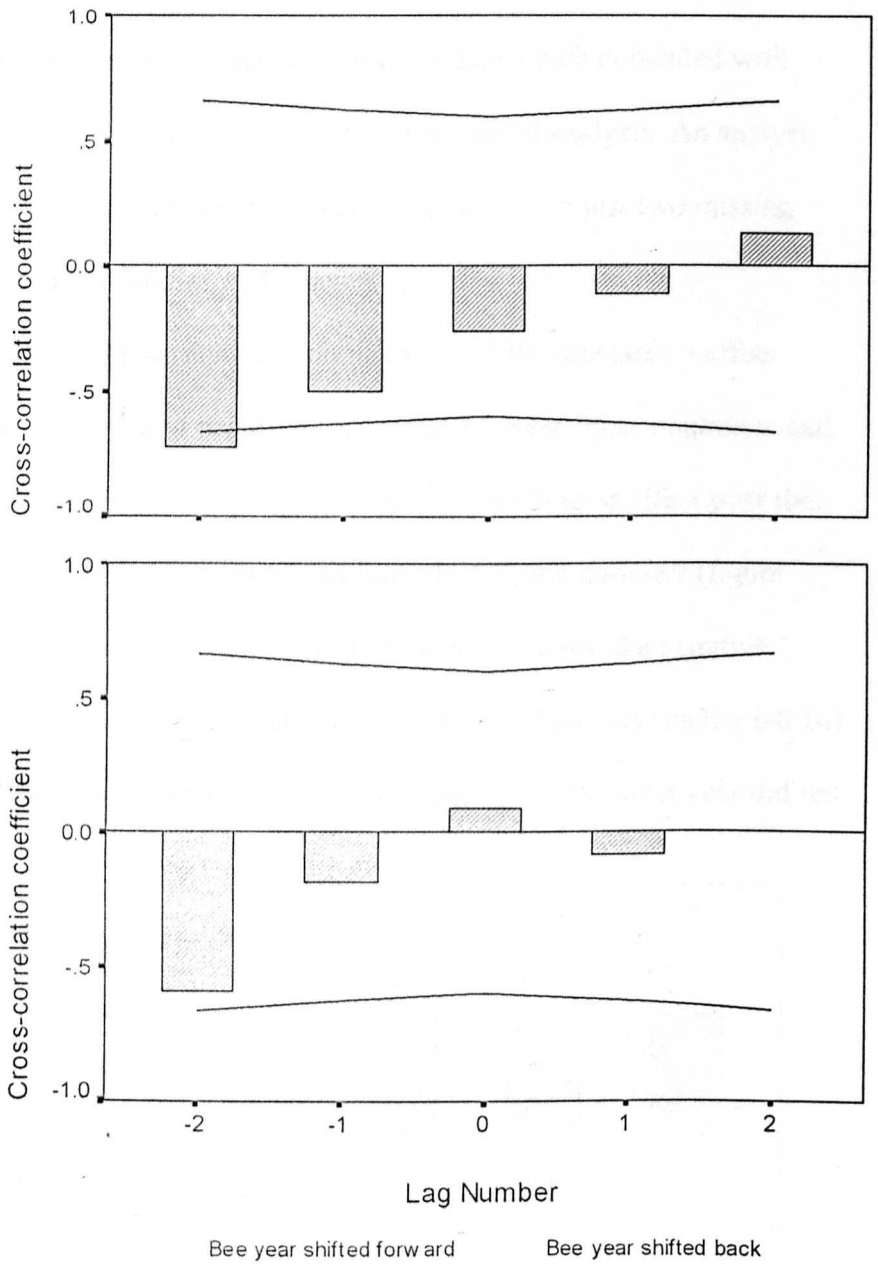


Figure 2.15. Cross-correlations of annual honeybee catch with (a) annual non-mimetic hoverfly catch (b) honeybee-mimetic hoverfly catch. Both 1984-1994. Two years of data are estimated from nine years' real data (see text).

Honeybee (*Apis mellifera*) cross-correlations (Table 2.7) with their mimics were more problematic because so few successive years of model data were

available. The greatest number of successive years data which coincided with hoverfly data was only six years, too few for a meaningful analysis. An analysis of eleven successive years (1984-1994) was carried out, with just two missing years filled with means from the other eleven.

Analysis of honeybees and non-mimics showed that the largest effect (figure 2.15a) was a significant negative correlation between mimic numbers and model numbers two years later (-0.73). This was also the biggest effect over the same years between honeybee numbers and honeybee mimic numbers (figure 2.15b, correlation coefficient = -0.55). Non-mimics also showed a negative correlation (-0.50) with honeybee numbers the next year. This was smaller (-0.14) with honeybee mimics. Honeybees and honeybee mimics in the same year did not

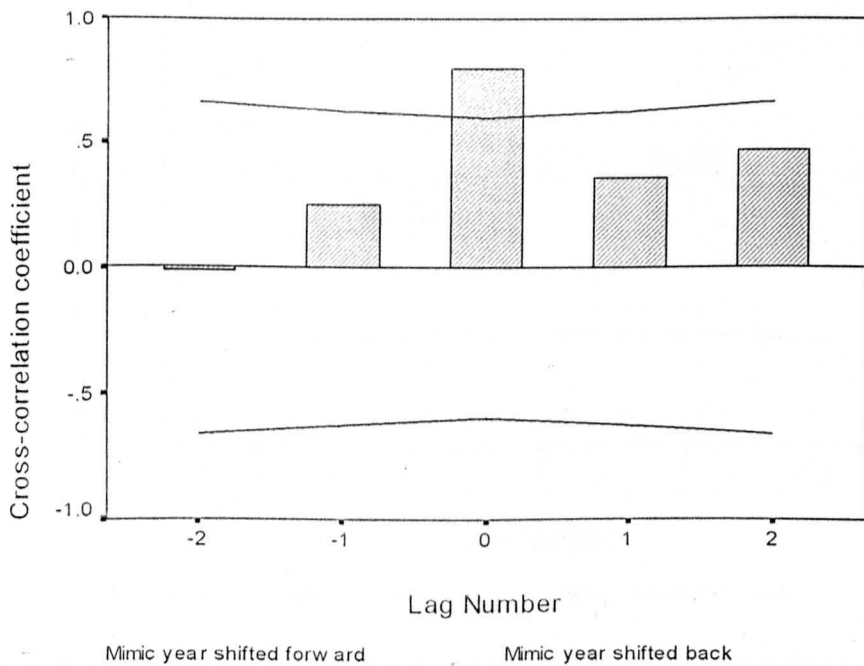


Figure 2.16. Cross-correlations of annual catch of honeybee-mimetic hoverflies with annual catch of non-mimetic hoverflies (1984-1994).

show the negative correlation seen between non-mimics and honeybees. For both honeybee mimics and non-mimics, there was barely any correlation between honeybee numbers and mimic numbers in subsequent years. As expected, there was a strong correlation (0.69) between honeybee mimic and non-mimic numbers in the same year (Figure 2.16), calculated only over the same eleven years as before.

Bumblebee mimics and non-mimic numbers were cross-correlated for the same 13 years as used for the bumblebee analysis (figure 2.17). There was not a large correlation in numbers in the same year, as seen in honeybee mimics.

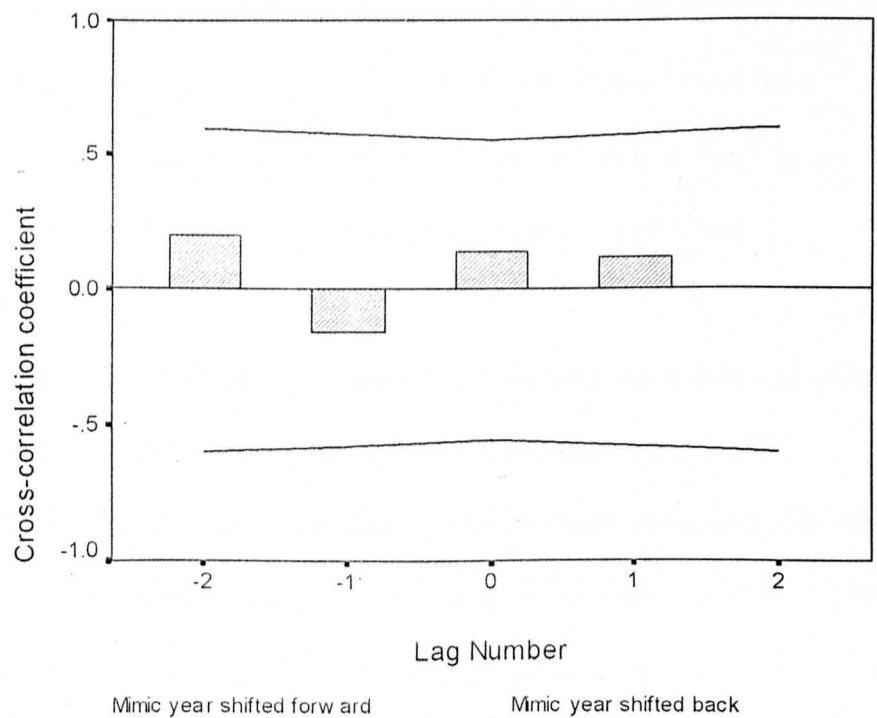


Figure 2.17. Cross-correlations of annual catch of bumblebee-mimetic hoverflies with annual catch of non-mimetic hoverflies (1982-1994).

2.4 Discussion

Weekly Malaise trap catches of hoverflies over 23 years indicate that, contrary to the expectations of Batesian mimicry, wasp mimics are generally more common than their models. This is in agreement with the findings of previous studies carried out with different counting methods (Dlusski 1984; Grewcock 1992; Howarth 1998), and hence is not simply an artefact of the trapping method. Mimics can still be protected at abundance levels higher than those of their models (Brower 1960; Turner 1984a), but only up to a limit of around ten mimics per model. The mean annual ratio of hoverfly wasp mimics to wasps is only 4.6:1, but this varies widely between years, from 0.6:1 in 1981 to 16.5:1 in 1975. Moreover, the ratio varies seasonally. The month with the highest mean ratio (13:1) is August, and in many years it rises above this level. It is difficult to see how a mimetic signal can maintain its deterrent to predators under these circumstances.

The mimics of honeybees (*Apis mellifera*) maintain a more balanced ratio to their models, though they do outnumber them slightly on average (1.7:1). Combined with their better quality of mimicry compared with many wasp mimics, and the presence of honeybees throughout the season, this is more consistent with the concept of classical Batesian mimicry. However, *Eristalis* spp. (which comprise the majority of the honeybee mimics) may be under-represented in the catch compared to their absolute abundance in the population (Owen 1991).

Bumblebee mimics conform to expectations to an even greater extent, being far outnumbered by their models (mean = 10.6:1), though this is an annual

ratio and the hoverflies are very seasonal. These are evidently good mimics, as not only do they appear good to the human eye, but also the same species have different colour morphs mimicking different species of bumblebee. Which morphs were caught was not recorded, but the species caught all have morphs that mimic bumblebee species common in this garden. For example, *Eristalis intricarius* mimics the common *Bombus hortorum*/*B. lucorum*/*B. terrestris* type, while the dominant *Merodon equestris* has morphs which resemble *B. pascuorum* (54% of all bumblebees caught), *B. pratorum* and others.

When discussing the relative abundance of models and mimics, it is the predator's encounter rate with them that is important, which may differ from the Malaise trap catch. This can be affected for example by prey behaviour; Dlusski (1984) reports that upon the approach of a predator, hoverflies flew away while bees and wasps did not, thus distorting the encounter rate of predators with models and mimics away from their relative proportions in the population. The ratios presented here may therefore bear little relation to the relative encounter rates of predators. Nevertheless, there is an indication that better mimics are less common than poor ones in relation to their models. This suggests that good mimics are more constrained by their relationship to models, because they are relying on their rarity to deceive predators. The poorer wasp mimics, in contrast, seem able to maintain high abundance levels without the protection of rarity, despite the fact that they probably deceive predators less than good mimics (Dittrich *et al* 1993). This pattern is borne out further by the fact that the few good

wasp mimics in the UK (*Chrysotoxum* and *Xanthogramma* spp.) are very rarely caught in comparison to their wasp models.

The large variation in model: mimic ratios is due to the considerable among-year variation in abundance of hoverflies and hymenopterans. Predation pressure is not the only selection pressure on hoverflies; food availability for larvae and adults, sufficient time for reproduction, suitable weather conditions and other factors will also affect their timing and frequency. However, if mimicry is the purpose of their colour patterns, the influence of model abundance should be detectable.

Models and mimics do not peak in the same years, so it is not a case of some years being 'good' or 'bad' for insects in general. There were positive correlations between wasp numbers and the abundance of their mimics in the following years, but the coefficients were smaller than those seen with non-mimics. Therefore this cannot be seen as evidence for the influence of model abundance on mimic numbers. Within the wasp mimics, 'good wasp mimic' numbers were better correlated than non-mimics with model abundance two years previously, though the correlation was not significant, but total numbers of good wasp mimics are very low, and many years they do not appear at all in the catch. The other very good mimics, the bumblebee mimics, did not correlate better with bumblebee numbers than non-mimics did, unless the dominant *Merodon equestris* was excluded. Hence the best bumblebee mimics do seem to be relatively highly influenced by model numbers. However, though the mimetic colouration of *M.equestris* may not be as accurate as other species, behaviourally it is very like a

Model	Hoverflies	Effect of hoverflies on models (negative lags)	Correlation in same year (zero lag)	Effect of models on hoverflies (positive lags)	Possible conclusion	Figure
Wasps	Non-mimics	At 1 year	-	-	Predation	2.10
	Mimic	Increases with lag	-	-	Predation	2.11
	Good mimics	-	-	Increases with lag	Protection	2.12a
	<i>Syrphus</i> group	Increases with lag	-	Increases with lag	Protection and predation	2.12b
	<i>E. balteatus</i>	At 2 years	-	-	Immigration	2.12c
	<i>H. pendulus</i>	-	-	-	No link	2.12d
Bumblebees	Non-mimics	-	Significant effect	-	Environmental fluctuations	2.14a
	Mimics	-	Some effect	Some at 2 years	Protection and environmental fluctuations	2.14b
	Mimics excluding <i>Merodon</i>	-	Some effect	At 1 and 2 years	Protection and environmental fluctuations	2.14c
Honeybees	Non-mimics	-	-	Increases with lag, negative	?	2.15a
	Mimics	-	-	Increases with lag, negative	?	2.15b

Table 2.8. Summary of main effects found across years between models and hoverflies, and some possible interpretations.

bee. Honeybee mimics, unlike wasp mimics and bumblebee mimics, did not even show positive correlations with honeybee numbers (though this analysis was for a limited number of years). Honeybee mimics thus seem more influenced by external factors that affect all hoverflies than by model abundance. This contrasts with the findings of Dlusski (1984) that a large drop in honeybee numbers coincided with dramatic decreases in their mimic abundance, relative to other hoverflies.

Unexpectedly, hoverfly (particularly non-mimic) numbers appeared to affect wasp numbers in some cases. This unpredicted positive effect could be due to wasp predation on hoverflies, since high abundance of hoverflies could lead to higher levels of prey for wasps, increasing their survival. *Vespula* wasps do prey on other invertebrates, including species of Diptera, and are the major predators of some species (Toft & Rees 1998; Beggs & Rees 1999). Furthermore, the fact that non-mimics affect wasp numbers more than mimics do could indicate that hoverfly patterns provide protection from wasp as well as bird predation.

Immigration of hoverflies into the garden could be masking some of the effects predicted of model abundance on mimic numbers. This is seen particularly in *Episyrphus balteatus* and *Eupeodes corollae* (a member of the *Syrphus* group) (Owen 1991), and is thought to occur mainly from agricultural land, especially after a warm spring with an abundance of aphids available as a larval food source. The harvesting of crops then leads to mass movements of these species of hoverfly. Hoverflies immigrating from other, possibly distant, areas will not have been influenced by local changes in model abundance and the consequent survival of mimics. Abundance of *Episyrphus balteatus* does indeed show little if any correlation with wasp numbers (though it is also known to breed in the garden). The significant effect of *E. balteatus* on model numbers (Figure 2.12c) could also be spurious because of large-scale immigration of this species.

The suburban nature of the garden may also result in low predation levels compared to a more 'natural' situation. Some species that are known to take hoverflies (Torp 1994), such as swallows (*Apus apus*), robins (*Erithacus rubecula*)

and great tits (*Parus major*) are recorded in the garden. However, these are mainly generalists and may not constitute a high risk of predation for hoverflies. Without a high predation rate, there is less reason to expect a link between model and mimic numbers.

Other factors may override the effects of predation via mimicry in influencing abundance of hoverflies. Competition among hoverfly species is unlikely to be one of these, as analyses of population dynamics and ecomorphological relationships on this community show that hoverfly species respond independently to fluctuations in essential resources (Gilbert & Owen 1990). The resource levels (e.g. of aphids) themselves may have a large influence on abundance, as well as external conditions such as the weather.

Model abundance is also expected to influence mimic seasonality within years. In this garden, wasp mimics generally appear well before their models are present in any numbers (similar to the temporal pattern found for wasp mimics by Dlusski (1984)). The presence of wasp mimics early in the season before wasps have built up in numbers seems to make little sense in terms of predator learning if hoverflies are imitating wasps. Numbers of wasp mimics in May and June are not high compared to later in the summer, but there are very few wasps present at this time.

It is advantageous to hoverflies to be able to emerge earlier than wasps, to take advantage of larval and adult food sources, and in some cases fit more generations into the season. One factor which may make this possible despite the lack of protection through model numbers is the presence of alternative prey;

early in the season non-mimetic hoverflies greatly outnumber wasp mimics. Therefore, while predators may not yet have learned the unprofitability of yellow-and-black patterns, wasp-mimetic hoverflies will be partially protected by the presence of so much alternative prey. The fact that some birds can retain memories of patterns they associate with unprofitability for a period of several months (Mostler 1935; Rothschild 1964; Evans & Waldbauer 1982), could also contribute to the protection of wasp mimics from predators at this time. This seems to be the case for wasp mimics in the U.S. (Waldbauer *et al* 1977; Waldbauer & LaBerge 1985), although these studies involve perfect mimics.

The timing of the large peak in wasp mimic abundance in August is also difficult to explain purely in terms of mimicry, since numbers increase dramatically before large numbers of wasps emerge, and thus before many predators will have encountered wasps. Again, this suggests that other factors such as food availability are playing a larger role than model abundance, and that mimicry may not be the primary selection pressure on the timing of putative wasp mimics. This is particularly evident when timing is compared with that of more obvious mimics, such as bumblebee mimics, honeybee mimics and good wasp mimics. Bumblebees are active from April until October, rising to a peak in mid-June (Owen 1991). *Merodon equestris*, the most common bumblebee mimic, times its appearance to coincide with this peak, and the other, rarer mimics emerge after this when predators have had experience of bumblebees for some months. Honeybee mimics also are mainly caught in the latter half of the season, when honeybees have been active for several months. Good wasp mimics too

were never caught (apart from one individual) before July. This again indicates that where a species is deceiving predators effectively, selection through predation constrains it to certain times of the year. The majority of the wasp mimics do not appear to be constrained in this way.

However, not all wasp mimics are alike. For example, nearly all *Helophilus* spp. are caught after the beginning of August and the large-scale appearance of wasps. They do not peak until some time later. This seems consistent with its status as a relatively good (though not perfect) mimic, being large in size and bright yellow in pattern. *Helophilus* are abundant, but much less so than wasps. In combination with other wasp mimics, their abundance is of course much greater than that of wasps. However, predators can differentiate between mimics of different quality (Dittrich *et al* 1993), and therefore there is probably not a 'rule of thumb' for predators choosing between either 'mimics' or 'non-mimics'. Therefore the low abundance of *Helophilus* should afford it some protection (though there seem to be no effects of wasp abundance on *Helophilus* numbers (Figure 2.12d).

How well predators distinguish between different mimics in the field may depend partially on the availability of resources at a particular time. In practice, for example, in times of high resource availability predators may be able to afford to avoid any insect with yellow markings, since plenty of alternative prey is present with no risk attached. At times of low resources, however, they may be forced to try more risky prey, probably starting with the poorest mimics (Srygley & Kingsolver 1998). The time of lowest resources is likely to be when birds are

fledging (Srygley & Kingsolver 1998), which could be one reason why there is a dip in hoverfly numbers around the end of June. Another reason for a dip at this time could be that this is when fledgling birds are learning about colour patterns and hoverfly phenology has been selected to not emerge at this time (Waldbauer & LaBerge 1985).

In contrast with *Helophilus*, the '*Syrphus* group' start emerging early, with a peak in May/ June before the time of high abundance in August. Abundance is also high relative to wasps, and the among-year data showed only a slightly larger correlation than for non-mimics with wasp numbers two years previously. There was an equally large effect in *Syrphus* group abundance on model numbers, again possibly indicating the effects of wasp predation. However, these effects are not significant. One alternative explanation for this apparent lack of constraint by models despite their distinctive colouration is that species in the *Syrphus* group are Müllerian mimics of each other. This could explain their similarity to each other (though they are also closely related phylogenetically (Rotheray & Gilbert 1999)), as well as their high abundance, which would serve to reinforce the message of fellow mimics. Their seasonality would also evolve to coincide with each other, not with wasps. Two possible messages Müllerian mimics could be reinforcing are distastefulness or escaping ability through flight agility. Even if these are Müllerian mimics, there could also be extra protection afforded by their superficial similarity to wasps, as there seems no reason why mimicry and aposematism should be mutually exclusive.

Whether the patterns seen in this garden are typical of other sites is difficult to establish, as long-term studies such as this one are rare. A setting with more 'natural' abundances of insects and their predators could help clarify whether the colour patterns of mimetic hoverflies, particularly wasp mimics, have really evolved to deceive predators.

Chapter Three

Reproductive characters and body size in hoverflies

3.1 Introduction

Allometric relationships with body size are often explored to give insight on the selection pressures that may have shaped variation in reproductive characters (*e.g.* Harcourt *et al* 1981). Though commonly encountered in the literature, such studies are still dominated by vertebrates (but see, for example Wiklund *et al* 1987; Gage 1994; Poulin 1995; Pitnick 1996).

Male characteristics of the testis and sperm show great diversity among species, which is often interpreted in terms of adaptiveness since there is high heritability in testis size (*e.g.* Coulter *et al* 1976). Inter-specific variation in testis size correlates with sperm production, and therefore reproductive potential (Short 1979; Møller 1988, 1989). There is less evidence in invertebrates, but given that the sole function of insect testes is to manufacture sperm (Chapman 1982) (unlike in vertebrates, where hormone production is also involved), it seems certain that testis size has an important role to play in reproductive potential.

Sperm number and sperm length both contribute to reproductive potential; inseminating with a larger number of sperm will be more likely to saturate a female's reproductive tract (particularly important with sperm competition), while longer sperm are more likely to participate in fertilisation than shorter ones (*e.g.* in *Drosophila*: Snook 1997; Snook & Karr 1998). Testis length is directly related to sperm length (Pitnick 1996, on *Drosophila*), indeed it can be used to predict

sperm length in *Drosophila* (Joly & Bressac 1994). Testis volume also takes into account sperm number; in *Drosophila*, 82% of interspecific variation in testis mass is explained by variation in the amount of sperm being produced (Pitnick 1996). The effect of sperm competition is clearly seen in the relationship between testis size and mating strategy: males of vertebrate species with polygamous females have larger testes than those with monogamous females (*e.g.* Møller 1991; Stockley *et al* 1997), consistent with the idea of sperm competition risk (Parker 1972) influencing the evolution of testis size. Studies on invertebrates confirm this idea; in a study of 74 butterfly species, relative testis size increased with risk of sperm competition, as defined by female mating frequency (Gage 1994). Tying in with this, ejaculate size (linked to testis size) correlates directly with risk of sperm competition in some insects (Gage 1991; Vahed 1998). Experiments show that the probability of fertilisation is proportional to the number of sperm introduced by the male, relative to those of other males (*e.g.* Martin & Dzink 1977). This is probably the reason for increased sperm number (and increased testis size) in vertebrates, in which the sperm of different males usually mixes in the female where multiple inseminations have occurred. In some cases, this may also be the case in invertebrates, but in many there appears to be little or no sperm mixing (Simmons & Siva-Jothy 1998). Increased sperm numbers through increased testis size can still be adaptive, since increased sperm number can also facilitate flooding of the female sperm storage organs and thus prevent other males gaining access (Simmons & Siva-Jothy 1998).

Hence in multiply mating species there can be strong selection pressures to produce large and long testes (as exemplified by the giant sperm produced in some species of *Drosophila*: Joly *et al* 1995), but a limit is set on this by the costs of testis production (Harcourt 1991). Previous studies in vertebrates have shown a significant positive allometric relationship between testis size and body size in many groups (*e.g.* Heske & Ostfeld 1990; Kusano *et al* 1991). In invertebrates, Pitnick (1996) found positive allometry between testis mass and body mass between *Drosophila* species, and Gage (1994) showed the same in butterfly species. Similarly, correlations have been found between spermatophore size and body size in butterflies (Svard & Wiklund 1989; Forsberg & Wiklund 1989), and ejaculate size and body size in bush crickets (Wedell 1997). In this study, the prediction that there is positive allometry of male reproductive effort is tested, using two measures of male reproductive potential: testis length, and testis volume.

Females are also under constant selection pressure to increase their inclusive fitness, with fecundity as a major component (Stearns 1992). Ovariole number is generally considered a direct measure of potential fecundity (*e.g.* Price 1975, 1977 on parasitoids; Fitt 1990 on *Dacus*, but see Leather 1994). Life-history theory predicts a trade-off between egg number and egg size (Parker & Begon 1986; Stearns 1992). Such trade-offs are frequently found in practice, for example in fish (Elgar 1990) and birds (Lack 1968), as well as insects such as crickets (Carriere & Roff 1995) and *Drosophila* (Montague *et al* 1981), though exceptions do occur (*e.g.* Fitt 1990). The strategy producing the optimal

compromise of offspring number, quality and survivorship (*e.g.* Sinervo 1990) should determine where a species falls along the trade-off line, and may be influenced by factors such as longevity (see Gilbert 1990), host range (Fitt 1990; Gilbert 1990) and oviposition opportunities (Wiklund *et al* 1987).

Across related animal species, body size is generally correlated with both egg size and egg number (Peters 1983). Real examples are plentiful; for example clutch size is linked with body size across salamander species (Tilley 1968), and body size and total fecundity are positively correlated across 35 nematode species (Morand 1996). In other cases the link is not so tight (*e.g.* Fitt 1990 on *Dacus*; Poulin 1995 on copepods), often in insects (Leather *et al* 1994), indicating that the history of change in egg traits has not purely been one of change in body size. Here the prediction of positive allometry of female reproductive effort is tested, using egg size, egg number and batch volume as measures of female reproductive potential.

The Syrphidae (Diptera) are used as the test taxon for this work, a large (>5500 species) family of flies distributed worldwide. Adults are virtually always flower feeders, whereas larvae show a great variety of feeding modes (Rotheray 1993; Gilbert *et al* 1994). Adults vary greatly in morphology, with at least a 400-fold difference in weight between the smallest and largest species. There is a trade-off between egg size and number, with larval feeding mode influencing where on the trade-off species lie: phytophagous species lay few, large eggs, predators lay an average number of average-sized eggs, and saprophages lay many small eggs (Gilbert 1990). Gilbert's (1990) analysis took no account of

phylogenetic relationships, since no phylogeny existed then. Recently, a generic-level phylogeny has become available (Rotheray & Gilbert 1999), permitting the phylogenetic analysis performed here.

In this study, ovariole number, egg volume and body size are used to test hypotheses about the selection pressures on female reproductive characters, taking phylogeny into account using the independent contrasts method (Felsenstein 1985). The same is done for males using testis length, testis volume and body size. For comparison, a similar analysis was carried out for a well-understood morphological character associated with foraging (tongue length), correlated with the corollae depth of flowers visited and the proportions of nectar and pollen in the diet (Gilbert 1981, 1985). Evolutionary changes in tongue length are very tightly correlated with changes in body size within a single genus, *Platycheirus* (Gilbert *et al* 1994), so it is expected to be more constrained by body size than are reproductive characters.

3.2 Methods

3.2.1 Morphological data

Morphological data derive from fieldwork in the USA (Arizona, Oregon and Maine), Poland (Bialowieza), the UK and the Russian Far East. Hoverflies were frozen on capture, and then measured under a binocular microscope with an ocular micrometer (details, see Gilbert 1981, 1985, 1990; Gilbert *et al* 1994) and then dissected. Measurements included tongue length, and thorax width, length

and height. The three thorax measures were multiplied together to give a measure of thorax volume, used as an index of body size. Female ovaries were removed into water, teased apart, and the number of constituent ovarioles counted per ovary. The length (L) and maximum width (W) of mature (chorionated) eggs was measured, and egg volume calculated using the formula for the volume of an ellipsoid $(4/3)\pi(L/2)(W/2)^2$, to enable a measure of ovary volume (or batch size). In males, the reproductive system was dissected out in water, and the length and maximum width of the testis recorded. Testis volume was calculated in the same way as egg volume. All characters were averaged over individuals to give a mean value for each species (see Appendix 1).

3.2.2 Comparative method and statistical analyses

It is now generally agreed that it can be misleading to compare morphological characters without taking phylogeny into account (*e.g.* Harvey & Pagel 1991, Martins & Hansen 1996; but see Ricklefs 1996). This is because species in a branching phylogeny are not independent points. If taken as independent, the significance of differences between taxa may be over-estimated; many traits are similar because of evolutionary descent rather than independent evolution (Harvey & Pagel 1991). Felsenstein's method of independent comparisons (Felsenstein 1985) was used to overcome this problem, implemented by the computer program 'CAIC' (Comparative Analysis by Independent Contrasts, Purvis and Rambault 1995).

Independent comparisons methods remove the effect of phylogenetic relationships by specifying a set of independent contrasts between pairs of species or other taxa (Felsenstein 1985), in contrast to phylogenetic autocorrelation (Gittleman & Kot, 1990) and maximum likelihood methods (Lynch 1991), where variation is separated into that associated with phylogeny and that independent of it. With independent comparisons, each contrast is scaled by its expected standard deviation. These standardised contrasts are then independent and normally distributed, and hence are suitable for standard statistical analyses.

Standardised contrasts were calculated for thorax volume and tongue length (229 spp), testis length and testis volume (157 spp), and egg volume, ovariole number and ovary volume (91 spp). All data were reciprocally transformed before calculating contrasts; this ensured that the data conform to Felsenstein's model of evolution of characters as a Brownian motion (or continuous walk) process (Felsenstein 1985; Purvis & Rambault 1995). When a set of contrasts for one variable is regressed on a set for another variable, a positive slope indicates that the two traits are co-evolving in the same direction. All regressions of contrasts were forced through the origin; the resulting slopes give the true relation between the variables in the absence of phylogenetic effects (Pagel 1993). A contrast between two nodes is assigned an arbitrary sign, depending which node value is subtracted from which (Garland *et al* 1992). CAIC deals with this by always assigning a positive sign to the independent variable; the other variable switches signs accordingly. All reproductive characters contrasts



Figure 3.1. Genus-level phylogeny of the hoverflies, based on 187 morphological larval characters.

were regressed on thorax volume contrasts. In addition, change in male and female characters was compared among species. The effects of body size were removed by using residuals from the regressions of reproductive traits on thorax volume.

For comparison with the regressions using contrasts, regressions of log-transformed species means (not through the origin) were also carried out, using the same species as used in the independent contrasts analyses. Logs of mean reproductive character species values were regressed on thorax volume, as for contrasts.

3.2.3 *Phylogeny*

A phylogeny of virtually all the Palaearctic genera of syrphids (Rotheray & Gilbert 1989, 1999) was used, based upon 187 larval morphological characters scored on 85 genera (Figure 3.1). Because this phylogeny is based on larval characters, the phylogeny is completely independent of the adult-derived data used here. The branch lengths are not known and hence equal branch lengths were used. Branch lengths are important because they are used to provide expected variances to standardise the contrasts; equal branch lengths assume a strictly punctuational view of evolution and it is not known if this is accurate for the syrphid phylogeny, but simulation work shows that even inaccurate branch lengths give reasonable results with CAIC (Purvis *et al* 1994).

CAIC has a particular advantage in that it allows multiple branches at a node where the true bifurcating structure is not known ('soft' polytomies). This

allowed consideration of the data at the species level, with several species of a genus branching from a node, despite the fact that the phylogeny is generic. It also allows missing values, and thus considers the contrasts for the whole tree even when values are not available for all species. Sample sizes for the regressions are lower than the number of taxa used, because they use standardised contrasts, not species means. Where specimens could only be identified to genus, data were only used for calculating contrasts if no other species were available for that genus, to avoid the possibility of contrasting a species with itself.

As well as comparing each character with body size for all species, the analysis was repeated for the two main subfamilies. The syrphids currently are classified into three subfamilies: the Microdontinae, Syrphinae and Eristalinae. The Microdontinae have occasionally been classified as a separate family (Thompson 1972): there is only data for four species here, and hence they cannot be analysed separately. The Syrphinae are a monophyletic group mainly aphidophagous as larvae, and they are fairly homogeneous in adult body design. It is possible that the Syrphinae are a rapidly diversifying, recently evolved clade; their relatively uniform adult form and larval feeding habits suggest this, but only molecular data will shed light on whether this is the case. The rest of the syrphids are classified as the Eristalinae, but are polyphyletic if the phylogeny of Rotheray & Gilbert (1999) is correct; they contain syrphids with very different adult designs and larval feeding habits.

3.3 Results

3.3.1 Is the evolution of body size related to changes in tongue length?

There was considerable interspecific variation in both tongue length and body size (thorax volume). Thorax volume varied from 2 mm³ in *Sphegina petiolata*, to 255 mm³ in *Criorhina quadriboscis*, while tongue length varied almost 10-fold, from 1.04 mm in *Heringia heringii*, to 9.8 mm in *Criorhina caudata*.

Analysis of 85 independent contrasts (from 229 species) revealed that tongue length and body size have evolved in a significantly positively correlated fashion (Figure 3.2a; $F_{1,84}=78.4$, $r^2=0.48$, $p<0.001$). This relationship had a slope of 1.03 ± 0.12 . There was a good relationship for both subfamilies, more so in the Syrphinae (Figure 3.2b; $r^2=0.58$) than the relatively more diverse Eristalinae ($r^2=0.31$). As further support for the relationship between the two variables, change in tongue length was positive in 74 of the 85 cases in which body size increased, significantly more than expected by chance alone (binomial test, $p<0.001$).

Log-transformed species means also had a significant allometric relationship ($F_{1,216}=404.6$, $r^2=0.65$, $p<0.001$), with a slope of $+0.32 \pm 0.02$.

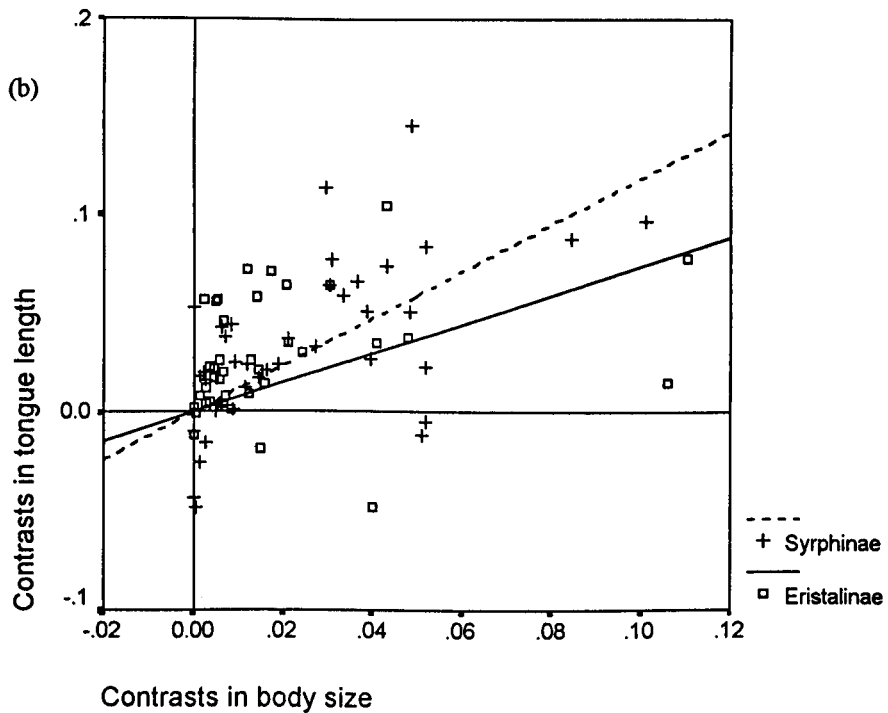
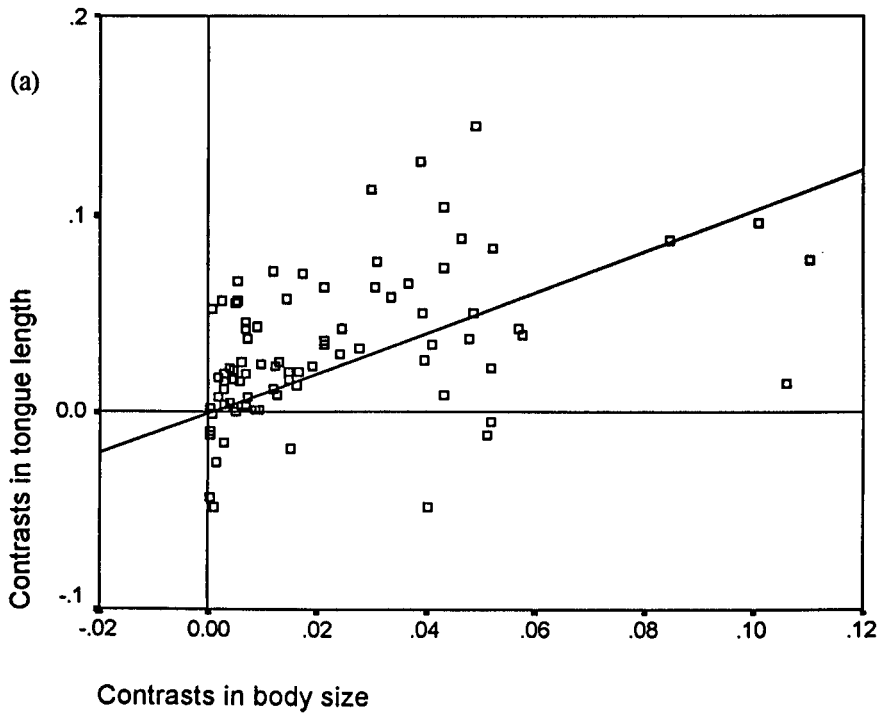


Figure 3.2. The interspecific relationship between (a) tongue length and body size (thorax volume) (b) tongue length and body size for two syrphid sub-families. Points are standardised independent contrasts. The regression lines were forced through the origin.

3.3.2 Are body size changes related to changes in parameters of egg production?

The interspecific variation in egg characters was again considerable, with ovariole number ranging from 8 in *Melanostoma mellinum* to 302 in *Criorhina caudata*. Egg volume varied from 0.02 mm³ in *Syrirta pipiens* to 0.51 mm³, in *Volucella bombylans*.

Analysis of 58 independent contrasts showed that ovariole number and body size have evolved in a significantly positively correlated fashion (Figure 3.3a; $F_{1,57}=24.7$, $r^2=0.30$, $p<0.001$). This relationship had a slope of 0.15 ± 0.03 . As further support for a relationship between the 2 variables, change in ovariole number was positive in 40 of the 58 cases in which body size increased, significantly more than expected by chance alone (binomial test, $p<0.001$).

The relationship between change in ovariole number and change in body size was stronger in the more diverse half of the phylogeny, the Eristalinae (Figure 3.3b; $F_{1,24}=24.5$, $r^2=0.51$, $p<0.001$) than in the more homogeneous branch, the Syrphinae ($F_{1,31}=15.9$, $r^2=0.34$, $p<0.001$).

Changes in egg volume were less tightly linked to changes in body size (Figure 3.3c; $F_{1,57}=16.2$, $r^2=0.22$, $p<0.001$), with a slope of 88.3 ± 22.03 . Change in egg volume was positive in 40 of 58 cases where body size increased, more than expected by chance alone (binomial test, $p=0.006$). The relationship was stronger in the Syrphinae (Figure 3.3d; $F_{1,31}=10.5$, $r^2=0.25$, $p=0.003$) than in the Eristalinae ($F_{1,24}=4.0$, $r^2=0.14$, $p=0.058$).

Using log-transformed species means (not contrasts), both ovariole number and egg volume also have significant allometric relationships with body

size (ovariole number: $F_{1,138}=83.0$, $r^2=0.38$, $p<0.001$ (slope $+0.47 \pm 0.05$), egg volume: $F_{1,85}=78.3$, $r^2=0.48$, $p<0.001$ (slope $+0.47 \pm 0.05$)).

The patterns with body size may be confounded by any trade-off between ovariole number and egg volume, so the relationship between the two was examined. The raw species means showed a negative relationship between the two characters if both were adjusted for body size (by generating residuals from egg volume/thorax volume and ovariole number/thorax volume regressions) (Figure 3.4a; $F_{1,84}=53.8$, $r^2=0.39$, $p<0.001$, slope $=-0.66 \pm 0.09$), confirming the clear trade-off between ovariole number and volume found by Gilbert (1990). Analysis of independent contrasts also found a negative relationship between egg number and egg volume (again adjusted for body size) (Figure 3.4b; $F_{1,57}=11.5$, $r^2=0.17$, $p=0.001$), with a slope of -0.0006 . However, ovariole number changed in the opposite direction to egg volume in only 30 out of 58 contrasts, which could be expected by chance alone (binomial test, $p=0.896$).

To rule out any possible problem with an egg number/egg volume trade-off, the two were multiplied together to produce another parameter, batch size (effectively ovary volume). Analysis of independent contrasts showed a strong relationship between batch size and body size (Figure 3.5a; $F_{1,57}=90.6$, $r^2=0.61$, $p<0.001$), with a slope of $+5.80 \pm 0.61$. 51 of 58 positive changes in body size were associated with positive changes in batch size (binomial test, $p<0.001$). The relationship was stronger in the Eristalinae (Figure 3.5b; $F_{1,24}=58.9$, $r^2=0.84$,

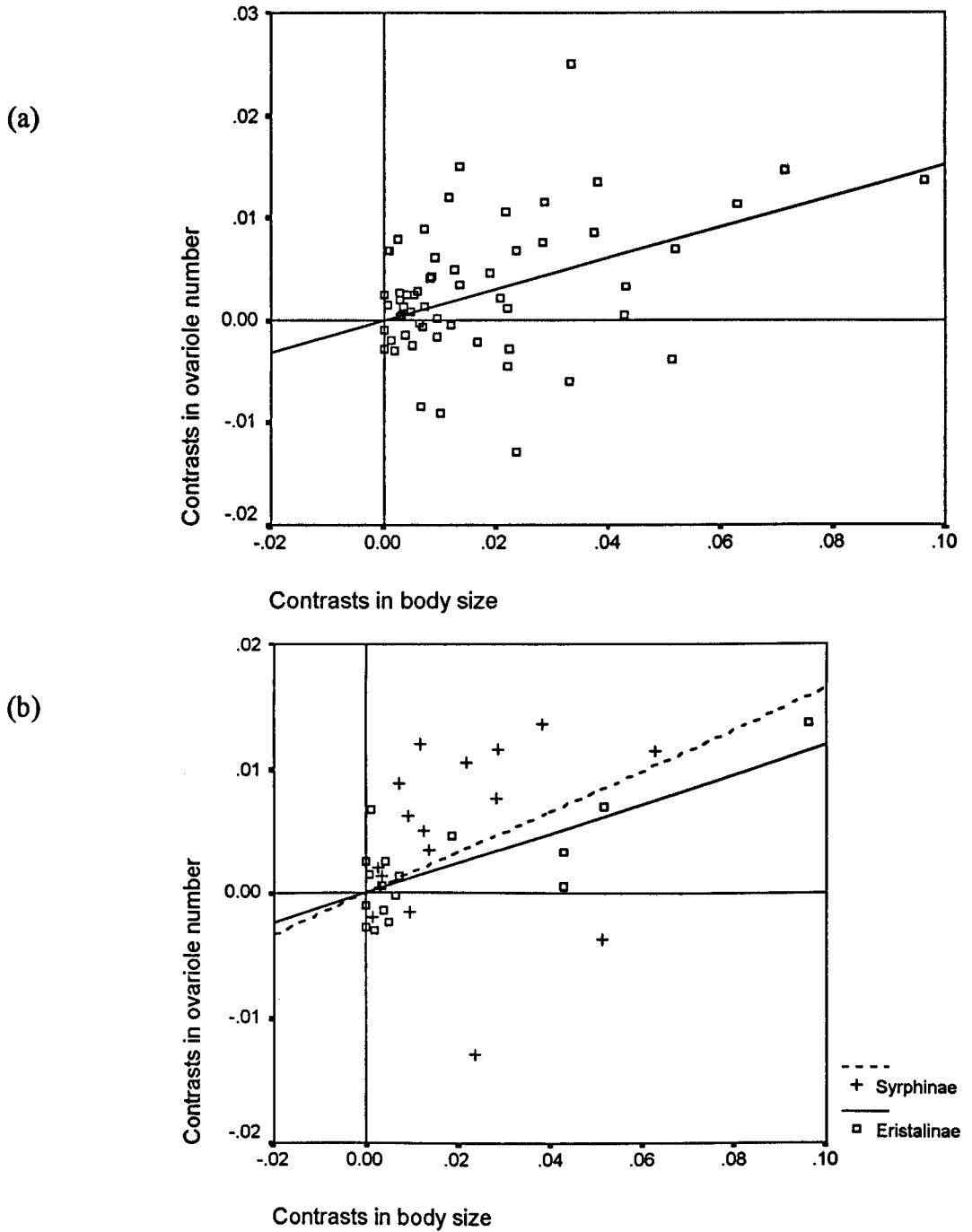
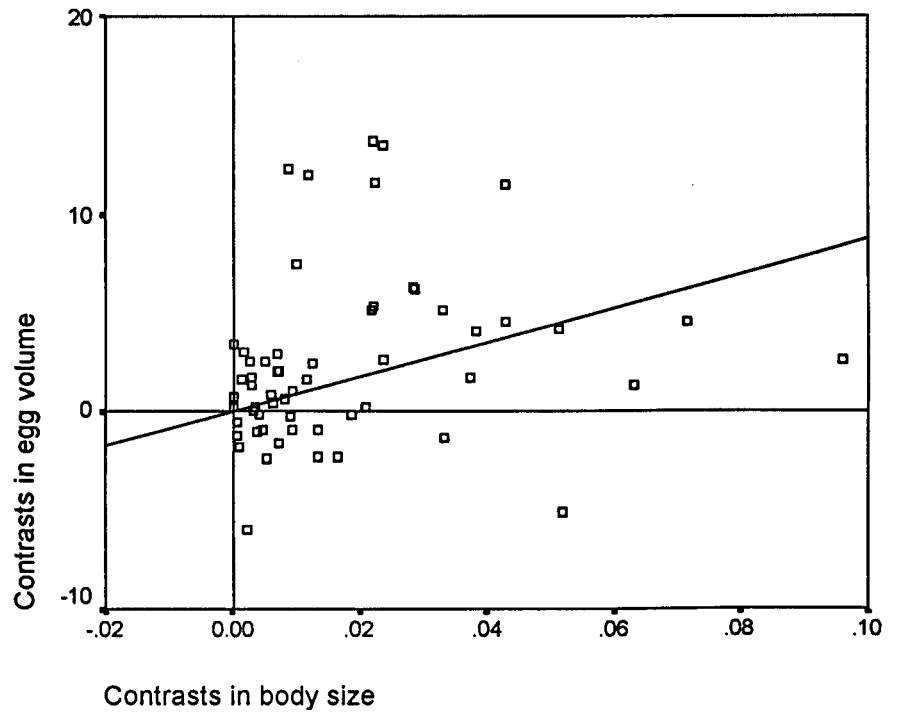


Figure 3. The interspecific relationship between (a) ovariole number and body size (thorax volume) (b) ovariole number and body size within two syrphid subfamilies. All points are standardised independent contrasts. Regression lines were forced through the origin. (Figure 3 continued over page).

(c)



(d)

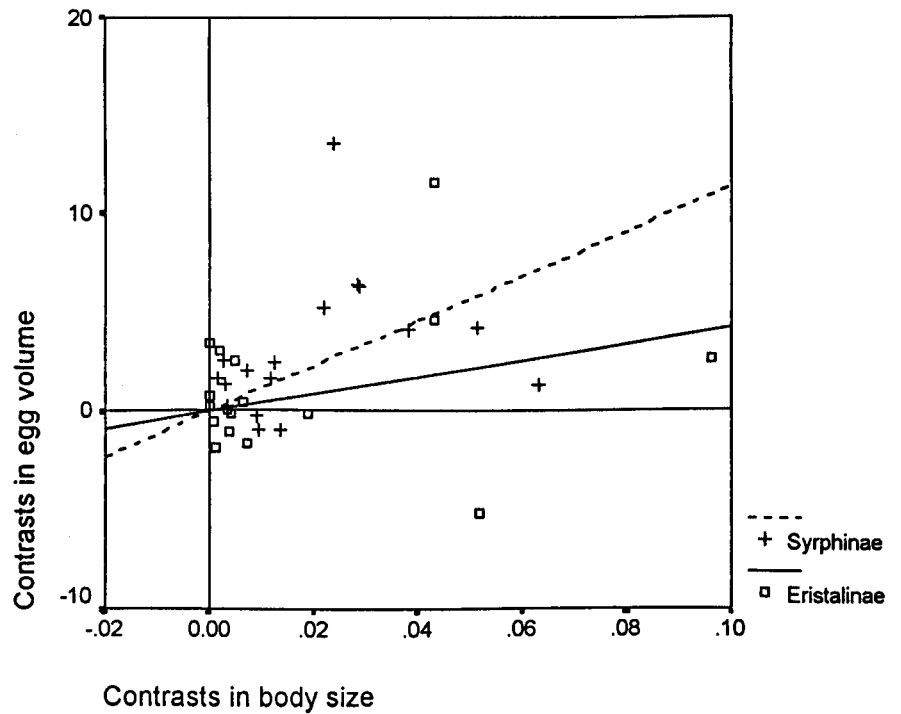


Figure 3 (continued) The interspecific relationship between (c) mature egg volume and body size (thorax volume) (d) mature egg volume and body size within two syrphid subfamilies. All points are standardised independent contrasts. Regression lines were forced through the origin.

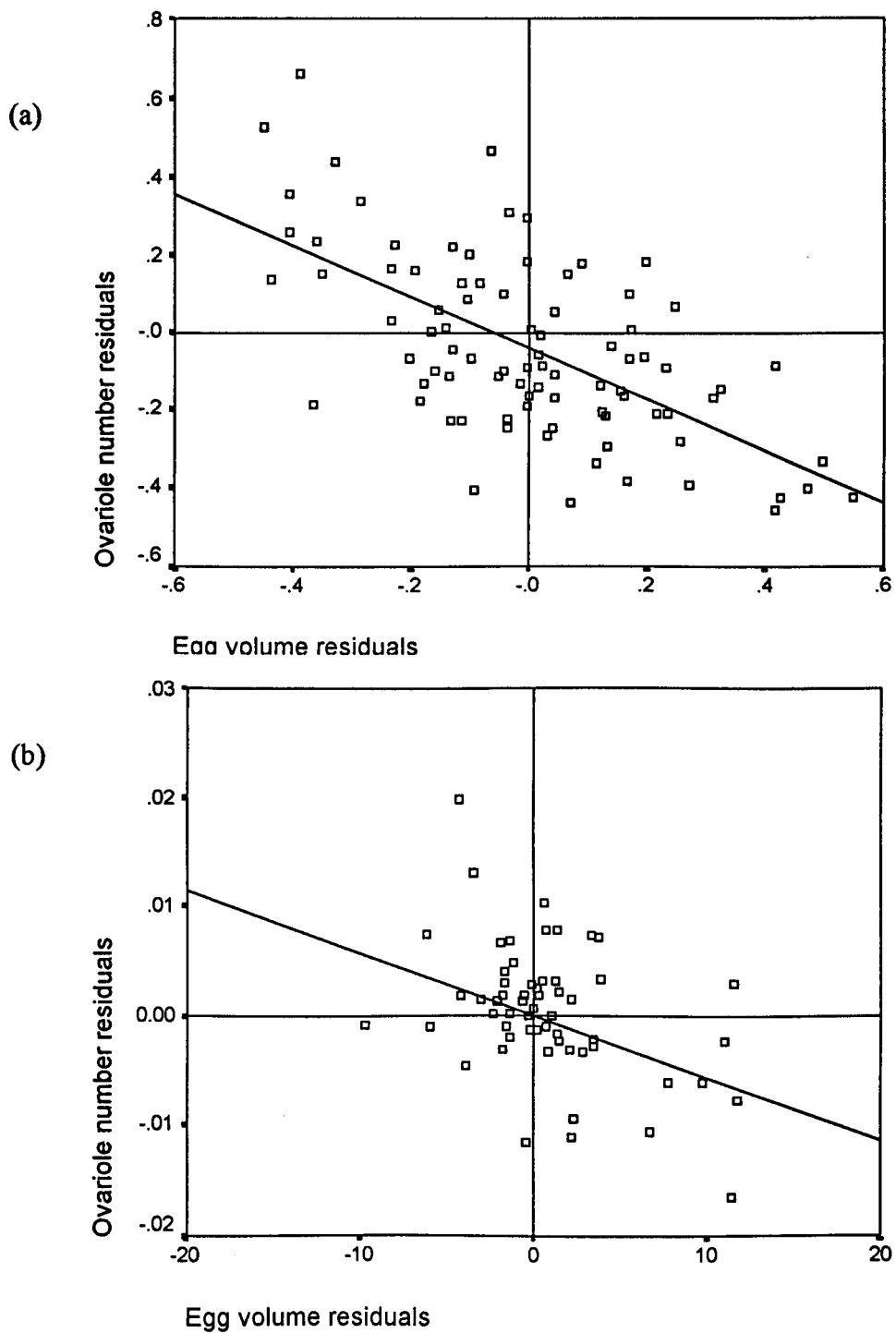


Figure 3.4. (a) The size-adjusted relationship between mean ovariole number and mean egg volume. Residuals of an egg volume/ body size regression were regressed on residuals of an ovariole number/ body size regression. (b) The size-adjusted relationship between ovariole number and egg volume, using independent contrasts. Residuals of an egg volume/ body size regression were regressed on residuals of an ovariole number/ body size regression.

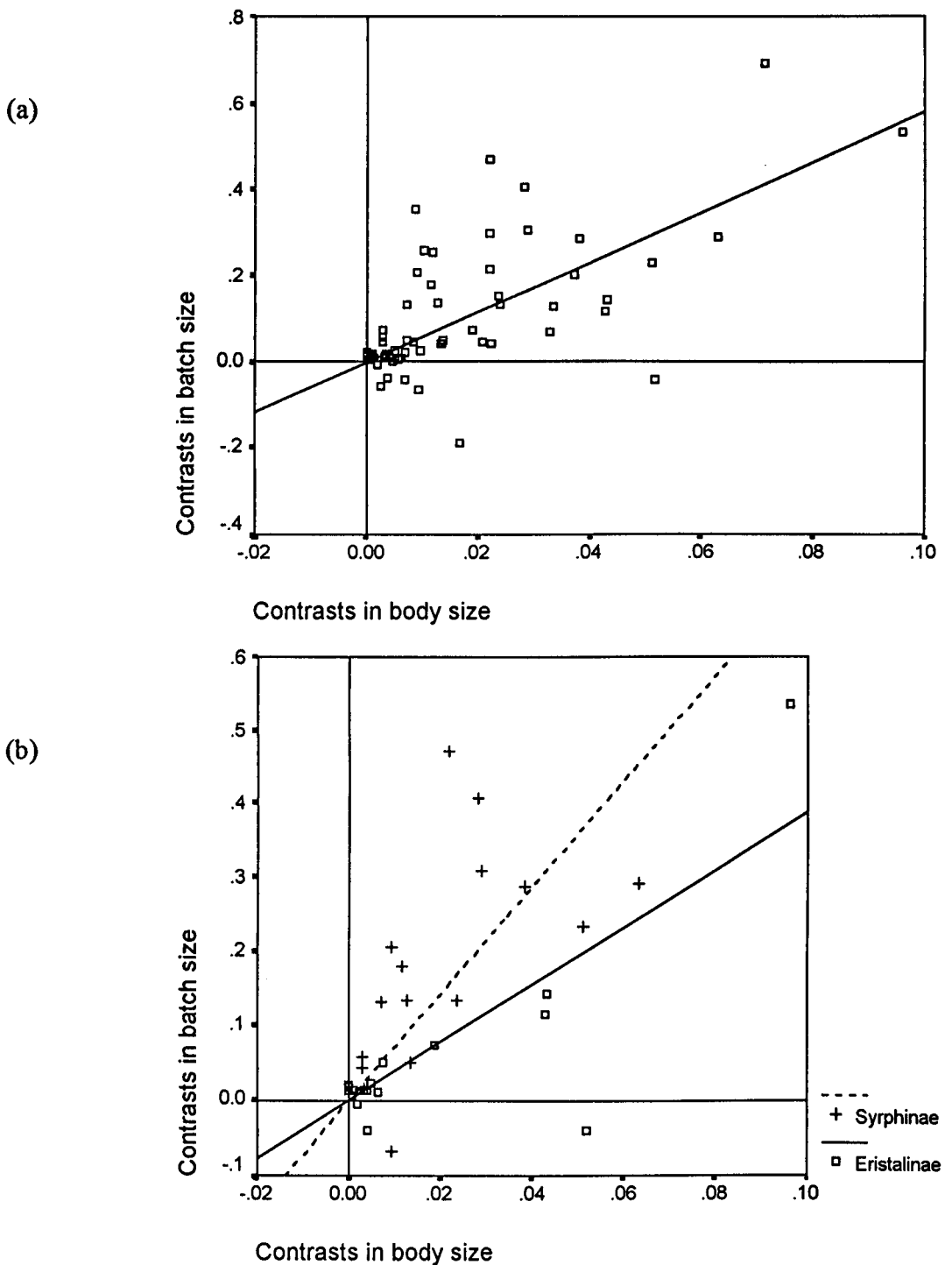


Figure 5. The interspecific relationship between (a) batch size and body size (thorax volume) (b) batch size and body size in two syrphid sub-families. All points are standardised independent contrasts. All regressions were forced through the origin.

$p < 0.001$) than in the Syrphinae ($F_{1,31}=68.0$, $r^2=0.69$, $p < 0.001$). There was also a positive significant relationship with analysis of log-transformed species means ($F_{1,84}=424.0$, $r^2=0.83$, $p < 0.001$), with a slope of 0.95 ± 0.05 .

3.3.3 Is body size related to parameters of sperm production?

Interspecific variation was again considerable, with testis length ranging from 0.32 mm in *Platycheirus discimanus* to 25 mm in *Criorhina kincaidi*. Testis volume ranged from 0.01 mm³ in *Heringia squamulae* to 11.6 mm³ in *Microdon*.

Analysis of independent contrasts revealed that testis size (volume) and body size have evolved in a positively correlated fashion, though this relationship was weaker than for female characters (Figure 3.6a; $F_{1,64}=6.6$, $r^2=0.09$, $p=0.013$, slope = $+59.0 \pm 23.0$). Further support for a relationship between the two variables was provided by examining the directions of the contrasts; change in testis size was positive in 49 of the 65 cases in which body size increased, significantly more than expected by chance alone (binomial test, $p < 0.001$). The relationship between testis volume and body size was stronger in the Eristalinae (Figure 3.6b; $F_{1,29}=6.9$, $r^2=0.19$, $p=0.014$) than in the Syrphinae ($F_{1,33}=3.7$, $r^2=0.10$, $p=0.063$).

Contrasts in another parameter of sperm production, testis length, were tightly linked with contrasts in testis volume ($F_{1,64}=85.6$, $r^2=0.57$, $p < 0.001$). Change in testis length was positively related to change in thorax volume (Figure 3.7a; $F_{1,67}=2.2$, $r^2=0.03$, $p=0.142$) with a slope of $+1.09 \pm 0.73$, but this was not significant, and was weaker than for testis volume. This was true in both the

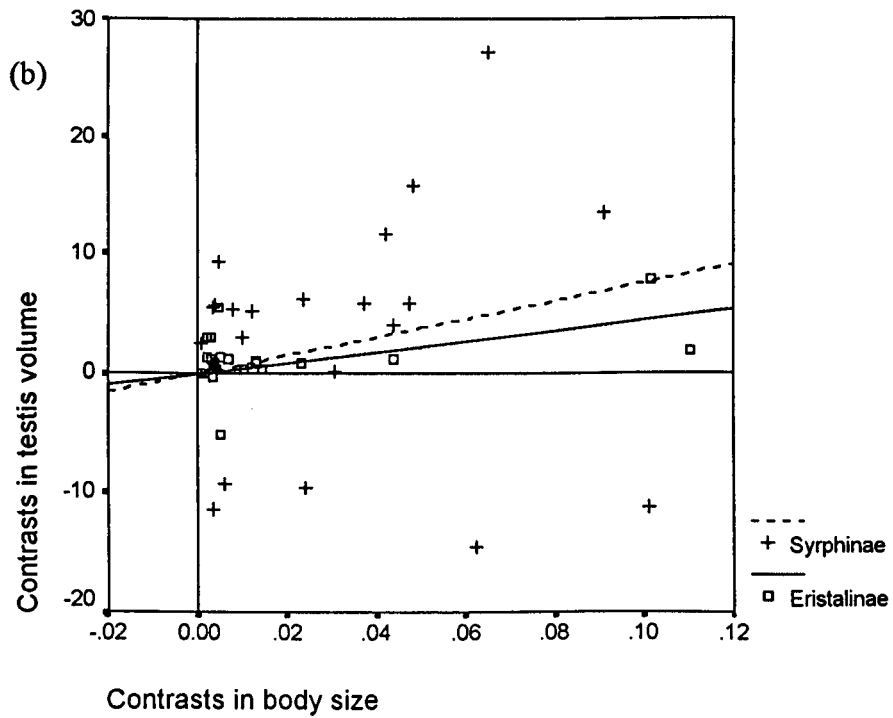
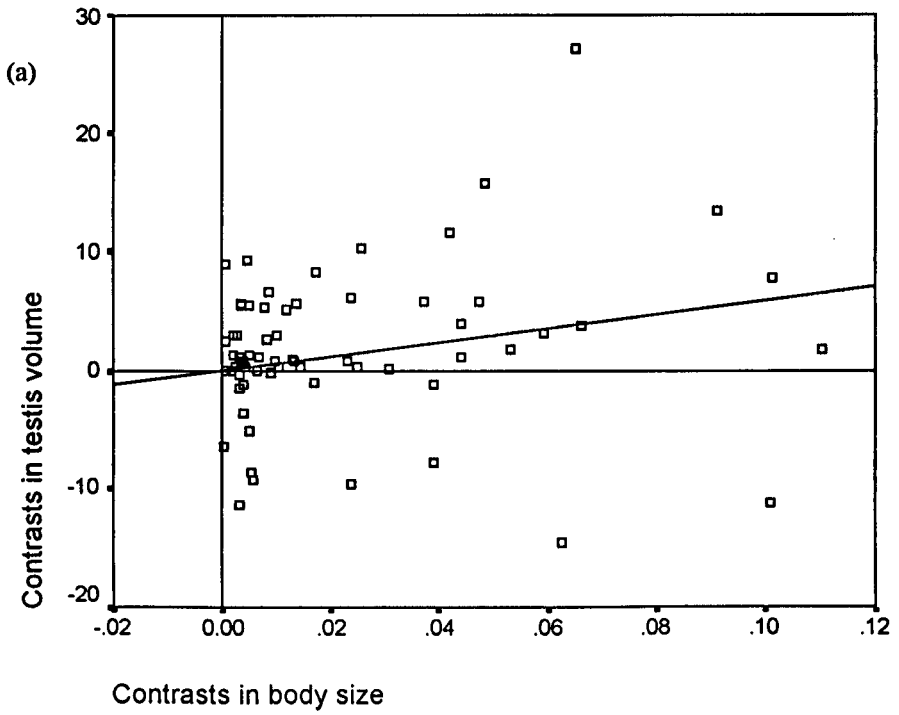


Figure 3.6. The interspecific relationship between (a) testis volume and body size (thorax volume) (b) testis volume and body size in two hoverfly subfamilies. Points are standardised independent contrasts. Regressions were forced through the origin.

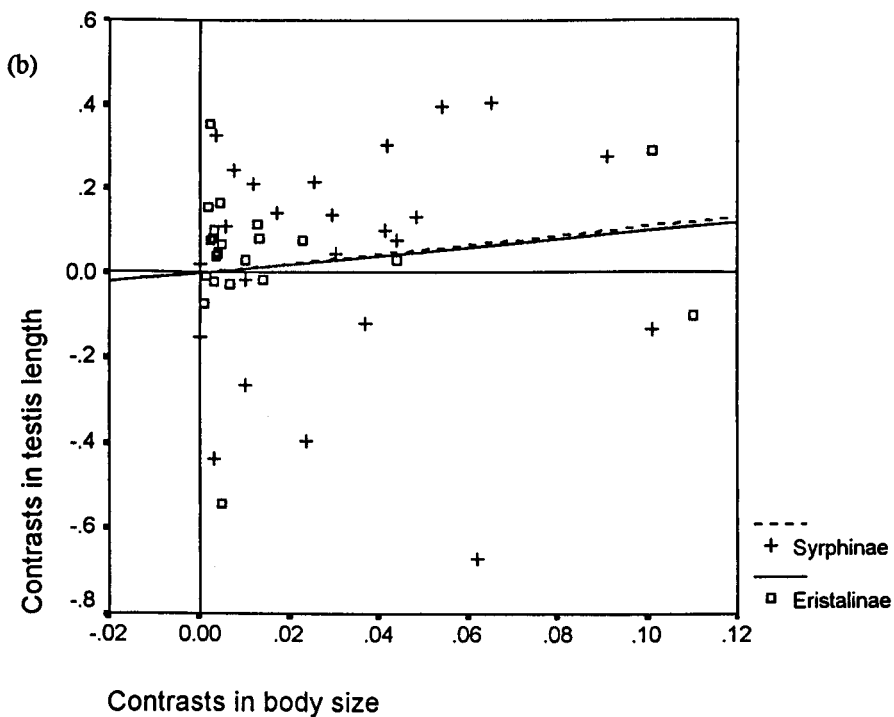
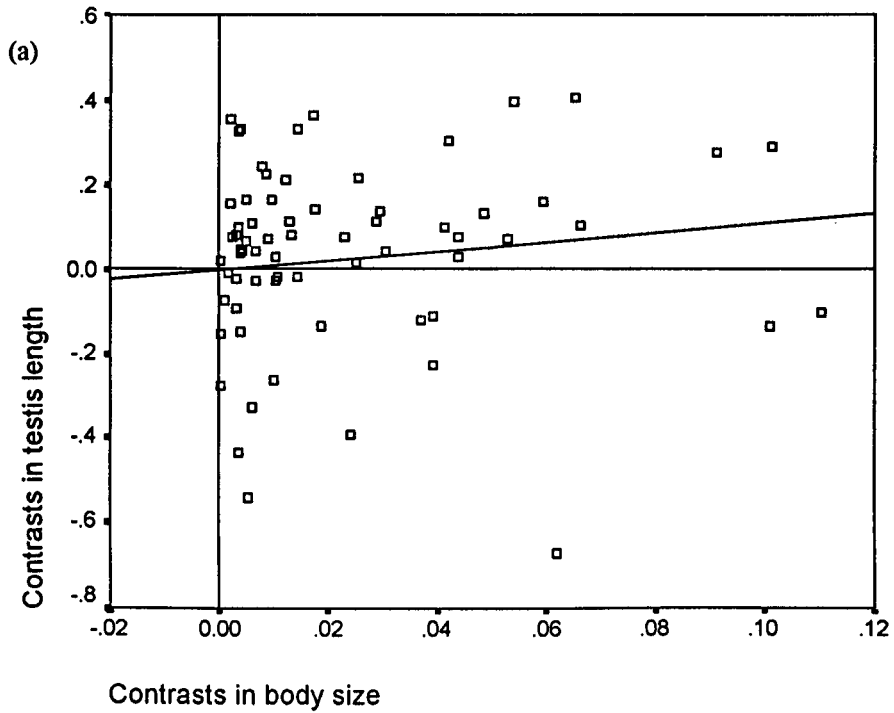


Figure 3.7. The interspecific relationship between (a) testis length and body size (thorax volume) (b) testis length and body size in two hoverfly subfamilies. Points are standardised independent contrasts. Regressions were forced through the origin.

Syrphinae (Figure 3.7b; $F_{1,35}=1.8$, $r^2=0.05$, $p=0.194$) and the Eristalinae ($F_{1,30}=0.9$, $r^2=0.03$, $p=0.889$). Change in testis length was positive in 45 of 68 cases where body size increases, (binomial test, $p=0.011$), again a weaker relationship than for testis volume or egg parameters.

Comparing log-transformed species means, both testis volume and testis length have significant allometric relationships with body size (testis volume: $F_{1,147}=51.1$, $r^2=0.26$, $p<0.001$ (slope = 0.70 ± 0.10), testis length: $F_{1,150}=43.7$, $r^2=0.23$, $p<0.001$ (slope = 0.46 ± 0.07)), stronger than in their evolutionary relationships.

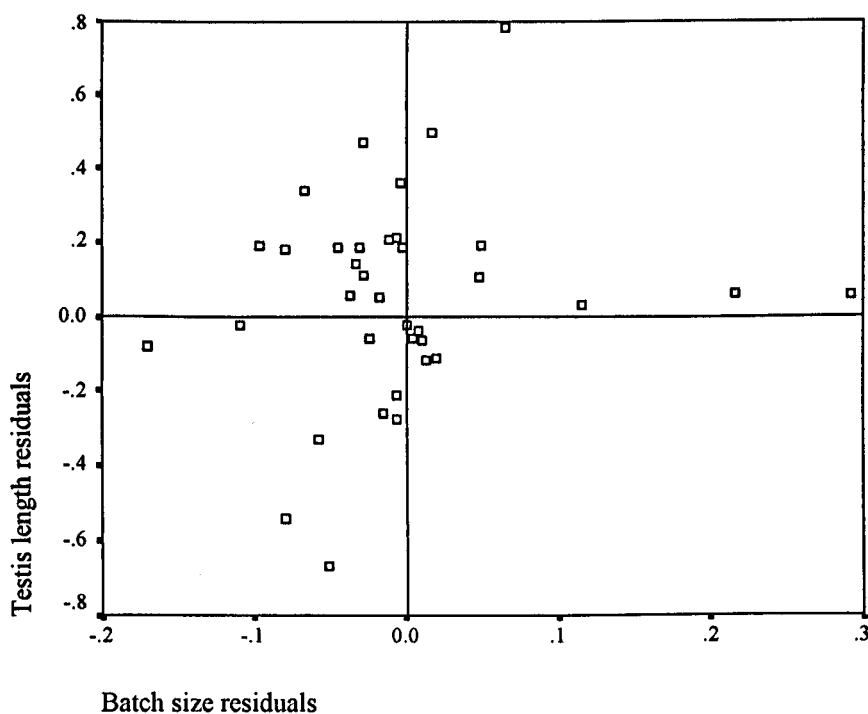


Figure 3.8. The size-adjusted interspecific relationship between batch size and testis length, using standardised independent contrasts. Residuals of a testis length/ body size regression are regressed on residuals of a batch size/ body size regression. Regressions were forced through the origin.

Comparing males and females among species, there was no association between change either of the testis characters and change in any of the egg characters, after adjusting both for body size (e.g. batch size contrasts and testis length contrasts Figure 3.8; $F_{1,35}=0.8$, $r^2=0.02$, $p=0.365$). Only 21 of 36 contrasts were in the same direction for males (testis length and females (batch size), which could be expected by chance alone (binomial test $p=0.405$).

3.4 Discussion

Allometric patterns can help explore the selection pressures that have shaped variation between species; if there are departures from orderly scaling patterns, adaptive explanations need to be sought. Tongue length in hoverflies showed no such deviation. As previously found within the genus *Platycheirus* (Gilbert 1990), there was tight covariance between tongue length and body size, both in species means and independent contrasts. Tongue length evolved in the opposite direction to body size in only 11 of the 85 contrasts considered; for example, *Syritta* has a smaller body size, but a longer tongue, than the closely related genus *Xylota*.

However, reproductive characters in both females and males did not show such orderly scaling patterns, implying strong selection pressures overriding the evolutionary covariance with body size. Across related animal species, body size is generally correlated with both egg size and egg number (Peters 1983). In hoverflies, this seems true of ovariole number; the results indicate that the history of change in fecundity was largely one of body size change. A regression of

independent contrasts was highly significant, and ovariole number frequently increased where body size increased between species. The relationship between change in egg volume and change in body size is weaker, especially within the diverse Eristalinae ($r^2=0.14$). Similarly Wiklund *et al* (1987) found that body size correlated significantly with egg number, but not with egg weight, in species of pierid butterfly, and Poulin (1995) found a similar pattern across copepod families using independent contrasts. There are contrasting selection pressures acting on egg volume; an increase in egg size may lead to increased offspring fitness, while a decrease in size could result in an increase in fecundity, because of the trade-off between egg size and number. Like Gilbert (1990), a trade-off was found between egg number and egg volume (once adjusted for body size) in hoverflies. However, r^2 was fairly low (0.17), and the trade-off does not appear very clear-cut (see Figure 3.4b), especially since ovariole number evolved in the opposite direction to egg size in only around half the contrasts (30/58).

These patterns between egg size, egg number and body size may be partly explained using the argument of Wiklund *et al* (1987), which runs as follows. 'Baseline' allometry between egg size and body size would be expected in the absence of variation in any particular selection pressures. However, if hoverflies are selected to maximise fecundity (ovariole number), this selection pressure could be strong enough to override any correlation between egg size and offspring fitness, and egg size would be reduced to a minimum, irrespective of body size (Labine 1968). Scaling of egg size to body size would only occur if there was some constraint on female fecundity. Wiklund *et al*'s hypothesis was supported

by the fact that Swedish satyrids, tolerant of low temperatures (whose fecundity may be constrained by the length of time during which temperatures are high enough for oviposition) did show scaling between egg size and body size, whereas sun-loving pierids (whose fecundity is not constrained by temperature) did not. Furthermore, two satyrid species which were sun-adapted fitted with the patterns of the pierids. It is possible that syrphids (especially the Eristalinae) may also be maximising their fecundity, and limiting their egg size to a minimum, regardless of body size. This would be most likely if the correlation between egg size and offspring fitness is not strong; the weak trade-off between ovariole number and egg size suggests this is sometimes the case. However, it is not clear why the fecundity of the Eristalinae should be less constrained relative to the Syrphinae.

Once these two measures are combined into one parameter, batch size, there is a much stronger relationship with the evolution of body size, in all parts of the phylogeny. Species means (rather than contrasts) show an equally strong link. This (like Gilbert 1990) implies that size was the major influence on the evolution of overall reproductive potential. Body size is bound to be influential; larger bodies can probably mechanistically produce larger ovarioles, and in 40/58 contrasts (more than expected by chance) egg volume did increase when body size increased. Therefore if eggs are sometimes reduced to a minimum size to maximise fecundity, they may well still be larger in larger hoverflies.

The evolution of batch size is less strongly linked with body size in the Syrphinae than in the Eristalinae. The cause of this could be the invariability of

the Syrphinae in adult form for reasons not connected with reproductive potential so oviposition strategies could have varied, whilst (relatively) body size has not.

Like egg variation in females, the patterns of testis variation in males were complex. While not as extreme as in *Drosophila bifurca*, where sperm length (and hence testis length) is twenty times longer than the male body (Pitnick *et al* 1995a), there are very large variations in testis length among species of Syrphidae, from 0.32 mm in *Platycheirus* to 25 mm in *Criorhina*. Drosophilids are equally variable (see diagrams in Patterson & Stone 1952). Since there is a tight correlation between testis length and sperm length, both observationally (Joly & Bressac 1994) and evolutionarily (Pitnick 1996) it is assumed here that in the hoverflies a long testis implies long sperm within it. Furthermore, though producing sperm is traditionally considered cheap (Trivers 1972), producing such long sperm is costly, increasing the costs of producing and maintaining testes (Pitnick *et al* 1995a), reducing sperm numbers (Pitnick 1996) and delaying male maturity (Pitnick *et al* 1995b). The data suggest that some species of hoverfly may also produce very long sperm, with the associated costs. The possible selective advantages are unclear (Pitnick *et al* 1995b); long sperm may give an advantage in the competition to fertilise ova, by swimming faster (Gomendo & Roldan 1991), have a post-fertilisation function, providing nutrients for offspring (Snook & Markow 1996) or function to flood the whole reproductive tract (Simmons & Siva-Jothy 1998). These would only provide a selective advantage in the presence of sperm competition. Nothing is known about this in hoverflies, but all species mate multiple times, as far as is known, and sperm competition is

widespread in other invertebrates and is considered nearly ubiquitous (Parker 1982, 1984).

The evolution of testis length and volume has clearly been less constrained by body size than female characters, suggesting that other pressures have had a strong influence. The most obvious selection pressure on testis size is sperm competition from other males. Variation in testis size suggests either variable risk of sperm competition among hoverfly species, or variable mechanisms to deal with it (for example, the very large sperm described above). Insects are known to differ widely in their mechanisms of either promoting their chances of fertilisation in sperm competition, or avoiding it altogether (Simmons & Siva-Jothy 1998), even within a family (e.g. the drosophilids). Different mechanisms within the hoverflies could therefore lead to different selective forces on testis size.

There was no evidence that the evolution of increased reproductive potential in females is associated with that in males. Again, this was probably because selective pressures on male testis characters are associated with diverse modes of dealing with sperm competition, which is sexual selection independent of any natural selection pressures shared with females.

The link between testis length and body size is weaker than that between testis volume and body size. Strong selection pressures on sperm length in some species may have caused this deviation from an orderly scaling pattern. This suggests that selection pressure is stronger on sperm length alone than when sperm number is also considered. If these selection pressures derive from sperm

competition, this again emphasises the importance of sperm length in the competition for fertilisation or as a post-fertilisation advantage.

There was a large influence of phylogeny on these relationships. The link between changes in batch size, testis size and testis length and changes in body size are all tighter if the species means are compared. Different conclusions would be reached with these, effectively non-independent points. This emphasises the need for incorporation of phylogeny into studies such as this; more such studies are needed to untangle the complex patterns of reproductive allometry in invertebrates.

Chapter Four

Exploring the measurement of similarity

4.1 Introduction

David Grewcock (1992) introduced the concept of using a computer program which objectively measures the similarity between model and mimic as a tool for studying mimicry. Similarity to wasps is very variable in hoverflies, and a way was needed of rating this quality without the use of subjective human judgement. He suggested that ‘the most immediate barrier to the study of apparently mimetic hoverflies was the diversity of abdominal patterns in the [mimicry] complex, and the fluidity of subjective judgements about the similarity of those patterns to that of the supposed model pattern’, and proposed a ‘technique ... which allowed the consistent quantification of pattern similarities, with minimal reliance on subjective judgements.’ This had potential uses for looking at specific aspects of mimicry. However, similarity as measured and the quality of mimicry are not the same thing. The latter is dependent on receiver psychology; it is how predators perceive the patterns that determines the quality of the mimicry. The main use of measured similarity values so far has been to determine how closely similarity and mimicry coincide (Dittrich *et al* 1993).

Grewcock’s method mapped images of abdominal colour patterns onto a grid, with each square containing only a single colour. Model and mimic images were compared using squares of progressively smaller size. The smaller the squares needed to discriminate between the images, the more similar they were.

Using this method, Grewcock (1992) successfully distinguished between a number of hoverfly species in comparison to a wasp model, as well as showing that the similarity of hoverflies to their wasp models was much lower than between the classic model-mimic pairing of the Monarch and Viceroy butterflies.

The technique was subsequently modified to make it faster and more convenient, directly comparing corresponding pixels of two bit-mapped images (described in detail later in this chapter). This discriminates successfully among various hoverfly species, which show a wide range of similarity to wasps, as expected. This way of measuring similarity is the approach used in this thesis. The other main advance in the development of the image analysis has been to look at the coincidence between actual and perceived similarity (Dittrich *et al* 1993). Though Grewcock always assumed at least some relationship between the two, experiments with pigeons have shown that they consistently rank images of different hoverfly species in a way highly correlated to the measured similarities (with some exceptions, see later discussion, and introductory chapter). The same rankings also occur using pinned insect specimens rather than bit-mapped images (Green *et al* 1999). These results are important to the use of the image analysis, as the kind of variation measured by the technique is relevant to and correlated with real biological decisions made by receivers.

In this thesis, the use of this helpful tool is expanded further for the study of mimicry. Similarity measures have been made on a wide range of hoverfly species, and then used in familiar and novel ways. One use has been to expand on

Grewcock's (1992) work, by using similarity values to approximate mimicry quality, to compare the 'mimicry profile' of disturbed and undisturbed habitats.

Secondly, similarity values are used in a completely novel way to examine the relationships between similarity to the model, reproductive potential and flight agility. Altogether, image analysis is carried out for 68 images of hoverflies compared to wasps, many more than the 10-15 images used in previous studies.

The use of similarity values on this large scale justifies some further examination of the way these values are generated, as well as checking whether the system reliably produces reasonable results. There are some problems inherent in testing the method; its very purpose is to be objective and therefore using human subjective judgement to test it would be inappropriate. However, the practical implementation of the system can certainly be judged, and assumptions made can be tested. Overall, the process should be reliable, repeatable, and relevant to real life. Specifically, this chapter aims to answer the following questions:

- How does the comparison of colour patterns work in theory and in practice?
- Does the program produce an intuitively sensible ranking of species? If not, why not?
- Is the use of a single *Vespula vulgaris* image justifiable?
- Is the use of a single similarity value for a colour pattern group justifiable?

4.2 How are the patterns compared?

4.2.1 How the image analysis technique works

Essentially, the method converts two-dimensional images to colour bitmaps, and then generates a single-value description of the similarity between them. This is done by superimposing the test and the reference image, and calculating the distance apart of their corresponding pixels in red-green-blue (RGB) colour space. There are three stages to this process.

Colour	Red value	Green value	Blue value
Black	0	0	0
Dark orange	230	120	40
Orange	240	155	25
Yellow	255	204	102
Pale Yellow	255	255	153
Grey	204	204	204
White	255	255	255

Table 4.1. Red-green-blue values for colours used in syrphid palette.

Firstly, the images were prepared. Photographs of hoverflies from Torp (1994) were individually scanned and manipulated using Adobe Photoshop so that the image consisted only of the abdomen (from scutellum to tip). (Though a few hoverfly genera have yellow patterns on the thorax (e.g. *Xanthogramma*, *Chrysotoxum*), in most it is uniformly dark). A field guide (Chinery 1993) illustration of *Vespula vulgaris*, the model, was treated in the same way. Some

hoverfly images not available from field guides were obtained by directly photographing specimens from the Natural History Museum, London. Small imperfections, reflections and so on were eliminated from the images manually. Using the program BitEdit™, the images were then reduced to a standard palette of six colours (Table 4.1), which adequately describe virtually all hoverfly colours, plus white as a background colour.

The images were standardised in size, such that all images were 90 x 100 pixels, with the image centred vertically to maximise overlap between images.

The orientation of images is shown in Figure 4.1.

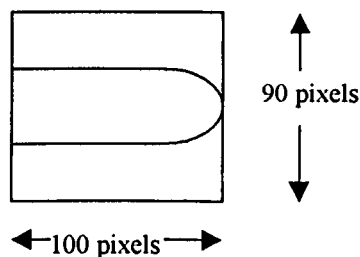


Figure 4.1. Orientation and size of images. The abdomen was centred vertically.

The first stage of the comparison was then carried out, by running the program BITMAP (see Appendix 1) under Qbasic™. This converts each bitmap file into a string of digits representing the colour pattern in each image.

In the third stage, another program (SHIFT: see Appendix 2) compares each mimic pattern file to that of the model, producing a similarity value. This is achieved by aligning the images in their bottom left corner (0,0), and shifting them vertically and horizontally to maximise the matching of pixels, thus allowing for slight orientation and positional differences between patterns.

To produce the similarity value, SHIFT calculates the sum of colour ‘matches’, and ‘mismatches’, summed over all corresponding positions in the two patterns. For comparisons involving black or white (the background), matches and mismatches are calculated simply as shown in Table 4.2.

Coincidence of white pixels are not counted as matches because white is the background colour, not part of the image. However, correspondence of white (background) and black or coloured pixels are counted as mismatches because they represent differences in body shape.

Colour of pixel	Colour of corresponding pixel (after shifting)	Match	Mismatch
White	White	0	0
White	Not white	0	1
Black	Black	1	0
Black	Not white or black	0	1

Table 4.2. Match and Mismatch values allocated to pixel comparisons involving black and white.

When black is paired with a colour (i.e. not black or white), a mismatch is scored, because this represents a difference in pattern distribution, since the coloured areas differ in location. However, where two non-black colours correspond in position, this does not necessarily mean that the patterns (in terms of distribution of black) at that position are different, since potentially only the colour of the pattern may differ. For example, it would not make sense to count a pairing between a yellow and a pale yellow pixel as just as much of a mismatch as

that between black and yellow (mismatch=1). Therefore matches between coloured pixels were calculated as shown in Table 4.3.

Colour of corresponding non-black-or-white pixel (after shifting)	Match	Mismatch
Same colour	1	0
Different colour	$1-p$	p

Table 4.3. Match and Mismatch values allocated to pixel comparisons involving colours (not black or white). Value of p is explained in text.

p measures the degree of mismatch, which is the distance apart of the two colours in RGB colour space (the numerator in the following equation), relative to the distance apart of black and white (the denominator). This is calculated as follows, using the RGB values of colour_m (mimic image) and colour_R (reference image).

$$p = \frac{\sqrt{[(red_m - red_R)^2 + (green_m - green_R)^2 + (blue_m - blue_R)^2]}}{255\sqrt{3}}$$

Hence p and the degree of mismatch increases in magnitude as colours become more dissimilar.

The matches and mismatches for the image are then summed. The overall picture similarity is calculated as the total number of matches divided by the total number of matches and mismatches

$$\frac{\text{Matches}}{\text{matches} + \text{mismatches}}$$

In this way, a similarity value is obtained which takes into account not just the proportion of yellow (or other colour) in the abdominal pattern, but also the distribution and shade of the colour.

4.2.2 *The role of colour*

The colour palette used for the images is shown in Table 4.1. A value for p was calculated for a comparison between each colour and yellow (colour of wasp pattern) (Table 4.4).

Colours paired	p -value
Yellow and yellow	0.00
Pale yellow and yellow	0.16
Orange and yellow	0.21
Dark orange and yellow	0.24
Grey and yellow	0.26

Table 4.4. p -values obtained from different colour pairings.

The smaller the value of p , the more matches and fewer mismatches. Therefore pale yellow is considered the most similar to yellow, followed by orange, dark orange and grey respectively. To get an idea of how the comparison of these colours works in practice, grids (100x100 pixels) were compared in different colours. These grids approximated to the pattern on the second tergite of a wasp (Figure 4.2a) and a putative mimic (Figure 4.2b). Those grid squares which are white in the figure were either yellow, pale yellow, orange, dark orange

or grey (see RGB values in Table 4.1). Grid A (model) in yellow-and-black was compared using SHIFT to either itself or Grid B (mimic). The results are shown in Table 4.5.

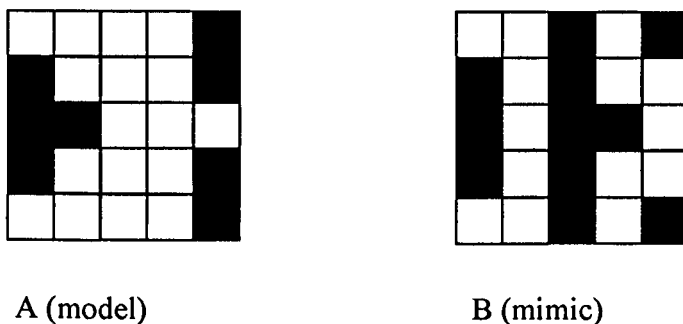


Figure 4.2. 5x5 grids used to compare colours.

Grid A (y-and-b) compared with:	Colour of grid	Similarity value (%)	Shift
Grid A	Yellow and black	100	(0,0)
Grid A	Pale yellow and black	89	(0,0)
Grid A	Orange and black	86	(0,0)
Grid A	Dark orange and black	83	(0,0)
Grid A	Grey and black	32	(0,0)
Grid B	Yellow and black	72	(0,0)
Grid B	Pale yellow and black	64	(0,0)
Grid B	Orange and black	64	(0,0)
Grid B	Dark orange and black	63	(0,0)
Grid B	Grey and black	25	(0,0)

Table 4.5. Similarity values produced by SHIFT for test grids.

In practice, then, a difference in colour from yellow makes a difference of 10-15% to the similarity score. Where a difference in pattern distribution is also involved, this is reduced still further. Contrasts to orange, dark orange and pale yellow all produce approximately equal differences from yellow, as expected from the relatively similar p -values. The exception to both of these is where the other colour is grey; here the drop in similarity is dramatic.

Where the pattern is different, comparing grid A to grid B, the colour plays a lesser part in determining the similarity value, because contrasts between black and colours produce bigger mismatches than contrasts between colours. This is nearly always the situation in nature, where there are both colour and pattern differences between model and mimic. Therefore differences in colour play a lesser role than pattern distribution in determining similarity values. What importance the shade of yellow has in signalling to predators is unclear; pigeons certainly can rate hoverfly images of different colours than yellow as highly similar to wasps (e.g. *Episyrphus balteatus*, which is orange in colour). Grey would seem much less of a warning signal than any yellow-based colour, and so probably deserves its lower ranking. Therefore, based on what little is known about the nature of colour perception in predators, the colour ratings obtained seem reasonable.

4.2.3 *The role of pattern distribution*

The distribution of black and a contrasting colour, then, is the main determinant of the similarity value. A few pattern distributions were studied, to

look at this in some more detail. Again, these were grids 5x5 squares (100x100 pixels) and the model was based on a simple version of the second tergite of *Vespula vulgaris*. The pattern distributions of the mimics were loosely based on the second tergites of *Syrphus ribesii*, *Temnostoma vespiforme*, *Episyrphus balteatus* and *Chrysotoxum arcuatum*. All grids were in yellow and black (Figure 4.3).

A range of similarity values were produced, as shown in Figure 4.3. None of the images were shifted to produce the maximal match by SHIFT. All 4 mimics had black parts towards the left and right of the image, with some yellow in the middle, and the lowest score was 53 %; hence even a general resemblance to a model feature is being acknowledged. Both shape and proportion of yellow were significant. For example, the '*S.ribesii* tergite' image had much less yellow (four squares) than the model (nineteen squares), and in '*C.arcuatum*' the directional pattern of the yellow was reversed from that of the model; both of these received the lowest scores. In '*E.balteatus*', the pattern was similar to '*S.ribesii*' except the area of yellow was expanded to eight squares; this resulted in a higher score. In '*T.vespiforme*', not only was the area expanded, but the shape of the yellow band was much more similar to that of the model; this produced the highest score of all. Hence the program does, at least with these test, seem to be sensitive to both the area of the yellow, and its shape relative to that of the model.

These grids also show another important point. '*S.ribesii*' and '*C.arcuatum*' had the same similarity score, though they do not resemble each other, because both had 10 matching grid squares and 15 mismatching grid

squares relative to the model. Several other patterns could also have produced this score. In other words, two images can have the same resemblance to the model, but different resemblances to each other. This is because the image analysis does not recognise and match particular features, but just looks at the magnitude of pattern differences. In practice, this should not present a problem, as any features which are mimicked, but in slightly different locations, should be brought together by the shifting process.

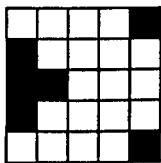
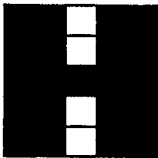
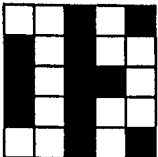
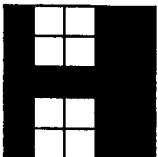
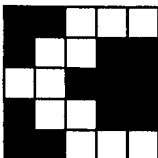
Model	Mimic	Similarity value	
		53	<i>'S.ribesii'</i>
		78	<i>'T.vespiforme'</i>
		66	<i>'E.balteatus'</i>
		53	<i>'C.arcuatum'</i>

Figure 4.3. 5x5 grids used to compare pattern distributions

4.3 Fine-tuning of the measurement of similarity

It cannot be stated whether the similarity values produced are ‘right’ or ‘wrong’, as the aim is to produce values unbiased by human subjective judgements. However, the program can still be checked to ensure that it is working to produce intuitively sensible rankings. The similarity values produced with SHIFT are shown in column 1 of Table 4.6. Good mimics, like *Temnostoma* species, *Xanthogramma* and *Chrysotoxum*, score relatively highly and very poor mimics like *Volucella pellucens* and *Leucozona lucorum* score poorly, as expected. However, two main anomalies occurred when using SHIFT which appeared counter-intuitive.

4.3.1 Allowing for different body sizes

Firstly, some small species produced very high similarity values, because all images were standardised for size in the analysis. For example, *Parasyrphus lineola* was ranked as second highest in similarity, despite the area of its abdomen being only around 30% that of *V. vulgaris*. Similarly, *Melangyna lasiophthalma* and *Meligramma guttata* were ranked 6th and 8th respectively, though their abdomen areas are only 37% and 22% that of *V. vulgaris*.

The relationship between size and distance in terms of pattern perception is likely to be complex. Humans tend to base their discrimination between wasps and hoverflies on size cues (Grewcock 1992). However, pigeons shown novel images of hoverflies with no control for size still mostly rated them the same as

when they were given standardised images (Dittrich *et al* 1993). However, the mimics used were all at the larger range of size of hoverflies; it does seem incongruous to have these small species ranked so highly. Therefore the similarity values were converted for size in the following manner.

Using the same photographs that were scanned to calculate the similarity values, the length and width of the abdomen were measured and multiplied to give an approximate abdomen image area. This was converted to a proportion of the abdomen area of a *Vespula vulgaris* worker, between 0 and 1. Where a mimic's abdomen was larger than that of the model, the proportion was converted to less than 1 accordingly; for example, *Didea alneti* had a proportion of 1.02, which was converted to 0.98. The areas ranged from 0.16 (*Sphegina flavimana*) to 0.98 (*D.alneti*) of *V.vulgaris*. Similarity values were adjusted to range from 0-100% (previous range: 52.31%-74.77%). These were then multiplied by the relative body size to give size-adjusted similarity values (see column 2 of Table 4.6).

For example, *P.lineola* was reduced in rank to 29th, *M.lasiophthalma* to 22nd, and *M.guttata* to 38th, of the 59 species measured, and larger species rose in rank accordingly (see Table 4.6). This is not to say that size has taken over as the primary determinant of the similarity value; large poor mimic species such as *Volucella pellucens* and *Leucozona lucorum* still ranked lower.

4.3.2 Allowing for all-black tergites

The other main anomaly of the similarity values produced by SHIFT was that some entirely black or metallic-coloured species such as *Chalcosyrphus nitidus* and *Ferdinandea cuprea* had relatively high similarity scores. When size-adjusted, these two species were ranked as 25th and 19th respectively of 59 species measures, despite a complete lack of any colour signals corresponding with those on a wasp. This is clearly because the model pattern has a large proportion of black pixels, which match with pixels on these black species.

To overcome this, a new system of matching images was devised such that large areas of black, with no colour patterns upon them, would not produce large match totals, but instead give a very low score. To do this, each abdomen image was split into four sections, corresponding to tergites 1, 2, 3 and 4+ (see Figure 4.4). Tergites 2, 3 and 4+ were then each compared separately, relative to the model's equivalent tergites. BITMAP remained the same, converting the bitmaps to descriptive text files, but a new program, SEGMENT (written by F. Gilbert) compared the tergites separately, replacing SHIFT.

SEGMENT tests each tergite by overlaying the midlines of the mimic and model tergite, and shifting them in the y-axis only to obtain the maximal match. Mismatches and matches are calculated for each of the three tergites separately, and a similarity value is calculated for each. To obtain an overall similarity value for the image, the matches and mismatches for all three tergites are summed and total matches/ matches + mismatches calculated as before. Hence the overall similarity value is not just the sum of the similarity values for each tergite.

By splitting up the pattern like this, any tergites which are totally black can be identified, and the match score can be brought down accordingly. Where a mimic tergite consists only of black pixels, the number of matches is counted as zero, though the mismatches are still counted. This brings down the overall matches considerably even if only one or two tergites are black; if all three are black, the total match number is zero and hence the overall similarity value is zero. For the wasp model image, 'tergite2' for the purposes of SEGMENT in fact also included part of the first tergite, because it contains some of the yellow pattern. In hoverflies, the first tergite rarely has any pattern on it.

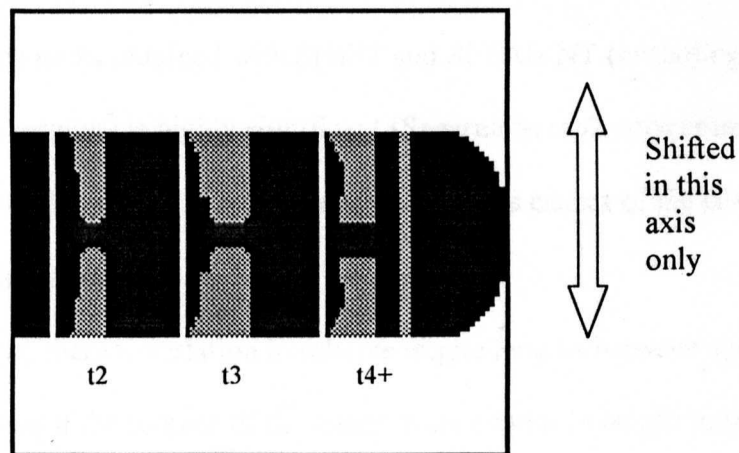


Figure 4.4. Abdomen image split into tergites.

The aim of using SEGMENT was to emphasise the influence of large black areas on lowering the similarity to wasps, whilst generally retaining the rankings of other species. The altered similarity scores can be seen in Table 4.6, and their rankings in Table 4.7. Black/metallic species *Chalcosyrphus nitidus*, *Chrysogaster solstitialis*, *Ferdinandea cuprea*, *Heringia heringii* and

Neocnemodon vitripennis have clearly been reduced to similarity values of zero. This objective was therefore successful.

However, the change of method to using separate tergites also influences the similarity values of other species. A check was needed to ensure that this new system did not undermine the validity of the image analysis.

Looking at the changes in similarity ranking in Table 4.7, columns 1 and 2 can be compared to show that the black species have been greatly reduced in similarity value. Columns 3 and 4 show how similarity ranks have changed for those species which have not been affected by possessing a black tergite. 71% of images have changed by 5 ranks or less, and 90% by 10 ranks or less. The correlation between ranks obtained with SHIFT and SEGMENT (excluding images with black tergites) is highly significant (Spearman's rank correlation (one-tailed) $r_s=0.90$, $p<0.000$, $n=48$). Nevertheless, the possible causes of the changes in rank are investigated briefly.

In particular, there is variation in relative tergite lengths between species, and it is possible that if the tergites of the mimic were similar in length to those of the model, this could be having an undue influence on the similarity score, not due to pattern distribution. Also, the lack of horizontal shift in the matching process could mean that corresponding features in slightly different locations are no longer being matched up.

However, the patterns on hoverfly abdomens can generally be split quite clearly into features on different tergites. There is generally one lunule or stripe per tergite, each potentially matching with those on a wasp's body, so it was

relatively straightforward to split up the images in an appropriate way.

Nevertheless, the lengths of the tergites varied; this gives variation in the potential amount of matching, since the degree of overlap of the images determines how much matching there can be.

A series of 3 images were compared to a model image using SEGMENT, whereby the mimics resembled the model except for the length of tergite 2. The

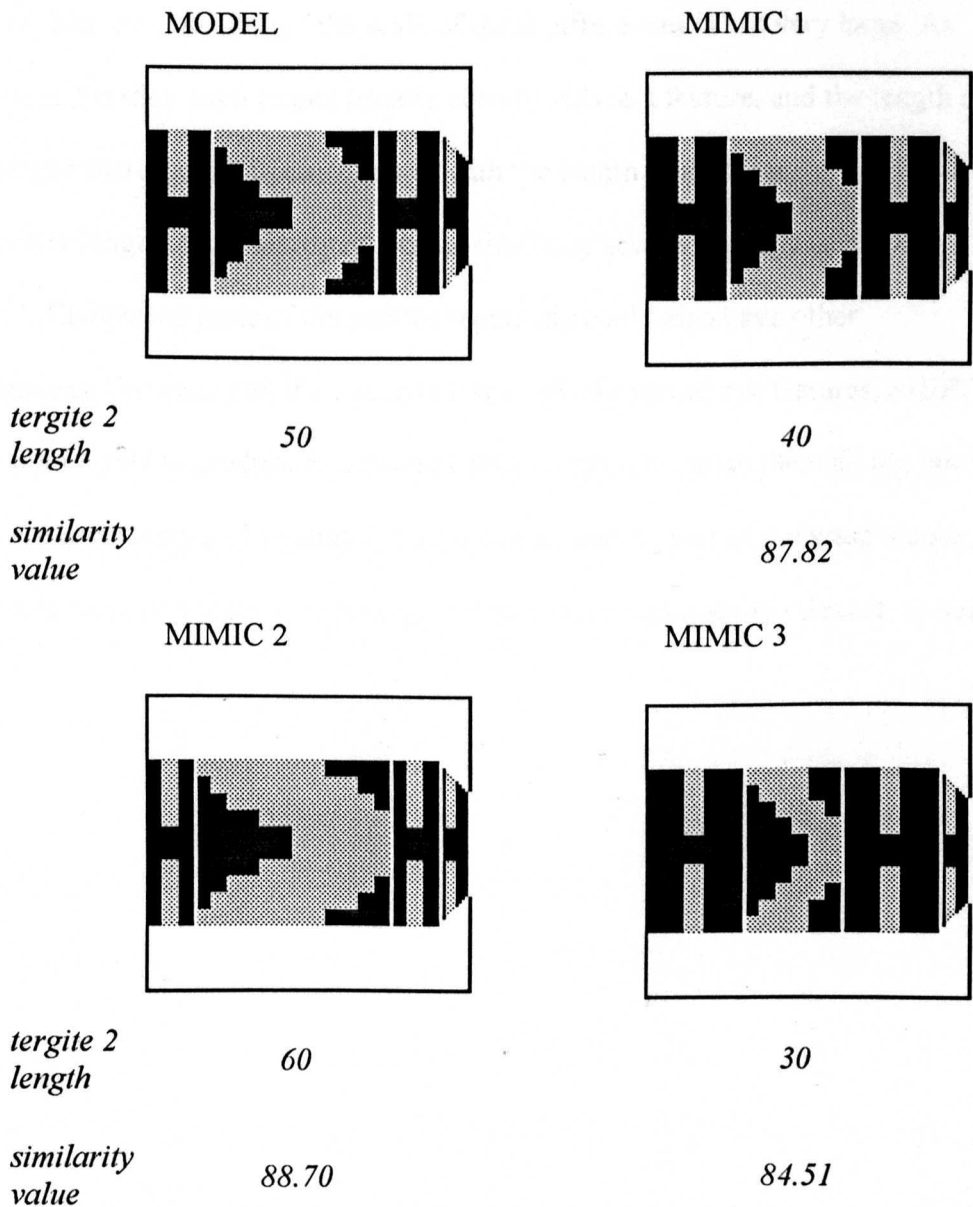


Figure 4.5. Images used to compare tergite lengths.

pattern on tergite 2 was stretched or compressed accordingly (see Figure 4.5). With each pairing, the images are lined up on their midlines, and in this case not shifted vertically, since they are already in the position of maximum matching. There was an overlap of 40 pixels length between Model and Mimic 1, 50 with Mimic 2, and 30 with Mimic 3. The image pairing with the widest overlap has produced the highest similarity value, and the other values rank the same as the size of their overlap, though the scale of these differences is not very large. As mentioned earlier, each tergite usually corresponds to a feature, and the length of the tergite therefore often corresponds with the length of that feature. For features of similar lengths to be allocated similar similarity scores seems reasonable.

Comparing parts of the pattern separately could also have other advantages. For example, if a hoverfly has relatively spread out features, SHIFT may not be able to produce a horizontal shift which will match them all up, but if they are each compared separately to the corresponding part of the wasp's body, it becomes more of a feature-matching, and thus more biologically relevant, system.

Table 4.6. Similarity scores obtained between 68 hoverfly images and *V.vulgaris* (contd over page)

Species	1 Similarity value using SHIFT	2 Size-adjusted similarity value using SHIFT	3 Similarity value using SEGMENT	4 Size adjusted similarity value using SEGMENT
<i>Allograpta micura</i>	N/A	N/A	48.11	9.52
<i>Anasimyia interpunctata</i>	73.12	29.18	41.33	27.49
<i>Anasimyia interpunctata</i>	74.22	23.29	38.52	19.52
<i>Aemosyrphus polygrammus</i>	N/A	N/A	33.34	18.60
<i>Baccha elongata</i>	69.73	12.01	2.40	0.77
<i>Blera confusa</i>	68.56	36.54	36.49	37.82
<i>Blera humeralis</i>	63.16	25.94	38.70	40.11
<i>Blera scitula</i>	65.92	31.35	38.03	39.42
<i>Brachyopa dorsata</i>	68.06	12.44	37.29	13.53
<i>Ceriana conopsoides</i>	76.14	73.84	31.54	46.95
<i>Chalcosyrphus nitidus</i>	75.42	32.57	0.00	0.00
<i>Chalcosyrphus piger</i>	74.54	31.44	24.57	16.59
<i>Chrysogaster solstitialis</i>	65.22	12.83	0.00	0.00
<i>Chrysotoxum arcuatum</i>	70.92	59.32	46.64	69.66
<i>Chrysotoxum bicinctum</i>	73.29	38.37	34.67	30.10
<i>Chrysotoxum sapporensis</i>	72.41	63.54	50.93	76.07
<i>Dasysyrphus bilineatus</i>	60.92	14.31	37.99	26.17
<i>Dasysyrphus venustus</i>	73.85	31.18	51.22	35.28
<i>Didea alneti</i>	60.52	35.37	30.94	54.65
<i>Doros aequalis</i>	N/A	N/A	31.13	27.45
<i>Epistrophe diaphana</i>	76.41	38.09	55.00	43.77
<i>Epistrophe elegans</i>	58.33	13.59	15.07	12.90
<i>Epistrophe melanostoma</i>	72.86	34.53	51.80	41.22
<i>Epistrophella euchroma</i>	77.85	42.04	55.57	44.22
<i>Episyrphus balteatus</i>	72.44	36.42	41.32	35.33
<i>Eumerus strigatus</i>	69.73	13.05	37.78	13.16
<i>Eupeodes corollae</i>	70.28	26.94	45.46	31.81
<i>Eupeodes nitens</i>	73.72	36.94	49.84	40.90
<i>Ferdinandea cuprea</i>	70.04	35.78	0.00	0.00
<i>Helophilus pendulus</i>	69.46	47.87	44.62	57.81
<i>Heringia heringii</i>	77.48	11.48	0.00	0.00
<i>Ischyrosyrphus glaucius</i>	64.14	33.20	31.32	38.69
<i>Ischyrosyrphus lateralis</i>	63.34	18.37	27.02	19.58
<i>Lejops vittata</i>	N/A	N/A	42.49	39.76
<i>Leucozona lucorum</i>	54.40	10.17	22.29	26.87
<i>Megasyrphus erraticus</i>	66.95	55.81	44.23	76.66
<i>Melangyna lasiophthalma</i>	77.13	34.75	52.26	35.05
<i>Melanostoma scalare</i>	75.06	17.25	46.06	16.71

Table 4.6 (continued)

Species	1 Similarity value using SHIFT	2 Size-adjusted similarity value using SHIFT	3 Similarity value using SEGMENT	4 Size adjusted similarity value using SEGMENT
<i>Meligramma guttata</i>	76.64	19.36	43.89	16.81
<i>Meliscaeva cinctella</i>	74.82	22.75	39.54	19.10
<i>Myathropa florea</i>	61.24	35.46	30.07	49.87
<i>Neocnemodon vitripennis</i>	75.44	14.91	0.00	0.00
<i>Paragus bicolor</i>	70.42	13.51	34.06	11.87
<i>Parasyrphus lineola</i>	78.33	30.33	55.52	31.33
<i>Parhelophilus frutetorum</i>	N/A	N/A	36.46	34.12
<i>Pipiza quadrimaculata</i>	68.01	17.94	38.95	20.42
<i>Pipiza signata</i>	71.99	16.52	39.11	15.48
<i>Platycheirus clypeatus</i>	75.36	20.37	39.53	16.73
<i>Platycheirus discimanus</i>	N/A	N/A	22.09	5.96
<i>Rhingia campestris</i>	61.87	15.85	33.78	23.71
<i>Scaeva pyrastris</i>	69.30	56.24	43.67	67.02
<i>Sericomyia silentis</i>	54.95	9.52	27.18	27.30
<i>Sphaerophoria philanthus</i>	72.57	17.56	19.53	8.01
<i>Sphegina flavimana</i>	73.76	13.57	19.86	5.98
<i>Spilomyia saltuum</i>	78.06	60.70	45.99	52.44
<i>Syritta pipiens</i>	73.39	13.64	21.26	6.53
<i>Syrphus ribesii</i>	65.76	38.80	44.21	57.28
<i>Temnostoma apiforme</i>	73.20	74.48	42.43	71.77
<i>Temnostoma bombylans</i>	75.56	72.20	53.68	79.91
<i>Temnostoma vespiforme</i>	78.56	94.58	47.00	82.04
<i>Triglyphus primus</i>	73.44	6.28	35.48	5.01
<i>Tropidia quadrata</i>	N/A	N/A	29.80	19.84
<i>Volucella pellucens</i>	52.31	3.85	15.35	13.18
<i>Xanthandrus comtus</i>	N/A	N/A	30.95	33.42
<i>Xanthandrus comtus</i>	N/A	N/A	47.80	51.61
<i>Xanthogramma pedissequum</i>	77.04	59.77	42.64	49.68
<i>Xylota coeruleiventris</i>	70.10	23.46	31.48	19.35
<i>Xylota coeruleiventris</i>	72.93	24.81	32.76	18.68

Table 4.7. Ranks in similarity of hoverfly images to an image of *V. vulgaris*. The images are listed in order of their ranking using size-adjusted SEGMENT scores (column 1).

These are the scores used in subsequent chapters. (Table continued on next page)

Species	Rank Similarities			
	1 Segment (size- adjusted)	2 Shift (size- adjusted)	3 Segment (size- adjusted) excl. those with black tergites	4 Shift (size- adjusted) excl. those with black tergites
<i>Temnostoma vespiforme</i>	1	1	1	1
<i>Temnostoma bombylans</i>	2	4	2	4
<i>Megasyrphus erraticus</i>	3	10	3	10
<i>Chrysotoxum sapporensis</i>	4	5	4	5
<i>Temnostoma apiforme</i>	5	2	5	2
<i>Chrysotoxum arcuatum</i>	6	8	6	8
<i>Scaeva pyrastris</i>	7	9	7	9
<i>Helophilus pendulus</i>	8	11	8	11
<i>Syrphus ribesii</i>	9	13	9	13
<i>Didea alneti</i>	10	21	10	19
<i>Spilomyia saltuum</i>	11	6	11	6
<i>Xanthandrus comtus</i>	11a			
<i>Myathropa florea</i>	12	20	12	18
<i>Xanthogramma pedissequum</i>	13	7	13	7
<i>Ceriana conopsoides</i>	14	3	14	3
<i>Epistrophella euchroma</i>	15	12	15	12
<i>Epistrophe diaphana</i>	16	15	16	14
<i>Epistrophe melanostoma</i>	17	23	17	21
<i>Eupeodes nitens</i>	18	16	18	15
<i>Blera humeralis</i>	19	32	19	29
<i>Blera scitula</i>	20	27	20	24
<i>Lejops vittata</i>	20a			
<i>Ischyrosyrphus glaucius</i>	21	24	21	22
<i>Blera confusa</i>	22	17	22	16
<i>Episyrphus balteatus</i>	23	18	23	17
<i>Dasysyrphus venustus</i>	24	28	24	25
<i>Melangyna lasiophthalma</i>	25	22	25	20
<i>Parhelophilus frutetorum</i>	25a			
<i>Xanthandrus comtus</i>	25a			
<i>Eupeodes corollae</i>	26	31	26	28
<i>Parasyrphus lineola</i>	27	29	27	26
<i>Chrysotoxum bicinctum</i>	28	14		
<i>Anasimyia interpunctata</i>	29	30	28	27
<i>Doros aequalis</i>	29a			

Table 4.7 (continued)

Species	Rank Similarities			
	1 Segment (size- adjusted)	2 Shift (size- adjusted)	3 Segment (size- adjusted) excl. those with black tergites	4 Shift (size- adjusted) excl. those with black tergites
<i>Sericomyia silentis</i>	30	57	29	48
<i>Leucozona lucorum</i>	31	56		
<i>Dasysyrphus bilineatus</i>	32	46	30	42
<i>Rhingia campestris</i>	33	44	31	41
<i>Pipiza quadrimaculata</i>	34	40	32	37
<i>Tropidia quadrata</i>	34a			
<i>Ischyrosyrphus lateralis</i>	35	39	33	36
<i>Anasimyia interpunctata</i>	36	35	34	32
<i>Xylota coeruleiventris</i>	37	34	35	31
<i>Meliscaeva cinctella</i>	38	36	36	33
<i>Xylota coeruleiventris</i>	39	33	37	30
<i>Aemosyrphus polygrammus</i>	39a			
<i>Meligramma guttata</i>	40	38	38	35
<i>Platycheirus clypeatus</i>	41	37	39	34
<i>Melanostoma scalare</i>	42	42	40	39
<i>Chalcosyrphus piger</i>	43	26	41	23
<i>Pipiza signata</i>	44	43	42	40
<i>Brachyopa dorsata</i>	45	53	43	47
<i>Volucella pellucens</i>	46	59		
<i>Eumerus strigatus</i>	47	51	44	46
<i>Epistrophe elegans</i>	48	48		
<i>Paragus bicolor</i>	49	50	45	45
<i>Allograpta micura</i>	49a			
<i>Sphaerophoria philanthus</i>	50	41	46	38
<i>Syrirta pipiens</i>	51	47	47	43
<i>Sphegina flavimana</i>	52	49	48	44
<i>Platycheirus discimanus</i>	52a			
<i>Triglyphus primus</i>	53	58		
<i>Baccha elongata</i>	54	54		
<i>Chalcosyrphus nitidus</i>	=55	25		
<i>Chrysogaster soltialis</i>	=55	52		
<i>Ferdinandea cuprea</i>	=55	19		
<i>Heringia heringii</i>	=55	55		
<i>Neocnemodon vitripennis</i>	=55	45		

4.4 Images used in the image analysis

The model used for comparison with hoverfly images was in all cases a single image of *Vespula vulgaris*, the common wasp. Though this certainly provided a good idea of the similarity between wasps and their putative mimics, there is variation in the abdominal pattern of *V. vulgaris*, which could potentially lead to significant differences in similarity measurements had another image been used. Other species of wasp could also be acting as models.

The similarity values obtained were ultimately used not only for the species concerned, but also other members of its ‘colour pattern group’. The assumption that the variation within such groups was relatively low also needed to be examined.

4.4.1 Use of one model image

A single *V. vulgaris* image was scanned from a field guide (Chinery 1993). This was a typical example of the most common caste, the workers. Wasp abdominal patterns are known to vary over the season and between colonies (e.g. Nevison 1989; Chinery 1993). Ideally, a mean value to several *V. vulgaris* images would have been calculated for each mimic, but for reasons of time and practical constraints, this was not possible. Therefore similarity values against another *V. vulgaris* image were measured, as an example of the difference if another image was chosen, and to get an idea of how accurate similarity values should be

considered. Whether the actual similarity scores were the same was less important than whether species were ranked in the same order. There could for example be differences in model pattern which shift all the similarity values in the same direction. If the system is robust to variation in wasp images, a strong correlation between similarity values, and little change in their ranking, would be expected.

The *V.vulgaris* image was scanned from another text (Spradbery 1973), and similarity values were calculated as before. To produce the greatest possible difference from the first image, an image of a queen was chosen. For practical reasons, only 44 of the 68 hoverfly images used previously were compared

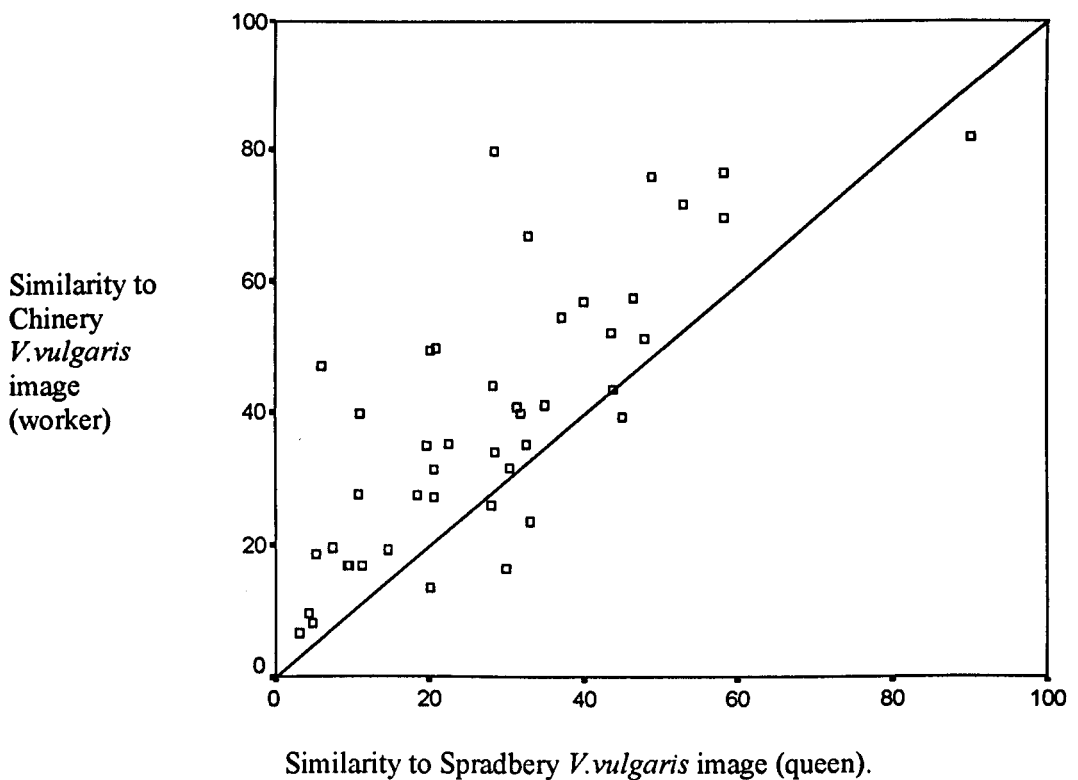


Figure 4.7. Similarity values of 41 hoverfly images, compared with 2 different images of *V.vulgaris*. Line shown is line of equal similarity.

against this second *V. vulgaris* image, again using SEGMENT and adjusting for size.

There was a highly significant correlation between the similarity values produced by the two images (Figure 4.7; Spearman's rank correlation, $r_s=0.77$, $p<0.000$, $n=44$).

On average, the difference in similarity rank between the two images for a mimic was 6 ranks (s.e. ± 0.94), though 26/44 (59%) changed by 5 or less. 9 species changed in rank by more than 10 places. In most cases, hoverfly images were more similar to the worker than the queen, which is biologically interesting in itself, since workers are much more common than queens in nature. The disparity between the images seems to be mainly because the Spradbery image was proportionally much wider than the original image, because it was a queen. Despite this, the general order was still the same, even between images of a worker and a queen, and probably the difference between worker images would be even less. This demonstrates the robustness of the similarity-measuring system.

4.4.2 Other model species

For the purposes of producing similarity values in this thesis, the model *Vespula vulgaris* was used. This is because it is the commonest social wasp species in the UK, and therefore seems the most obvious model candidate for hoverflies which mimic social wasps. However other social wasp species do of course exist. In the UK, these are mainly *Vespula* and *Dolichovespula* species, though in other locations genera such as *Polistes* can be abundant. Malaise trap

data from Leicester (J. Owen, unpublished data), show that in the UK *V. germanica* is the next most common social wasp after *V. vulgaris* (Figure 4.8).

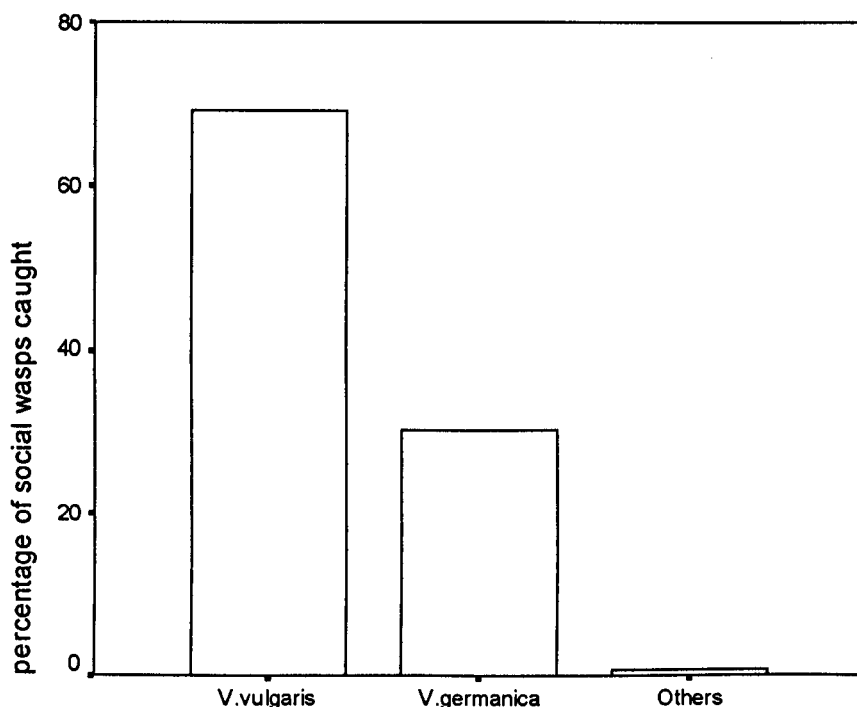


Figure 4.8. Percentages of *Vespula* and *Dolichovespula* species caught in Leicester malaise trap in the 21 years 1972-1992. N=6164 individuals. 'Others' comprise *D.norvegica*, *D.sylvestris*, *V.austriaca* and *V.rufa*.

Other *Vespula* and *Dolichovespula* species form a negligible proportion of the total number of wasps trapped. Of course many other insects also have elements of yellow-and-black coloration, but wasps combine the features of noxiousness, flight and abundance, and thus have been considered the main potential Batesian models for hoverflies.

The abundance data suggest that if hoverflies are Batesian mimics, convergence on the pattern of *V.vulgaris* is the primary selective force on their

colour patterns. Nevertheless, some influence of other model species, notably *V. germanica*, is also possible.

As similarity values are used as an indication of quality of mimicry later in this thesis, it must be ensured that the rankings produced would not be dissimilar using *V. germanica*. The expectation is that they will not be significantly different, as *V. vulgaris* and *V. germanica* are similar in many respects in their abdominal patterns. In fact, *Vespula* species are not readily distinguishable by their abdominal patterns, and thoracic and facial markings are usually used to discriminate between them.

An analysis of similarity values was carried out using SEGMENT and adjusting for size as before. Two *V. germanica* images from field guides (Chinery

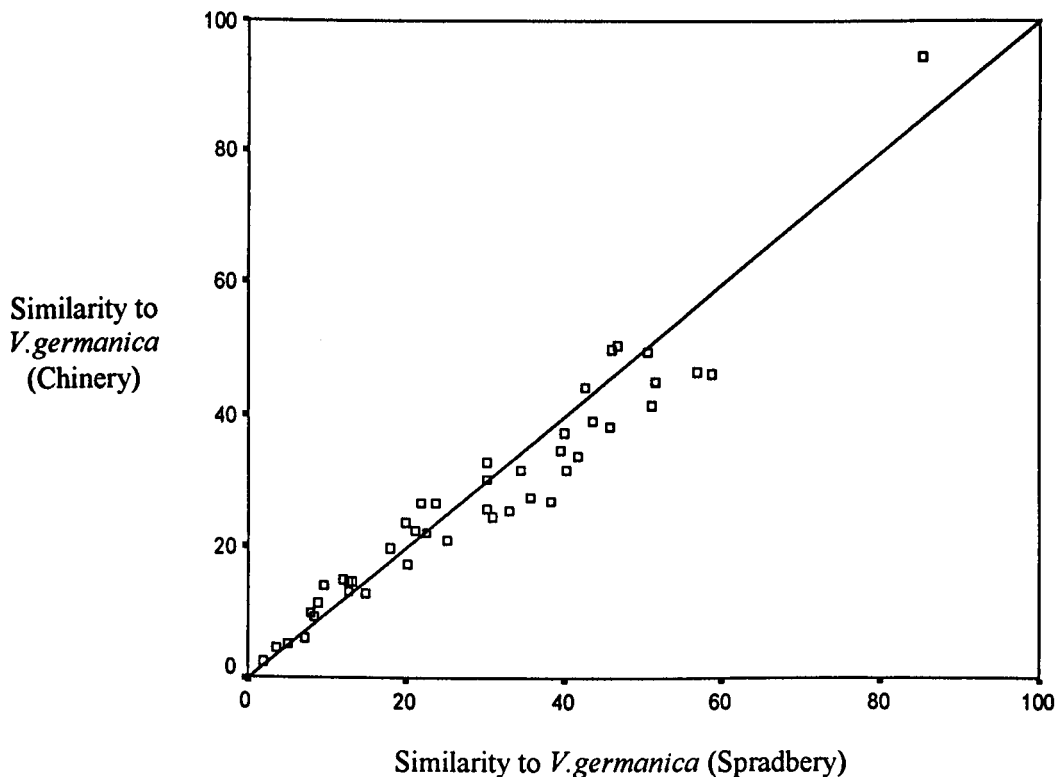


Figure 4.9 Similarity values of 44 hoverfly images compared with two different images of *V. germanica*. Line shown is line of equal similarity.

1993; Spradbery 1973) were compared with the same 41 mimic images as for *V.vulgaris*.

The similarity values produced by the two *V.germanica* images were extremely similar, as shown by the highly significant Spearman's rank correlation (Figure 4.9; $r_s=0.97$, $p<0.000$, $n=44$). The average difference between ranks of mimic images with the two different *V.germanica* images was only 2.5 ranks (± 0.28), equivalent to an average difference in similarity value of $4.08 \pm 0.40\%$.

To compare *V.vulgaris* and *V.germanica*, mean similarity values and mean ranks were calculated for each of the two wasp species. The mean similarity values were very similar for the two model species (Figure 4.10a; $r_s=0.90$, $p<0.000$, $n=44$), and the order in which species were ranked was even more highly correlated (Figure 4.10b; $r_s=0.92$, $p<0.000$, $n=44$). On average, an image's similarity value differed by 3.5 ranks (± 0.45) between the two wasp species, or by 6.61 % (± 0.98).

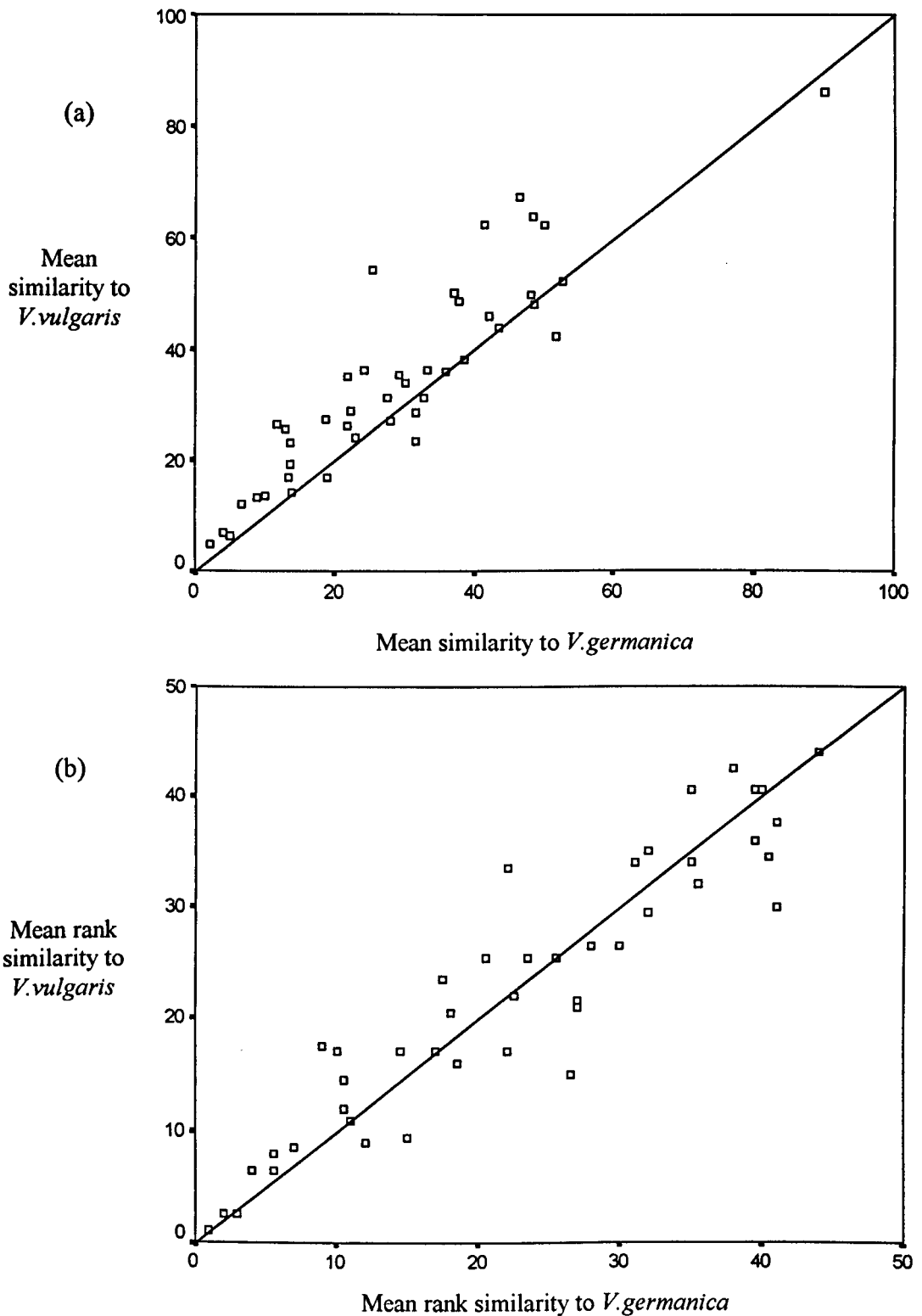


Figure 4.10(a). Mean similarity values to 2 *V.vulgaris* images, and mean similarity values to two *V.germanica* images, for 44 hoverfly images. (b). The mean rank similarity to two *V.vulgaris* images, and the mean rank similarity to 2 *V.germanica* images, for 44 hoverfly images.

4.4.3 Colour pattern groups

Similarity values were not calculated for every species. Species were allocated to colour pattern groups, and just one species' similarity to a wasp was measured for each group. A group usually comprised a genus or part of a genus. For example, all species in the genus *Helophilus* were given the similarity value of the species *H.pendulus*.

Species were not assumed to resemble each other because they were congeneric; they were only designated to the same colour pattern group if they were known to resemble the measured species. Where the appearance of a species was unknown and no reference image could be found, the species was not allocated a similarity value and was excluded from the analysis. These formed a small proportion of the total number of species used in chapters 5 and 7 (7.2%). For the disturbed habitat work, hoverflies were not identified in the field to species level anyway, but rather to the colour pattern groups directly.

Nevertheless, three species from each of two sample colour pattern groups were tested, to compare variation within the groups to the similarity values of other groups. *Sphaerophoria* and *Helophilus* are two common genera used extensively in the analyses in other chapters, and are also genera where there is some variation within the genus which could potentially invalidate allocating just one similarity value to all species. The results are shown in Table 4.8.

The similarity scores obtained did not vary greatly from those of the reference image. Mean similarity scores of the two other species in the genus did not differ significantly from that of the reference image. The mean similarity

value for all three *Helophilus* species was 53.40%. *H.pendulus* is ranked 8th in similarity to *V.vulgaris* (see Table 4.7); if this mean were used, it would be ranked 10th. The mean similarity value for the three *Sphaerophoria* species was 6.66%, which would stay at the same rank at 50th.

Species	Size-adjusted similarity scores
Reference image: <i>Helophilus pendulus</i>	57.81
<i>Helophilus affinus</i>	49.71
<i>Helophilus trivittatus</i>	52.69
Reference image: <i>Sphaerophoria philanthus</i>	8.01
<i>Sphaerophoria menthastri</i>	4.05
<i>Sphaerophoria scripta</i>	7.91

Table 4.8. Similarity values to *V.vulgaris* of different members of 2 colour pattern groups.

From this small sample, it would seem that the assumption of consistency across colour groups is valid, since variation within these groups is small compared to that between groups.

4.4.4 Discussion of images

It is inevitable that there will be some variation between images, certainly within colour pattern groups and between model species, and even within model and mimic species. Some of this is due to natural variation, and some due to the parts of the method where a degree of subjective input is unavoidable. At each of

these stages, care was taken to minimise the variation. For example, mimic images were used from the same source (Torp 1994) to minimise differences from image definition, variation between authors' drawing style etc. These images were all photographic, and were supplemented only where necessary by a standard set of photographs taken from a museum collection. During scanning and preparing the images, every care was taken to use the image manipulation programs in the same way for all images.

However, a part of the variation between images is real, from natural inter- and intra-species variation. One wasp image was compared with all hoverfly images to produce the similarity values, and it was important to check that another image would not have produced entirely different similarity rankings. In fact, the ranking of mimic similarity values stayed fairly consistent using two *V.vulgaris* and two *V.germanica* model images, in most cases changing just a few ranks or similarity points in either direction when a different model image was used. It seems, therefore, at least from these four images, that within-*Vespula* variation does not make much difference when comparisons are made to hoverfly images. Not surprisingly, the biggest difference was between queen and worker *V.vulgaris* images used as models.

The variation within the two colour pattern groups examined was also not very extensive, compared with variation between groups. The few percentage points difference between species in a group were small compared to the difference to the groups nearest to them in similarity, only leading to a change in one or two rankings at most. *Helophilus* and *Sphaerophoria* species were

deliberately chosen to be dissimilar and distinguishable in appearance; within other colour pattern groups (e.g. the genus *Syrphus*) this variation would appear to be even lower. Since there was so little variation within these groups, it seems unlikely that variation at an even lower level, within a species, could be a problem. Though such variation certainly exists, it should be very low compared to the range of similarity values seen here.

4.5 Conclusions

The image analysis technique used to measure model-mimic similarity has been successfully adapted for use in a wide range of model: mimic pairings. The underlying basis for the comparison of colour proportion and distributions is sound, with pattern distribution playing a larger role than colour, except where there is an extreme colour shift. Generally, obviously ‘good’ mimics were ranked highly, and ‘bad’ mimics were given low rankings. Whereas under the unmodified technique very small species and black species were obtaining high scores relative to good mimics, the modified technique makes no such errors, with minimal effect on other species.

Though variation among models exists, different images of *Vespula* have a relatively small effect on the rank similarities of different hoverfly species, including using images of the other common UK wasp species. The use of a single similarity value for different species in a colour pattern group was also validated.

Intraspecific variation in the size, shape and colour patterns of both models and mimics mean that none of the similarity values or rankings should be considered as absolutely or relatively very accurate. This needs to be borne in mind when using the similarity scores later on. However, the technique certainly gives a good idea of the main differences in similarity among hoverfly species; small differences in similarity, or close rankings, are less reliable.

The other main considerations when using these similarity values is that they cannot be considered definitive measures of mimicry quality. While the use of real receivers (pigeons) has confirmed that similarity rankings do concur with the mistakes real receivers make in judging colour patterns, this has not been confirmed for all the species considered here. In addition, disparities between measured and perceived similarity can occur; two hoverfly species (*Episyrphus balteatus* and *Syrphus ribesii*) were not ranked the same by pigeons as they were by the image analysis. It also needs to be borne in mind that the relationship between measured similarity and perceived degree of mimicry is not linear; a small increase in measured similarity can lead to a large increase in perceived similarity (Dittrich *et al* 1993).

Nevertheless, as I shall demonstrate in this thesis, the expansion of the similarity-measuring tool is a very useful one in the further study of mimicry in hoverflies.

Chapter Five

Testing the disturbed habitat hypothesis¹

5.1 Introduction

Mimicry has been a source of fascination for biologists ever since the beginning of modern evolutionary thought. Bates published the first adaptive explanations for mimetic relationships between species in 1862. This original theory of "Batesian mimicry" described how the patterns of unpalatable species (models) can be imitated by unrelated, palatable species, affording the mimics a degree of protection from visual predators. Bates' theory originated from his observations in Brazil of the similarities between the red-and-yellow-patterned ithomiine heliconiids and some species of pierid butterfly (Dismorphiinae), which had almost identical coloration even though Dismorphiinae are generally white. In this case, a palatable mimic is thought to deceive predators by imitating an unpalatable model. Batesian mimicry is often contrasted with Müllerian mimicry, where unpalatable species evolve to resemble one another. Recent modelling suggests that this distinction may (Turner & Speed 1996) or may not (MacDougall & Dawkins 1998) be artificial, with the two categories either distinct, or part of a continuum, depending on the assumptions made about predator behaviour.

A frequently cited example of Batesian mimicry involves the black-and-yellow patterns of social wasps (Hymenoptera: Vespidae), imitated by the unrelated hoverflies (Diptera: Syrphidae). However, this complex throws up a

¹ A modified version of this chapter has been published as: Azmeh, S., Owen, J., Sørensen, K., Grewcock, D. and Gilbert, F. (1998) Mimicry profiles are affected by human-induced habitat changes. *Proceedings of the Royal Society of London B* 265:2285-2290.

number of discrepancies with the predictions of Batesian mimicry. Since Bates' time, theories about mimicry (e.g. Fisher 1930; Sheppard 1959, 1975; Turner 1984a; Malcolm 1990) contain some fundamental universally accepted predictions. Firstly, a close resemblance to the model evolves due to strong selection pressures (Fisher 1930; Sheppard 1975; Huheey 1984). However, in hoverflies, close morphological and even behavioural resemblance to wasps (e.g. Waldbauer 1970) occurs in some species (e.g. *Temnostoma vespiforme*), but is unusual. Most common European hoverfly species have a much less faithful resemblance to their wasp models. Here, these are called "poor mimics", assuming them to be mimetic since birds make similar mistakes to humans in distinguishing them from wasps (see Dittrich *et al* 1993). A variety of hypotheses address this problem, including a non-mimetic aposematic function to hoverfly colour patterns, advertising either flight agility (Srygley 1994; Pinheiro 1996) or distastefulness (Malcolm 1981, 1992), or predator perceptions of imperfect mimicry differing from human ones (Dittrich *et al* 1993; Howse & Allen 1994).

Furthermore, mathematical models of mimicry suggest that there is a limit to the number of mimics compared with models: there may be more mimics than models in some circumstances, but even under extreme circumstances the ratio still has limits of 10 mimics per model (Brower 1960; Estabrook & Jespersen 1974; Sheppard 1975; Luedemann *et al* 1981; Turner 1984a). However, all these studies only consider perfect mimicry. In the case of hoverflies, seemingly poor mimics often outnumber their supposed models (Gilbert 1986; Owen & Gilbert 1989; Owen 1991) by much larger factors than allowable by any theoretical model. One

possible explanation for this is a shift in the natural abundance of mimics and models due to the artificial effects of habitat disturbance by humans (Grewcock 1992; Dittrich *et al* 1993). Evidence for the influence of human disturbance on mimicry dynamics already exists in a different context (Linares, 1997).

In this study, the problem of the relative abundances is addressed, specifically, the idea that the very high relative abundance of poor mimics is a direct result of human-caused habitat disturbance. If mimics are common relative to models, their mimicry should gradually be lost, since predators learn if colour patterns do not indicate noxiousness (Turner 1984a). In hoverflies, poor wasp mimics are much more abundant than high-fidelity mimics, but their relative abundance may be artificially inflated by human-induced changes to habitats. If in the past mimics were not so common, it could be that the mimicry has simply not been lost yet.

The potential reasons for changes in hoverfly relative abundances are connected with larval food resources; while adults all feed on pollen and nectar, larval feeding habits vary remarkably widely (see Rotheray 1993). Most of the common poor-mimic species are aphidophagous as larvae (e.g. *Syrphus* spp.), while many good mimics feed as larvae in tree holes or rotting wood (e.g. *Temnostoma* spp). Most Palaearctic hoverflies are species of open glades in forested habitats (Speight *et al.* 1975; Speight 1983), and their colour patterns probably evolved in the ancient forests that covered the Palaearctic, now mostly changed to the urban/ agricultural landscapes common in Western Europe. These landscape changes may also have hugely boosted abundance of aphids, since

aphids are also insects of open or edge habitats (Dixon 1973). While this hypothesis does not directly address the issue of why poor mimicry exists, it does provide an explanation for the current relative abundance of poor mimics to good mimics, and also the abundance of poor mimics relative to models.

There is indirect evidence of a link between aphid numbers and large changes in hoverfly abundance; years of mass immigration of aphidophagous hoverflies into suburban gardens are associated with hot spells early in the year where there was an abundance of aphids (Owen 1991). Grewcock (1992) conducted a preliminary study on the disturbed habitat hypothesis, a novel use of similarity values. A comparison of census walks of two English woodlands and a relatively undisturbed site in southern France, showed some indication that more good mimics were present in the less disturbed site, though both sites were dominated by poor mimics. However, overall hoverfly abundance was very low in the undisturbed site due to the lack of vegetation at the time of year, and it was a habitat type not native to the UK. This study uses disturbed and undisturbed sites at a similar latitude, and the undisturbed sites are mixed coniferous/ deciduous ancient forests, which once covered the UK (though there are climatic differences).

The disturbed habitat hypothesis is tested here by comparing median mimetic similarities of hoverfly communities in sites varying in their degree of disturbance. Hoverfly abundances are measured in each site, and plotted against calculated similarity values to produce 'mimicry profiles'. The prediction is that in undisturbed sites the median similarity is greater than in disturbed habitats. As a further test, data on hoverfly abundance are collated from the literature, and

assessed in the same way, assigning each habitat a broad category of degree of disturbance. Less disturbed habitats supported proportionally more good mimics, suggesting a significant role of habitat disturbance in the relative abundance of mimetic hoverflies.

5.2 Materials and methods

Changes in relative abundance of good and poor mimics were tested to see whether poor mimics have increased in frequency in disturbed habitats. Mimicry profiles were contrasted for sites differing in degree of disturbance, by measuring the frequency distributions of hoverfly taxa and converting them into frequency distributions of mimetic similarity by measuring similarity of each taxon to wasps. New and literature data on relative abundances were analysed, by comparing the median mimetic similarities of hoverflies in different types of habitat.

5.2.1 Measuring similarity to wasps

Model-mimic similarity in abdominal pattern only was measured, since behavioural mimicry is difficult to quantify. The model used in all cases was *Vespula vulgaris*, the commonest wasp type at all three sites and therefore the presumed model. The method of Dittrich *et al* (1993) was used, since they established using photographs and bitmapped images that humans, pigeons and computers all largely agreed in their assessments of relative similarities. Although pigeons can see UV light, and normal photographs do not record the UV patterns (Cuthill & Bennett 1993), UV photography of the relevant hoverfly species show

that there are no extra UV components of the colour patterns (Gentle 1995; P.R.Green *et al* unpubl. data).

To measure the similarity of a hoverfly species to *Vespula vulgaris*, a photograph of a specimen was scanned into a PC. Pictures were obtained from specimens from the Natural History Museum (London) and from colour plates (Torp 1994). Images were standardised in size to a height of 100 pixels, and reduced to a standard set of 7 colours (RGB values in brackets): black (0,0,0), dark orange (230,255,255), orange (240,155,25), yellow (255,204,102), pale yellow (255,255,153), grey (204,204,204) and white (255,255,255). Each hoverfly abdomen was compared with a standard wasp image using the image analysis technique described in Dittrich *et al* (1993; see also Grewcock 1992). The technique generates a single-value percentage description of the similarity between two patterns, achieved by comparing images pixel by pixel, and measuring the Euclidean distance apart of each pair of corresponding pixels in red-green-blue colour space. The images are shifted slightly to obtain the maximal match between them. (For a fuller explanation of how the similarity value is calculated see Dittrich *et al* 1993) [see also chapter 4].

Some hoverflies are obvious mimics of honeybees (*Apis* spp.), bumblebees (*Bombus* spp.), or other hymenopteran models; such species (e.g. *Eristalis* spp., *Volucella bombylans*) were excluded from the analysis. Similarity values were not calculated for every species, but rather for exemplar species representing a colour-pattern group, usually comprising a genus or part of a genus. Species were only allocated to a colour-pattern group if it was known that their abdominal pattern

was identical or almost identical to the exemplar species. A small minority of species whose appearance was unknown, or whose image was unavailable, were not used in the analysis. To take size differences between hoverflies into account, the similarity values were scaled by each hoverfly's difference in size from the wasp model.

There is some variation within hoverfly species in abdominal colour pattern (e.g. Holloway *et al* 1997). In this study, just one individual from each species was compared to a wasp image, but differences between colour-pattern groups were much larger than within-species variation.

5.2.2 *New data on hoverfly abundance*

Hoverfly abundances were recorded in May and June from three areas: the Far East of Russia (pristine forest habitat), Bialowieza, Poland (undisturbed forest habitat) and Leicester, UK (highly disturbed habitat). The emergence of wasp mimics in May and June does not necessarily coincide with that of their models [see chapter 2]. The analysis was therefore restricted to relative abundance of different types of mimic, and did not include model numbers.

Data on a pristine site were gathered from forested areas surrounding Komsomolsk-na-Amure in the Far East of Russia. This is true virgin mixed forest, with huge areas of woodland occasionally punctuated by human disturbance, at approximately the same latitude as central Britain (50.32N, 136.59E). During six weeks in May and June 1997, numbers of hoverflies and wasps of all types were counted during 10-minute periods at flowers throughout the day (0700-1600).

Flowers were patchily distributed through the forest, mostly in well-lit forest gaps such as disused roads, paths or railway lines. Ideally, individual hoverflies would be marked (Holloway & McCaffery 1990) or removed from the population when measuring abundance, to avoid counting the same individuals twice. However, this would have confounded the counting method by disturbing the hoverflies feeding in the patch. To avoid counting the same individuals in different patches, many different areas were used within the sites, 1-100 km apart. Within these sub-sites, almost all patches were separated by a minimum of 50 m. Some data from June 1995 from the same sites are also included, collected during census walks (F.Gilbert, unpublished data).

The most undisturbed mixed-forest habitat in Western Europe is the Bialowieza forest (1250 km²) in Poland and Belarus, part of which (47 km²) is a UNESCO-protected World Heritage site. It was in glades and small open areas around this protected area that the data on hoverfly abundance were collected. The forest is also at about the same latitude as the British study site (52.41N, 23.50E). Data were collected, again by observing for ten-minute periods, during six weeks in May and June 1996, after a preliminary survey of the habitat for suitability (Sørensen & Gilbert 1997).

The third set of data came from a long-term Malaise trap study (partially published in Owen 1991 [and see chapter 2]) of a suburban garden in Leicester, UK (52.38N, 1.05W), well stocked with a variety of flowers suitable for adult hoverfly feeding (see Owen 1991). Most of the UK should naturally have a climax vegetation of mixed forest, now long since disappeared, so this was classified as a

highly disturbed site. A 23-year dataset (1972-1994) was used from catches of hoverflies in the trap, and abundances from May and June were extracted for comparison.

A mimicry profile was produced for each of the three sites by plotting the frequency distribution of similarity values. The prediction was that similarity values would be lower in more disturbed sites, so the means of ranked similarity values would fall into the order: Russia>Poland>Britain. Similarity values for individual flies were used as the data, not means of sites. A non-parametric ANOVA for an ordered expectation was used, since normality can not be assumed. This was available in the form of a “specific Anova” (as advocated in the integrated non-parametric system of Meddis 1984), otherwise known as Jonckheere’s test for ordered alternatives (see Siegel & Castellan 1988).

For practical reasons, only these three sites were considered; to avoid pseudo replication (Hurlbert 1984), these cannot be generalised to represent all disturbed or undisturbed habitats. Thus, this is testing a prediction of the disturbed habitat hypothesis for particular sites.

5.2.3 Literature data

Data were also obtained from publications containing European hoverfly abundance or frequency data (Table 5.1). Each study site was classified into one of four broad habitat categories: ancient undisturbed forest, ancient disturbed woodland, recent disturbed woodland, or highly disturbed habitat (urban parks and gardens). In total, 117 datasets were compared (collated by K.Sørensen),

representing very wide variation in method used for surveying hoverflies (time of year, scale of study, etc.). It could not be verified that *Vespula vulgaris* was the dominant model in all cases: however, good mimics of other wasps (e.g. *Polistes* spp.) rate highly on the similarity scale, and the aim was to test only broad differences between habitat categories in terms of mimicry profile. Similarity values were assigned to each individual in every hoverfly community (again only including those species that to human eyes appear candidates for wasp mimics), and a median similarity calculated. Where data were given in abundance form (i.e. in abundance categories, for example “rare”, “frequent”), these were converted to frequency form (i.e. actual numbers) using a set of conversion factors. Each set was scaled approximately exponentially between frequencies of 1 and 100, varying according to the number of categories used in a dataset. The factors were as follows (least abundant category first): seven abundance categories (x2, x4, x10, x20, x50, x100), six (x2, x6, x15, x40, x100), five (x3, x10, x30, x100), four (x3, x20, x80), three (x5, x50) and two (x7).

Table 5.1. Literature data used to compare mimicry profiles across four broad habitat types: 1=Ancient undisturbed forest, 2=Ancient disturbed woodland, 3=Recent disturbed woodland, 4=Highly disturbed habitat. *n* is sample size: 'A' indicates the use of abundance categories, which were converted to frequencies as described in text. Table 5.1 continues on next two pages.

Reference	Country	<i>n</i>	Category	Median similarity
Azmeh <i>et al</i> 1998	Russia	A	1	34.53
Azmeh <i>et al</i> 1998	Poland	A	1	36.94
Bankowska 1995	Poland	A	1	35.78
Bankowska 1995	Poland	A	1	31.18
Bankowska 1980	Poland	A	2	31.18
Bankowska 1980	Poland	A	2	26.94
Bankowska 1980	Poland	A	2	20.37
Bradescu 1986	Romania	A	2	20.37
Cepalac & Ruzicka 1966	Slovakia	A	2	32.43
Chemini <i>et al</i> 1986	Italy	34	2	30.33
Daccordi <i>et al</i> 1980	Italy	86	2	38.8
Daccordi <i>et al</i> 1980	Italy	127	2	38.8
Daccordi <i>et al</i> 1980	Italy	40	2	34.53
Daccordi <i>et al</i> 1980	Italy	335	2	20.37
Gilbert & Perry 1982	England	2063	2	20.37
Gilbert 1981a	England	1220	2	20.37
Hanson 1985	England	A	2	20.37
Kula 1981	Czechoslovakia	113	2	36.42
Kula 1981	Czechoslovakia	47	2	36.42
Kula 1981	Czechoslovakia	200	2	30.33
Kula 1981	Czechoslovakia	47	2	38.8
Kula 1981	Czechoslovakia	37	2	36.42
Kula 1981	Czechoslovakia	118	2	36.42
Kula 1981	Czechoslovakia	77	2	36.42
Kula 1981	Czechoslovakia	181	2	30.33
Kula 1981	Czechoslovakia	40	2	30.33
Kula 1981	Czechoslovakia	59	2	36.42
Kula 1981	Czechoslovakia	82	2	31.18
Kula 1981	Czechoslovakia	255	2	30.33
Kula 1981	Czechoslovakia	251	2	36.42
Kula 1981	Czechoslovakia	125	2	30.33
Kula 1981	Czechoslovakia	57	2	36.42
Kula 1981	Czechoslovakia	211	2	30.33
Kula 1981	Czechoslovakia	179	2	36.42
Kula 1981	Czechoslovakia	90	2	36.42
Kula 1981	Czechoslovakia	57	2	36.42
Kula 1981	Czechoslovakia	68	2	26.94

Table 5.1 (continued)

Reference	Country	<i>n</i>	Category	Median similarity
Kula 1981	Czechoslovakia	325	2	30.33
Macgowan 1981	Scotland	A	2	28.64
Parmenter 1950	England	A	2	20.37
Röder 1979	Austria	A	2	22.75
Simic & Vujic 1987	Yugoslavia	A	2	22.75
Simic 1987	Yugoslavia	A	2	26.24
Speight & Lucas 1992	Lichtenstein	A	2	16.52
Speight & Lucas 1992	Lichtenstein	A	2	24.85
Speight & Lucas 1992	Lichtenstein	A	2	20.37
Speight & Lucas 1992	Lichtenstein	A	2	31.18
Speight 1983	Ireland	A	2	30.33
Stollar 1971	Slovakia	1326	2	35.46
Stollar 1984	Czechoslovakia	914	2	36.42
Van der Goot 1967	Holland	A	2	20.37
Watts 1983	England	6177	2	20.37
Watts 1983	England	4593	2	20.37
Cepelak & Zajonc 1962	Slovakia	A	3	35.46
Cepelak & Zajonc 1962	Slovakia	A	3	28.18
Cepelak 1982	Slovakia	577	3	36.94
Chemini <i>et al</i> 1983	Italy	51	3	35.46
Chemini <i>et al</i> 1983	Italy	36	3	30.33
Chemini <i>et al</i> 1983	Italy	16	3	30.33
Chemini <i>et al</i> 1983	Italy	87	3	35.46
Jentzsch 1991	Germany	A	3	17.56
Kormann 1993	Germany	A	3	35.46
Kormann 1993	Germany	A	3	38.8
Kormann 1993	Germany	A	3	47.87
Kormann 1993	Germany	A	3	31.18
Kormann 1993	Germany	A	3	36.42
Kormann 1993	Germany	A	3	36.42
Kormann 1993	Germany	A	3	3.85
Kormann 1993	Germany	A	3	20.37
Kormann 1993	Germany	A	3	35.46
Laurence 1950	England	A	3	17.56
Laurence 1950	England	A	3	46.33
Röder 1979	Germany	A	3	20.37
Röder 1980	Germany	679	3	20.37
Speight 1983	Ireland	A	3	15.45
Speight 1983	Ireland	A	3	36.42
Speight 1983	Ireland	A	3	32.97
Speight 1983	Ireland	A	3	31.18
Speight 1992	Lichtenstein	A	3	17.41

Table 5.1 (continued)

Reference	Country	<i>n</i>	Category	Median similarity
Speight 1992	Lichtenstein	A	3	35.46
Speight 1992	Lichtenstein	A	3	17.25
Ssymank 1991	Germany	283	3	34.57
Stollar 1974	Slovakia	255	3	35.46
Torp 1964	Denmark	766	3	19.36
Torp 1983	Denmark	A	3	20.37
Torp 1983	Denmark	A	3	26.94
Veltman 1979	Holland	A	3	20.37
Veltman 1979	Holland	A	3	10.59
Veltman 1979	Holland	A	3	30.33
Veltman 1979	Holland	A	3	17.56
Bankowska 1981	Poland	A	4	36.42
Bankowska 1981	Poland	A	4	17.25
Bankowska 1981	Poland	A	4	36.42
Bankowska 1981	Poland	A	4	36.42
Bankowska 1982	Poland	A	4	22.75
Bankowska 1982	Poland	A	4	22.75
Bankowska 1982	Poland	A	4	20.37
Bankowska 1982	Poland	A	4	20.37
Bankowska 1982	Poland	A	4	22.75
Barkemeyer 1992	Germany	2043	4	20.37
Chemini <i>et al</i> 1985	Italy	49	4	36.42
Chemini <i>et al</i> 1985	Italy	37	4	26.94
Chemini <i>et al</i> 1985	Italy	43	4	26.94
Dawe & McGlashan 1987	England	516	4	36.42
Fassotte & Grootaert 1981	Belgium	221	4	20.37
Gilbert 1981a	England	3660	4	36.42
Gilbert 1981a	England	3205	4	36.42
Jacob-Remacle 1980	Belgium	391	4	26.94
Kormann 1993	Germany	886	4	34.75
Owen 1991	England	23213	4	20.37
Parmenter 1942	England	A	4	20.37
Parmenter 1954	England	A	4	26.94
Pellmann & Nahhal 1991	Germany	7493	4	26.94
Plant 1986	England	A	4	20.37
Speight 1983	Ireland	A	4	31.68
Torp 1983	Denmark	A	4	22.75
Zucchi & Fischer 1991	Germany	A	4	31.18

The test was of the *a priori* hypothesis that human-induced disturbance artificially boosts the relative abundance of poor mimics (because these are largely aphidophages). This predicts that the average median similarities will fall into the rank order: undisturbed forest > ancient woodland > recent disturbed woodland > disturbed urban habitats.

This was again tested using a specific non-parametric one-way ANOVA (Meddis 1984). Using the median similarity from each site as the raw data, the rank sums R_i were calculated for each group (*i.e.* habitat type) ($i = 1$ to 4), and a Z-score calculated according to the formula:

$$Z = (L-E) / \sqrt{V}$$

$$\text{where } L = \sum \lambda_i R_i$$

$$E = (N+1) \sum n_i \lambda_i / 2 \text{ and}$$

$$V = (N+1) [N \sum n_i \lambda_i^2 - (\sum n_i \lambda_i)^2] / 12$$

(λ_i = predicted order for the groups, n_i = sample size for each group, $N = \sum n_i$)

Z-scores greater than 1.64 are adjudged to be significant at the 5% level.

5.3 Results

The similarity values obtained described 99% of individuals from Leicester, 91% from Poland and 85% from Russia. For the data from the literature, the similarity values covered on average $94\pm 1\%$ of the data.

For the new data, the null hypothesis that the mean ranks would not follow the predicted pattern (Russia>Poland>UK) was rejected using a specific ANOVA ($Z=24.07$, $p<0.001$). The peak in abundance moved to higher similarity values as the habitat became less disturbed (Figure 5.1a, b, c). In Leicester, the similarity value range with highest frequency was 5-15% similarity to models, while in Poland the highest frequency was in the 15-25% range. In Russia the peak frequency had moved even higher, to 25-35% similarity.

The whole population tended to have higher similarity values in the less disturbed habitats; in the Leicester dataset almost half of the hoverflies had similarity values of 15% or below, while Poland and Russia had only 5% and 10% respectively in this category. Conversely, the Leicester community had only 1% of individuals with 45% similarity or above, while Poland had 38% and Russia had 16%. This resulted in a higher overall median similarity in the undisturbed habitats: 36.9% similarity in Poland and 34.5% in Russia, compared with 17.3% in Britain.

For the overall test of the hypothesis using the literature data, there was also a trend of lower median similarity with increased habitat disturbance (Figure 5.2), and statistically the predicted pattern of similarity with habitat type did indeed occur ($Z = 1.69$, $p<0.05$). There is a large jump in mean similarity between

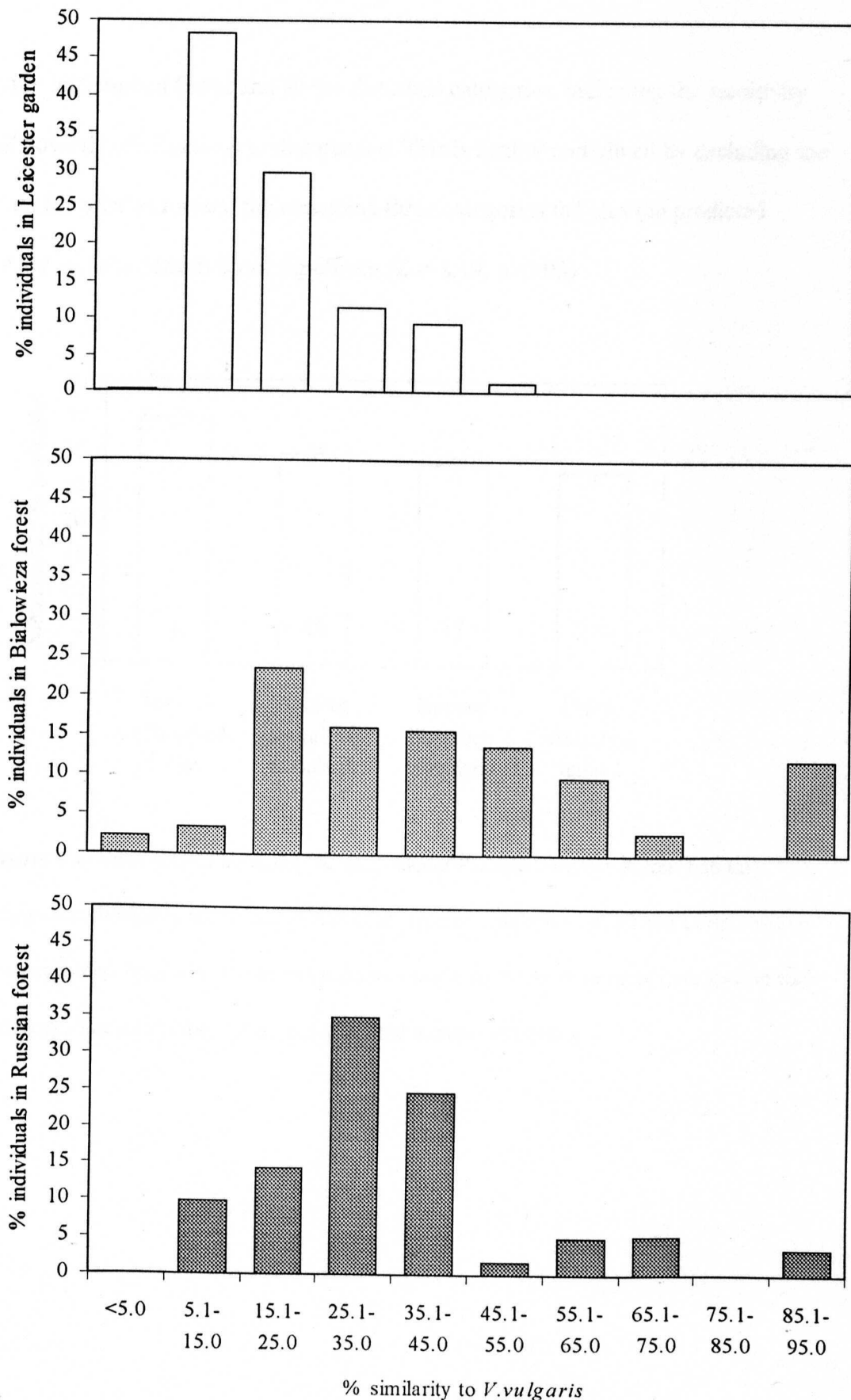


Figure 1. Abundance of hoverflies categorized by degree of similarity to *Vespula vulgaris*, in (a) a Leicester garden in June 1972-1994, (b) Bialowieza forest, Poland, in June 1996 and (c) Russian Far East forest in, in June 1995 and 1997.

truly undisturbed forest and all the disturbed categories, indicating the sensitivity of hoverfly communities to disturbance. This is further underlined by excluding the data for pristine forests; the remaining three categories fall into the predicted order, but the pattern is not significant ($Z = 1.19, p > 0.05$).

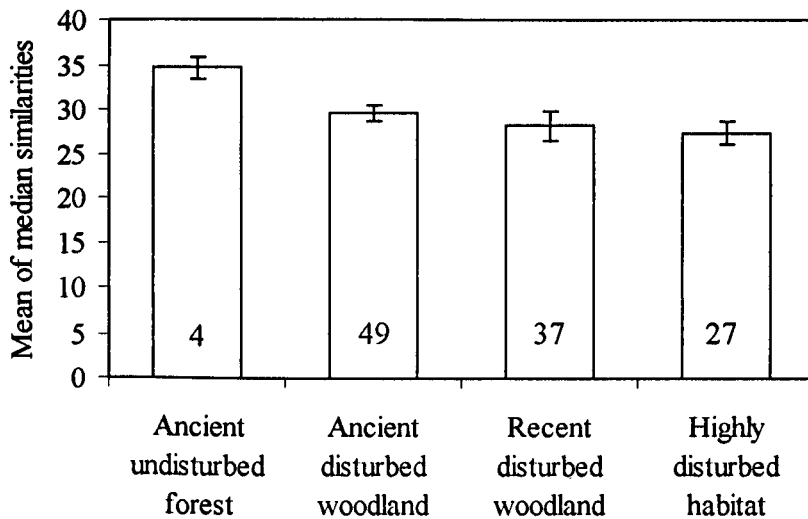


Figure 5.2. Similarity of hoverflies to wasp model *Vespula vulgaris* in four habitat categories. Similarity values are means of the median similarities of all sets of data within each category. Numbers in columns indicate sample sizes (the number of data sets) in each category. The similarities follow the predicted monotonic pattern.

5.4 Discussion

This study demonstrates that the disturbance of forest habitats has a large effect on the relative frequencies of hoverfly species. A shift towards lower similarities to wasps was found when habitats were disturbed. This suggests a reason why so many poor mimics may be present in the highly disturbed landscapes of Western Europe; the change to urban and agricultural environments has increased food resources for the larvae of poor mimics, while simultaneously decreasing them for good mimics. Indeed, in Leicester, there were no high-fidelity mimics at all over the 23 years of the study.

The paradox of mimics outnumbering models could therefore be explained thus. Evolution of colour patterns due to changes in model/ mimic ratios may be slow (Turner 1984a) so mimicry patterns seen now in disturbed habitats may be in the process of being lost. Predator pressure is the factor which would cause mimicry to be lost by natural selection. Here, habitat disturbance may have overtaken it in its role of regulating mimic abundance, though it may eventually catch up.

Theoretical models of mimicry (Huheey 1964; Pough *et al* 1973; Estabrook & Jespersen 1974) are generally based on measures of abundance, model noxiousness, prey spatial distribution and the profitability of alternative prey. These parameters, however, are rarely measured in the field. More extensive studies of frequency data, including model frequencies, would provide further elucidation of the complex systems described here.

In this study, the Russian forest was less disturbed than the Bialowieza

forest in Poland, where human activity does exist in most areas outside the central strict reserve. The hoverflies in Poland, however, had a higher mean similarity to wasps, and the distribution of similarity values was generally further to the right (Figure 5.1b, 5.1c). This might be due to stochastic differences between years (see Owen 1991 [and chapter 2]) since these studies covered only 1-2 seasons: in the Russian Far East, 1997 in particular was a poor year for hoverflies due to a previous series of dry seasons. It should be noted, though, that the peak in hoverfly abundance was at a higher similarity value than in Poland. This type of problem emphasises the usefulness of (a) long-term datasets such as the Leicester one, and (b) the type of large-scale literature survey used here, which gives a general picture despite variation in many aspects of the studies.

An area for further study would be to measure model abundance relative to mimics. This study concentrated on proportions of mimics relative to one another. Studies of the whole year such as that in Leicester would be needed to examine model:mimic ratios correctly.

Even in the untouched environments surveyed here, there are still many poor mimics, though they are proportionally fewer than in disturbed habitats. The imperfection of these mimics still requires some explanation (see various hypotheses in chapter 1), but this is a neglected area of research into mimicry. The following two chapters examine some possible explanations.

These results demonstrate that human-derived habitat change does alter the relative frequencies of good and poor mimics, and hence probably of mimics and models. This needs to be borne in mind when using community data to test ideas

about the evolution of mimetic complexes, since any but data from pristine habitats could be misleading.

Chapter Six

Are hoverflies really mimics?

6.1 Introduction

Since Batesian mimicry was first described by Bates in 1862, and subsequently accorded the status of a paradigm of Darwin's theory of evolution by natural selection (Fisher 1930; Turner 1987; Malcolm 1990), the colour patterns of a wide range of species, mostly insects, have been attributed to it (see Wickler 1968; Rettenmeyer 1970). In Batesian mimicry, an unpalatable (or otherwise unprofitable) model is imitated by an unrelated palatable species (the mimic). The mimicry is driven by the selective pressure of visually hunting predators such as birds. Batesian mimicry can be contrasted with Müllerian mimicry, where unrelated species are both unprofitable and share a colour pattern, thus sharing the costs of predator education. The distinction between Batesian and Müllerian mimicry may not be a rigid one; it has been suggested that they are two extremes of a continuum (Speed 1993a; but see MacDougall & Dawkins 1998).

The conditions under which Batesian mimicry could operate have been described using many mathematical models (see Huheey 1988; Speed 1999), using model and mimic parameters (e.g. frequencies) and characteristics of predators (e.g. learning and forgetting times). Experimental evidence has also been found for Batesian mimicry (e.g. Brower 1960, Jeffords *et al* 1979, review in Gilbert 1983). However, nearly all mathematical models and experiments concentrate on perfect (or almost perfect) mimicry. Experiments

that have examined imperfect mimicry have shown that it too can act as protection against predators provided models are frequent and highly unprofitable (Duncan & Sheppard 1965, Goodale & Sneddon 1977, Lindström *et al* 1997).

In hoverflies (Diptera: Syrphidae), imperfect mimicry of social wasps (Hymenoptera: Vespidae) is widespread (Dittrich *et al* 1993). The yellow-and-black abdominal patterns of the wasps are ‘mimicked’ in many syrphid species (e.g. *Syrphus* spp, *Scaeva* spp) by simpler yellow stripes or lunules across a black background. This is in contrast to well-known Batesian butterfly mimicry complexes (e.g. the Monarch-Queen-Viceroy complex (Brower 1958a,b, but see Ritland & Brower 1991)) where the mimicry is much more detailed. Imperfect mimics are often considered an intermediate stage during the evolution of perfect mimicry (e.g. Duncan & Sheppard 1965), or a breakdown of mimicry as a consequence of lack of predator pressure (Carpenter & Ford 1933; Turner 1984). Yellow-and-black patterns are found in species across much of the syrphid phylogeny, and it is improbable that so many genera are at the same point in their evolution towards perfect mimicry, especially considering their high abundance. Moreover, imperfect mimicry is advantageous only if models are frequent and highly unprofitable (Duncan & Sheppard 1965; Goodale & Sneddon 1977; Lindström *et al* 1997). Social wasps are indeed highly noxious models, with their very unpalatable tissues and harmful stings (Mostler 1935). However, they are not frequent in comparison to their supposed mimics, at least in the UK (Owen 1991).

A variety of hypotheses addresses the existence of these poor mimics, including the possibility that predator perceptions of imperfect mimicry differ

from human perceptions (Dittrich *et al* 1993; Howse & Allen 1994). In this paper, a different hypothesis is addressed (though the two are not mutually exclusive), suggesting that the colour patterns are not mimetic. Specifically, the patterns have a non-mimetic, aposematic function. Aposematism (see Mallet & Singer 1987; Guilford & Dawkins 1991) is widespread in the insect world, and is most commonly thought of as a warning to predators of unpalatability. Several unpalatable chemicals have been identified in brightly-coloured insect species (Brower 1984). Hoverflies, however, are almost certainly all palatable (Mostler 1935). Though toxic cardiac glycosides were found in the aphidophagous hoverfly *Ischiodon aegyptius* (Malcolm 1976), the results could not be reproduced and the hypothesis that they were transferred from plants via aphids was falsified (Malcolm 1981, 1992). Moreover, hoverflies form a proportion of the diet of many bird species (McAtee 1932; Krištín 1994; Torp 1994).

Bright colours can also advertise other forms of unprofitability (Rettenmeyer 1970; Baker & Parker 1979); one example of this is warning of escape ability from predators (Gibson 1980; Mallet & Singer 1987; Srygley 1994, 1999; Pinheiro 1996). Such escape ability (through flight agility) is a well-established alternative to unpalatability for escaping bird predators in butterflies (Kammer & Heinrich 1978; Srygley 1994; Srygley & Kingsolver 1998). Hoverflies are expert fliers, with excellent vision, and capable of high acceleration and sudden changes of direction (Ellington 1984; Gilbert 1986). They therefore seem likely candidates for this form of aposematism, which has been identified in two *Morpho* butterfly species (Pinheiro 1996) (see discussion).

This study tests the hypothesis that hoverflies are advertising their escape ability due to good flight agility. Two alternative evolutionary scenarios are postulated which could have led to the observed colour patterns, one if the colour patterns are mimetic, and one if they are aposematic. From these two scenarios, predictions are made about the relationship across species between flight agility and similarity to the wasp model. These predictions are then tested, using computer-generated measures of similarity to wasps. Flight agility is not measured directly, but a trade-off assumed between flight agility and reproductive potential. Many authors have found such trade-offs, both within (Denno *et al* 1989; Fleming & Gross 1989; Groeters & Dingle 1989) and among species (Shine 1980; Kaitala 1991). In particular, there is a trade-off in Neotropical butterfly species between flight muscle as a proportion of body mass and ovary mass (Marden & Chai 1991).

In the first evolutionary scenario, it is assumed that the colour patterns have evolved through mimicry; all hoverflies are initially agile, and some species evolve patterns mimetic of wasps. Predation pressure is reduced in these mimetic species, allowing decreased resource allocation to flight muscle (and thus increased allocation to reproduction). The more faithful the mimicry, the more predation pressure is reduced. Flight muscle is not the only component of flight agility (Ellington 1984), but it does contribute greatly to some aspects such as acceleration (Marden 1987), known to be important in hoverflies. Hence the prediction if the patterns are mimetic is a negative relationship between flight agility and similarity to the model, and a positive relationship between reproductive potential and similarity.

If the colour patterns are advertising flight agility, a second evolutionary scenario can be suggested; all hoverfly species are not particularly agile, but some evolve extra agility, and evolve convergent colour patterns to advertise the fact. The prediction from this is that there is no correlation between degree of similarity to the wasp and flight agility (or reproductive potential). Furthermore, species with 'mimetic' colour patterns should be more agile than 'non-mimetic' species, and via the postulated trade-off, should have lower reproductive potential.

In this paper, independent contrasts methods (Felsenstein 1985) are used to test these hypotheses across hoverfly species. No strong evidence is found from reproductive and similarity data that hoverflies are mimetic (if there is a reproductive gain from being mimetic). Additionally, there is suggestive but inconclusive evidence that hoverflies may be using their colour patterns to advertise their ability to evade capture.

6.2 Methods

To test whether hoverflies' colour patterns could be advertising escape ability, allocation to reproduction was compared with similarity to a wasp model. Egg batch size in females, and testis length and volume in males, were regressed against computer-generated similarity values, using comparative methods which take phylogeny into account.

6.2.1 Morphological data

Morphological data derive from fieldwork in the USA (Arizona, Oregon and Maine), Britain, Poland (Bialowieza forest), and the Russian Far East. Hoverflies were frozen on capture, and then measured under a binocular microscope with an ocular micrometer (for details, see Gilbert 1981, 1985, 1990; Gilbert *et al* 1994). Measurements included thorax width, length and height. An index of thorax volume was used to represent body size, calculated by multiplying together the three thorax measures. The hoverflies were then dissected. In females, the ovaries were removed into water and teased apart into their constituent ovarioles. The number of ovarioles was counted, and, if present, the length (L) and maximum width (W) of mature (chorionated) eggs were measured. Egg volume was calculated by using the formula for volume of an ellipsoid $(4/3)\pi(L/2)(W/2)^2$. Egg volume and ovariole number were multiplied to give a measure of maximum batch volume. Batch size is considered a reasonable measure of allocation to reproduction in females (Gilbert 1990). In males, allocation to testis production was measured by dissecting out the reproductive system in water, and measuring the length and maximum width of the testis. Testis length was considered an indication of reproductive potential in males, as it is strongly associated with sperm length in *Drosophila* (Joly & Bressac 1994; Pitnick 1996). Long sperm are more likely to be involved in fertilisation than short sperm (Snook 1997; Snook & Karr 1998), so it is assumed that long testes may have evolved via reproductive advantage. Testis size is also connected with sperm number (Pitnick 1996), and larger numbers of sperm again provide a reproductive advantage, especially in the event of sperm competition (Parker 1972). Sperm

production is often considered cheap (Trivers 1972) but, like in *Drosophila* (Pitnick 1996), hoverflies show a great deal of variation between species in testis length [Chapter 3], and some species have very large testes. Large testes are costly to produce and maintain (Pitnick *et al* 1995b), so here investment in testis length is considered a significant cost. All characters were averaged over individuals to give a mean species value.

6.2.2 Measuring similarity to wasps

Model-mimic similarity was measured using the method of Dittrich *et al* (1993). This directly compares two images pixel by pixel by measuring the distance apart of each pair of corresponding pixels in Red-Green-Blue colour space (for details, see Dittrich *et al* 1993 [and chapters 4 & 5]. Assessments of pigeons correlate with the similarities generated by this method (Dittrich *et al* 1993; Green *et al* 1999). One difference from the method of Dittrich *et al* (1993) was introduced; any tergite which was entirely black was allocated a similarity value of zero. This avoided the situation where black species were given relatively high similarity values because of overlap with the black on the wasp's body.

The bitmaps compared by the similarity program are of equal size. To consider size differences between species, the resulting similarity values were scaled by each species' size in relation to the model. *Vespula vulgaris* was used as the model, as it is the most ubiquitous social wasp in the UK, including at sites where hoverflies are abundant (Owen 1991, Azmeh *et al* 1998) [chapter 5].

Similarity values were not calculated for every species separately, but for colour-pattern groups. A group consisted of species whose abdominal patterns were identical or almost so, usually a genus or part of a genus. A similarity value was calculated for one species in the group and used for all species in the group. Hoverflies that are mimics of honeybees (*Apis* spp.) or bumblebees (*Bombus* spp.) were not included in this analysis.

6.2.3 Comparative method and statistical analyses

Taxa in a branching phylogeny can not be considered independent points for purposes of statistical analysis (e.g. Harvey & Pagel 1991, Martins & Hansen 1996). Differences between taxa may be over-estimated if they are considered independent points, because traits might be shared by taxa due to common evolutionary descent, not independent evolution (Harvey & Pagel 1991, but see Ricklefs 1996). This study used the computer program 'CAIC' (Comparative Analysis by Independent Contrasts, Purvis & Rambaut 1995) to take the phylogeny of the syrphids into account. This uses methods based upon Felsenstein's method of independent comparisons (Felsenstein 1985). Computer simulations have shown that CAIC is a more valid method of comparing taxa than using species means, even where the phylogeny is poorly resolved or branch lengths are incorrect (Purvis & Rambaut 1995). Furthermore, simulations show that it is at least as valid as phylogenetic autocorrelation methods (Gittleman & Kot 1990), and a more powerful test provided the phylogeny is at least fairly resolved.

Independent comparisons methods remove the effect of phylogenetic relationships by specifying a set of independent contrasts between pairs of species or other taxa (Felsenstein 1985). Each contrast is standardised by scaling by its expected standard deviation. These standardised contrasts are then independent and normally distributed, and standard statistical analyses can be performed upon them. Felsenstein's method can only be used for continuous variables; where a categorical variable is used (here, mimics v. non-mimics), CAIC uses modifications to the method (see Purvis & Rambaut 1995).

Standardised contrasts were calculated for thorax volume, testis length and batch size. All data were reciprocally transformed before calculating contrasts; this ensured that the data conformed to Felsenstein's model of evolution of characters as a Brownian motion (or continuous walk) process (Felsenstein 1985; Purvis & Rambaut 1995).

To examine the relationship between similarity and reproductive potential, regressions of contrasts were forced through the origin; the resulting slopes give the true relation between the variables in the absence of phylogenetic effects (Pagel 1993). The effects of body size on testis and batch size were removed prior to analysis, since there are allometric relationships between the reproductive characters and body size (S.Azmeh and F.Gilbert, unpub. data) [chapter 3]. This was done by regressing the reproductive trait contrasts on thorax volume contrasts. The residuals of these regressions were then regressed on similarity contrasts. A contrast between two nodes in the phylogeny is assigned an arbitrary sign, depending on which node value is subtracted from which (Garland *et al* 1992). CAIC deals with this by always

assigning a positive sign to the independent variable; the other variable switches signs accordingly.

To compare the reproductive potential of mimics and non-mimics, the effects of body size were again removed prior to analysis by regressing testis length and volume contrasts on thorax volume contrasts, and regressing batch size contrasts on thorax volume contrasts. The slopes of these regressions were then fitted to the raw species means, and residuals were taken from the line. These residuals, effectively the magnitude of the reproductive trait relative to body size, were then compared between the categorical characters (mimic vs. non-mimic) again using CAIC (Purvis & Rambaut 1995).

Species were assigned the status of 'mimic' or 'non-mimic' according to their similarity values; those with values below 27% were designated non-mimics (see Figure 6.3 for how genera were categorised). This cut-off point was chosen subjectively, as species above 27% generally have yellow-and-black stripes of some kind. Non-mimics were mostly either black (e.g. *Chrysogaster* spp., *Heringia* spp.) or of a shape and pattern very dissimilar to a wasp (e.g. the small and elongate *Baccha* spp. and *Melanostoma* spp.). Bee mimics were not used.

6.2.4 Phylogeny

A genus-level phylogeny of the syrphids was used (Figure 6.1), based upon 187 larval morphological characters (see Rotheray & Gilbert 1999). The phylogeny consists of 85 genera, nearly all those in the Holarctic. It is completely independent of the adult characters used in this study, because it uses larval data. The branch lengths for the phylogeny are unknown, and

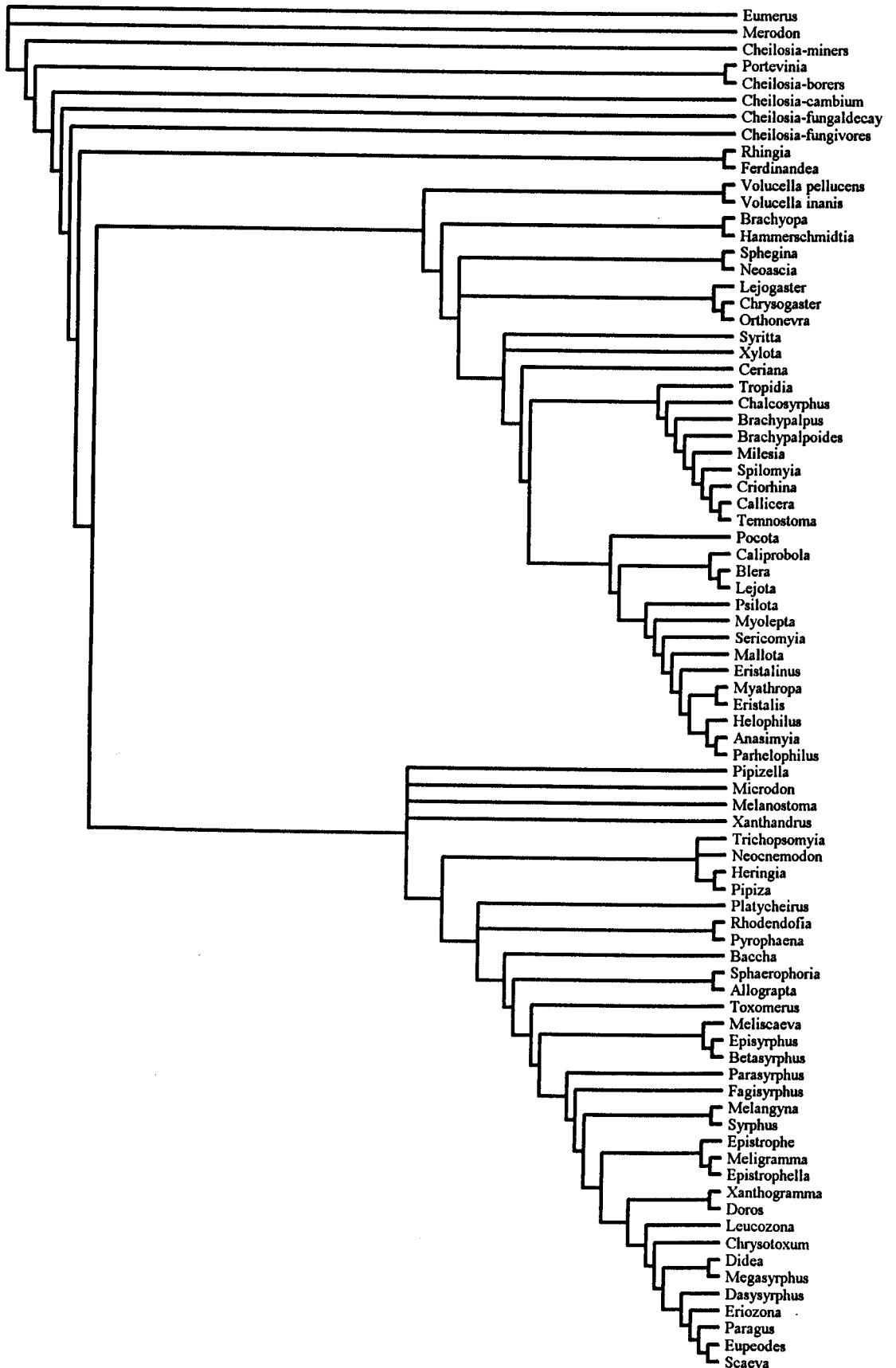


Figure 6.1. Genus-level phylogeny of the hoverflies, based on 187 morphological larval characters.

therefore equal branch lengths were used, despite this assuming a strictly punctuational view of evolution (see e.g. Harvey & Pagel 1991). Computer simulations show that using inaccurate branch lengths still gives reasonably accurate results (Purvis *et al* 1994).

The data were considered at the species level even though the phylogeny is only generic; therefore all species within a genus simply branch from the same node (a 'soft' polytomy). This is taken into account by CAIC using the logic of Pagel (1992); the true phylogeny is assumed to be bifurcating, and the daughter taxa at a multiple node are conservatively arranged according to their values of the independent variable.

6.3 Results

6.3.1 Is there a positive relationship between the evolution of mimetic similarity and reproductive potential?

For females, 40 sets of contrasts were obtained from data on 60 species. For males, 48 contrasts were obtained from 101 species.

Analysis of independent contrasts showed no indication that (size-adjusted) batch size and similarity to wasps have evolved in a correlated manner (Figure 6.2; $F_{1,39}=2.82$, $r^2=0.07$, $p=0.101$). Furthermore, reproductive potential had increased where similarity increased at only 24 of the 40 contrasts in the phylogeny. This is no different from random expectation (binomial test, $p=0.27$).

For males, changes in size-adjusted testis length also showed no significant relationship with changes in similarity to wasps (Figure 6.3a;

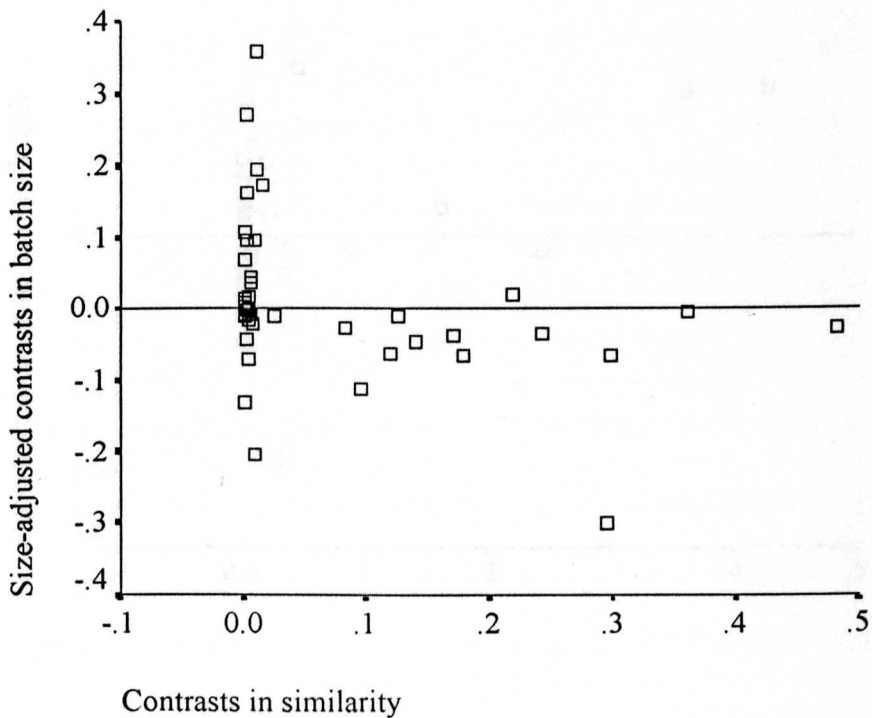


Figure 6.2. The relationship in females between body size-adjusted batch size (see text) and similarity to a *Vespula vulgaris* model in 60 species of hoverfly. All points are standardised independent contrasts.

$F_{1,47}=1.57$, $r^2=0.01$, $p=0.216$), while testis volume contrasts were weakly positively related with similarity contrasts (Figure 6.3b; $F_{1,44}=4.36$, $r^2=0.09$, $p=0.043$). Testis length increased in only half (24/48) of the cases where similarity increased (binomial test, $p=1.00$), while testis volume increased in 31/47 cases (binomial test, $p=0.07$).

6.3.2 Is the evolution of 'mimicry' associated with a reduction in reproductive potential?

For female batch size data, there were 5 nodes in the phylogeny (Figure 6.4a) where 'mimicry' had arisen (i.e. contrasts between mimics and non-mimics). 61 species were used in the analysis. For male data, there were

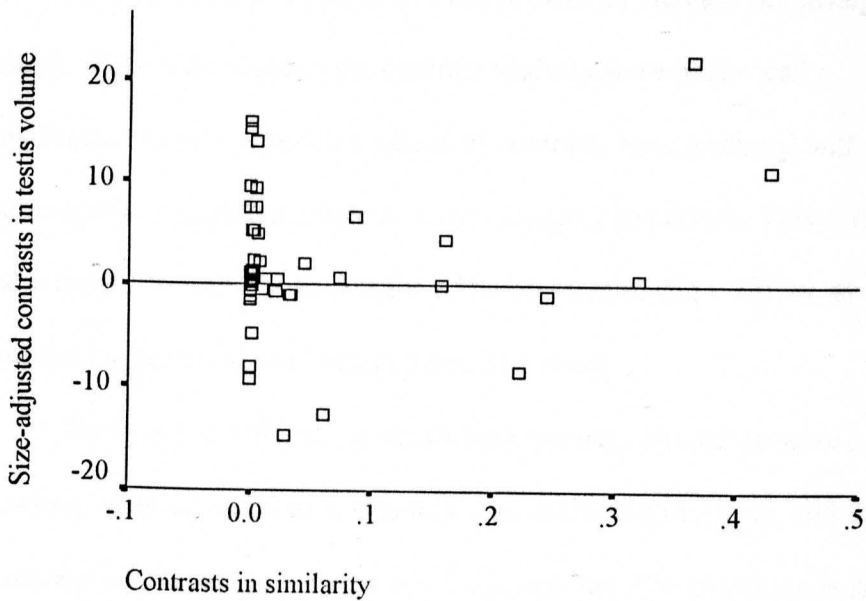
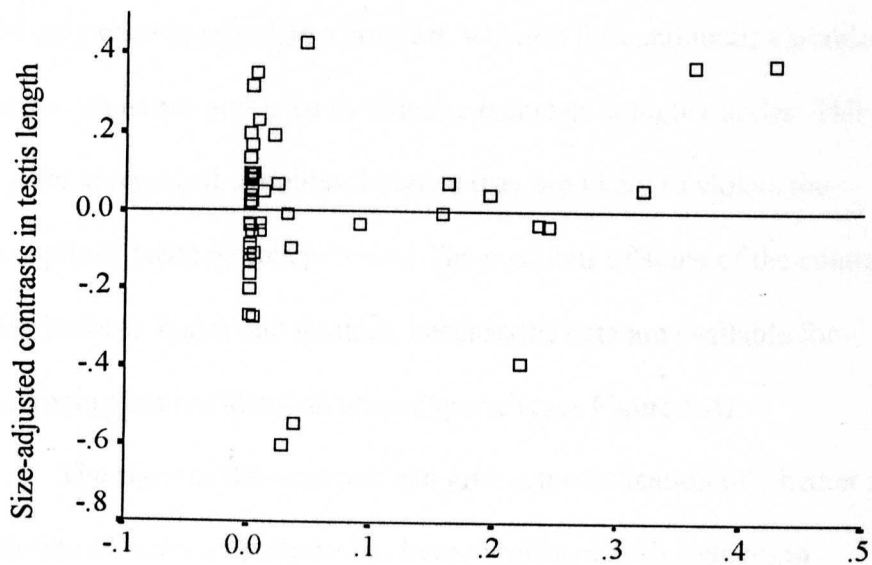


Figure 6.3. The relationship in males between similarity to a *Vespula vulgaris* model and (a) body size-adjusted testis length in 101 species of hoverfly. (b) body size-adjusted testis volume in 98 species of hoverfly. All points are independent contrasts.

also 5 such contrasts, obtained from 105 species for testis length, and 102 for testis volume. These low numbers of contrasts are due to the use of a categorical variable. (For categorical variables, the value for each species is

used only once to calculate a contrast, whereas for continuous variables, species values are also used to estimate contrasts at higher nodes. This is not done for categorical variables, because they are likely to violate the assumptions made by this process.) The positions of some of the contrasts differ between males and females, because the data are available for overlapping but not identical sets of species (see Figure 6.4).

The signs of the contrasts can give some indication of whether the evolution of mimicry patterns has been associated with changes in reproductive potential. If the sign of a contrast is positive, a transition from 'non-mimic' to 'mimic' status is associated with an increase in the dependent variable. The values used in the contrast analysis were reciprocally transformed; therefore positive values of contrasts are associated with the lowering of reproductive potential where mimicry has arisen. This is the prediction if 'mimicry' is in fact the advertisement of flight agility, and reproductive potential has been reduced as a result.

For females, 4 of the 5 nodes where mimicry has arisen were associated with an increase in size-adjusted batch size residuals, and therefore a decrease in size-adjusted batch size (Figure 6.4a). The exception was a small increase in batch size associated with the contrast between *Dasysyrphus bilineatus* and 2 other species in the same genus.

In males, 3 of the 5 contrasts between non-mimics and mimics were associated with decreases in size-adjusted testis length (Figure 6.4b). The exceptions were where mimicry arose in the genera *Spilomyia* and *Temnostoma*, and in the *Aemosyrphus/ Helophilus* group. For testis volume, the contrasts were in the same positions as for testis length, since most of the

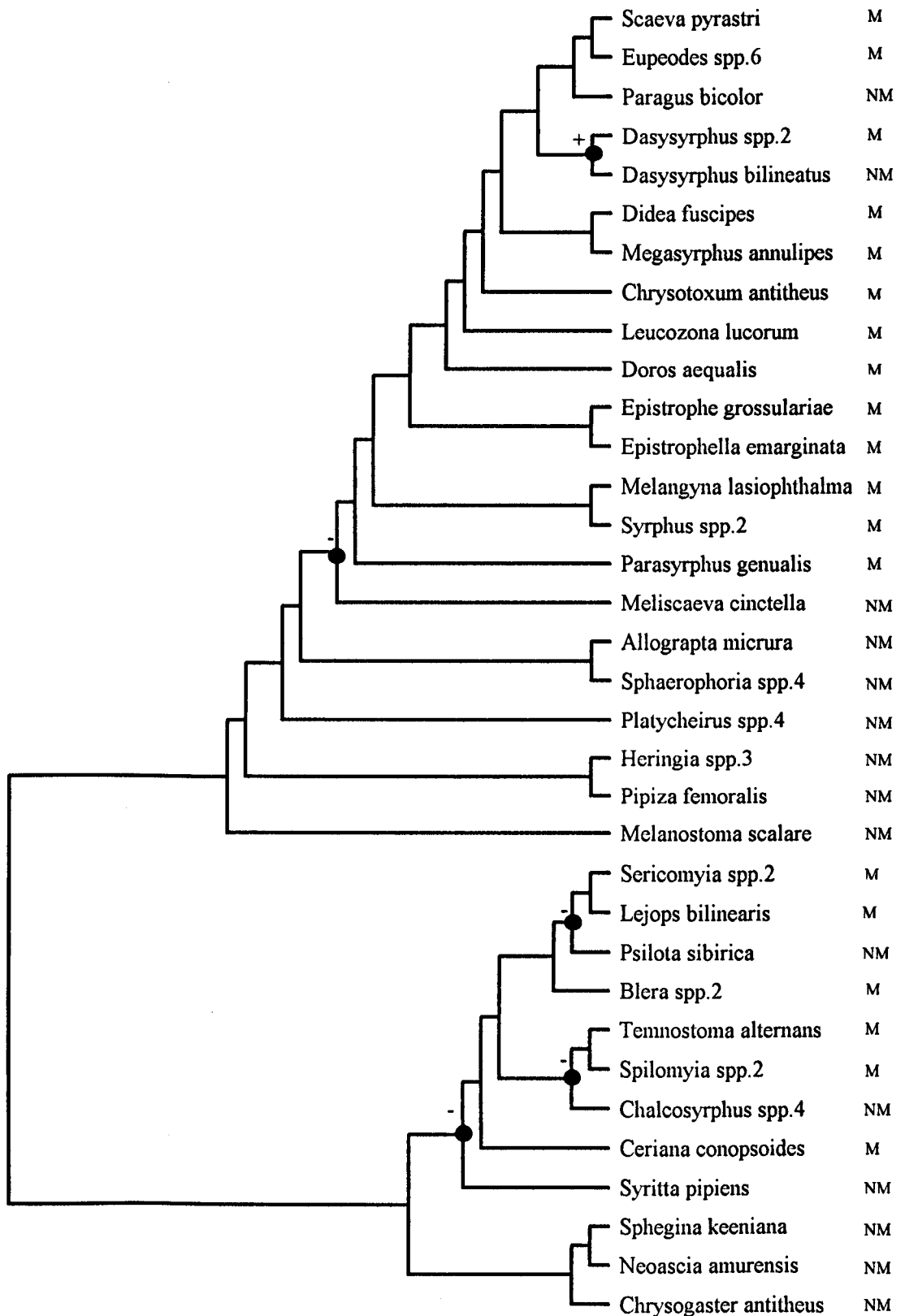


Figure 6.4a Phylogeny of the hoverflies showing only those taxa for which data were available on batch size and mimicry status (though the analysis used the complete phylogeny). Dots indicate nodes where one mimicry state (M or NM) has arisen from the other (see text) and thus where contrasts were calculated. '+' indicates an increase and '-' indicates a decrease in reproductive potential at the node, relative to transitions from NM to M. Numbers show the number of species used, in genera where more than one species had the same mimicry status.

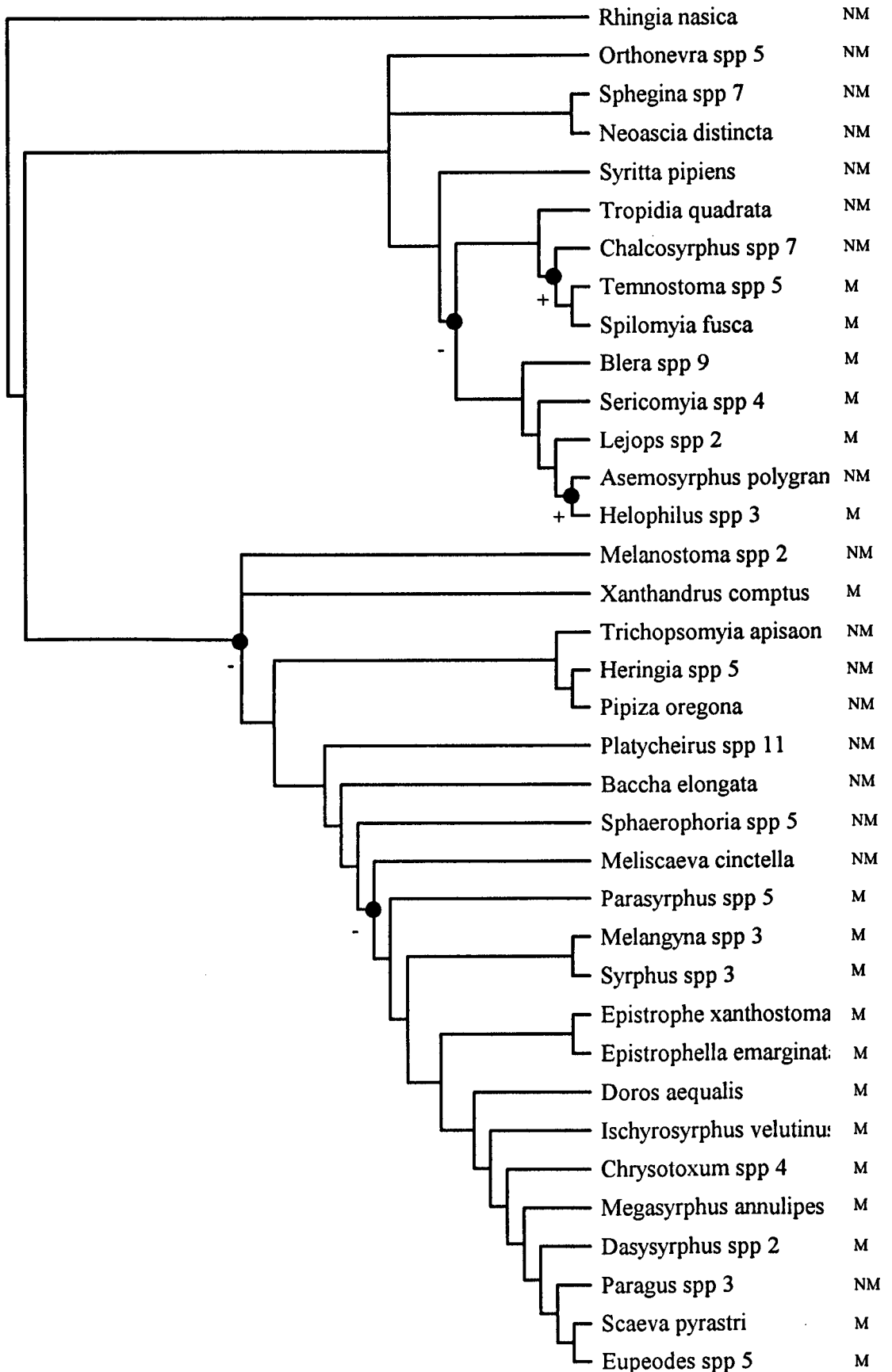


Figure 6.4 b Phylogeny of the hoverflies showing only those taxa for which data were available on testis length and mimicry status. For explanation of figure, see Figure 6.4a.

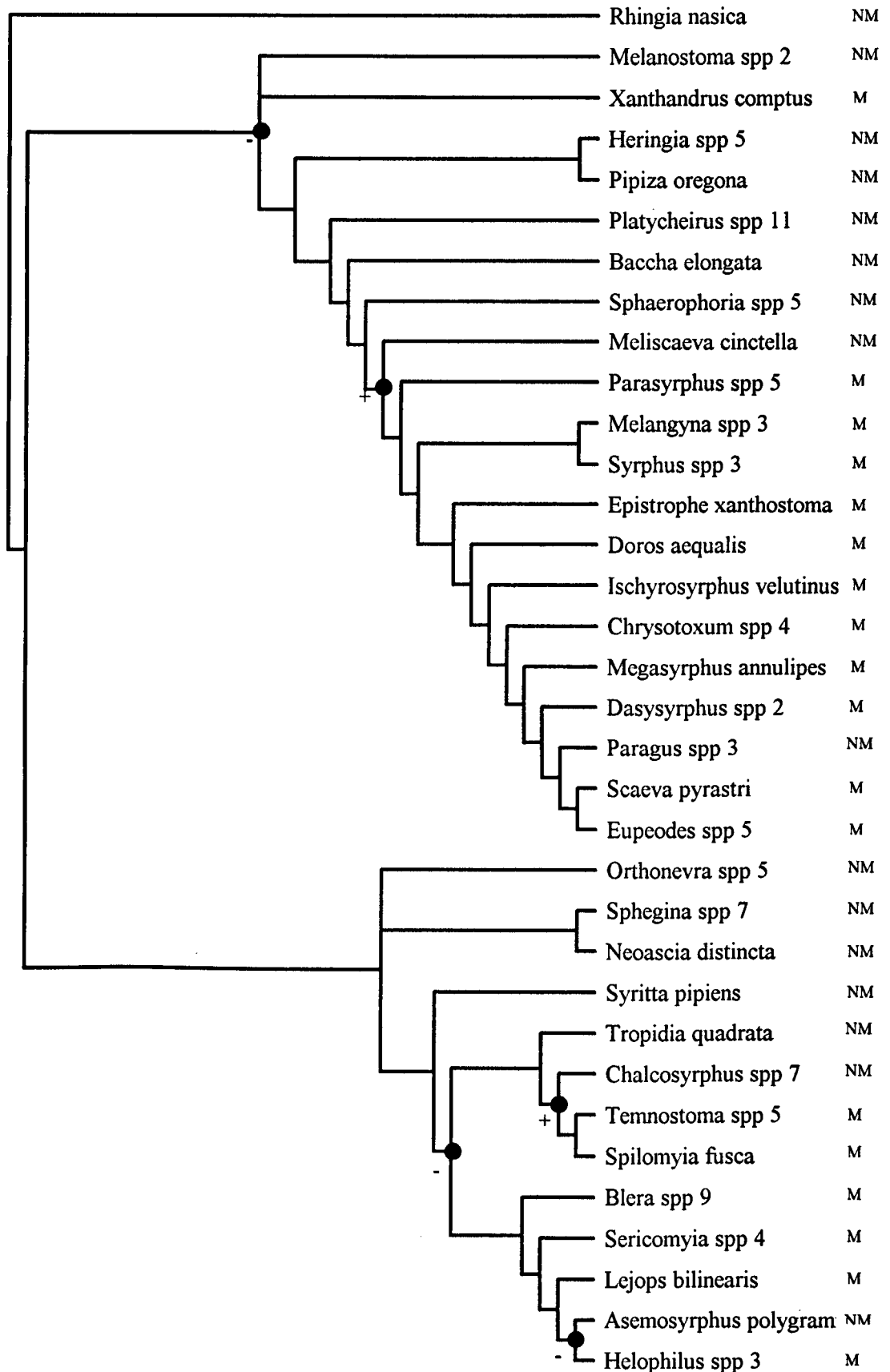


Figure 6.4c Phylogeny of the hoverflies showing only those taxa for which data were available on testis volume and mimicry status. For explanation of figure, see Figure 6.4a.

species used were the same. Again, in 3 out of 5 cases the change from non-mimic to mimic was associated with a decrease in reproductive potential; the exceptions were where mimicry arose in *Spilomyia* and *Temnostoma*, and in the subfamily Syrphinae (Figure 6.4c).. Considering male and female results, 7 out of 10 cases are in the predicted direction; however, low numbers of contrasts mean that statistical tests of these results have little power.

6.4 Discussion

Yellow-and black striped hoverflies are generally considered to be Batesian mimics of wasps (Stubbs & Falk 1983; Grewcock 1992; Lindström *et al* 1997). Mimicry may confer the advantage of an increase in reproductive potential due to reduced predation pressure, and a resultant decrease in the need for flight agility, as seen in butterflies (Srygley & Chai 1990a; Marden & Chai 1991; Chai 1996). This phylogenetic, contrast-based study shows no strong evidence that hoverflies are Batesian mimics, if there is a reproductive advantage to mimicry. Furthermore, data on reproductive characters suggest that ‘mimetic’ hoverfly species have lower reproductive potential than their non-mimetic counterparts, and thus may be advertising their escape ability through flight agility.

The lack of correlation between the evolution of reproductive potential and degree of similarity to wasps suggests that there is no reproductive advantage to increasing similarity to the model. Hoverflies are traditionally considered imperfect mimics (e.g. Dlusski 1994) and thus assumed to be in the process of converging onto their model, not having yet attained perfect mimicry (Duncan & Sheppard 1965; Alcock 1971). This situation might for

example persist if mimics and models are in the process of a coevolutionary chase, with the model constantly 'escaping' in pattern from the mimic, and the mimic converging on the new pattern (Nur 1970; Rettenmeyer 1970; Huheey 1988; Turner 1987; Gavrilets & Hastings 1998, but see Joron & Mallet 1998). However, even imperfect mimicry is associated with a decrease in predation due to the partial similarity to the model (Mostler 1935). Therefore, even imperfect mimics should show a decreased need for escape ability, and the resultant increase in reproductive potential, and as the imitation improves, the decrease in predation should be even greater. This pattern was not supported by evidence from female reproductive data in hoverflies.

In males, however, there was a weak positive association between increase in similarity and increase in reproductive potential (Figure 6.3), bordering on statistical significance. If this indicates a mimetic function to the colour patterns, males appear to be gaining more advantage from their similarity to wasps than are females. Srygley & Chai (1990a) suggest that females may also be more variable in their abdominal mass than males because they produce and oviposit eggs, an alternative possible reason for the lack of correlation between reproductive potential and similarity in female hoverflies. However, even in males the relationship between these variables is not strong, and the sign test of the contrasts shows no evidence of any association.

Another reason why Batesian mimics are expected to show decreased flight agility (and increased reproductive potential) is that flight behaviour itself, as well as the colour pattern, can act as a signal to the predator (Srygley & Chai 1990; Srygley 1994; Chai 1996). To imitate the relatively slow flight

of their models, Batesian mimics could be expected to have a body shape and flight morphology normally associated with poor flight agility. Observations suggest that common yellow-and-black hoverflies are not imitating the flight of wasps, since their quick, darting flight is quite unlike the slow, meandering flight of wasps (pers. obs.). Once more, this suggests that the primary force behind the evolution of colour patterns in these species has not been the imitation of wasps. However, Batesian mimics may sometimes retain some aspects of escape ability, since, unlike unpalatable species, they are unlikely to be released if captured by predators. For example, the butterfly *Dismorphia amphiona* has a large thoracic mass relative to its models (Chai 1996), increasing its flight speed and acceleration. Also, the Batesian mimic *Consul fabius* retains manoeuvrability by positioning its centre-of-body-mass near the wing base like other palatable species, while imitating other aspects of its models' flight pattern (Srygley 1994). Nevertheless, a pattern of decreasing flight agility (and increasing reproductive potential) with increasing similarity to the model is still expected, since the better the imitation, the less need there is for the retention of flight agility.

It is also possible that, unlike in butterflies, waterstriders, and other groups (Marden & Chai 1991; Kaitala 1991), there is in fact no trade-off between thoracic and abdominal mass allocation. In this case, the lack of correlation in this study would not necessarily imply that hoverflies are not mimics. This can be clarified in the future by analysing flight agility data directly, rather than indirectly using reproductive potential.

If the trade-off does exist, and hoverflies are not mimics of wasps, alternative explanations are needed for the evolution of their colour patterns.

Heal (1979, 1982) suggested that the colour patterns of *Eristalis* (a bee mimic, not included in this analysis) could have a thermoregulatory function, as well as a mimetic one. This view is based on the area of black colour overlying the dorsal blood vessel, which could facilitate the warming of the blood. However, not all mimics have a black band in this area, and experiments on pale and dark colour forms have shown contradictory results to the predictions from a thermoregulatory function (Ottenheim & Kuijt 1998). While thermoregulatory considerations may have a role to play in the evolution of colour patterns in hoverflies, they are unlikely to be the driving force.

Another explanation proffered for the imperfect colour patterns of syrphids is that predators have a different perceptual system to ours, and perceive imperfect mimicry as more perfect than humans do. For example, Dittrich *et al* (1993) found that, while pigeons rated hoverflies as mimics in much the same way humans (and the similarity program) do, two 'poor' mimics were rated relatively highly. This infers the presence of perceptual biases different from our own. This study suggests this is not the case, since if poor mimics were in fact perfect mimics, they should show even further increased reproductive potential. Howse & Allen (1994) suggest that the ambiguous nature of the patterns in poor wasp mimics may cause confusion in the predator, enabling time to escape ('satyric mimicry'). If this were the case, the colouration should still provide protection from predation (like mimicry), and allow a lower flight agility and higher reproductive potential; this was not found in this study.

The data suggest another explanation, namely that hoverflies are advertising their own flight agility. Predators could learn that it is not worth

attempting to catch hoverfly prey, given the small chance of capture. The analysis shows that where yellow-and-black colour patterns have arisen from non-mimetic patterns, this tends to be associated with a lowering of reproductive potential. In this case, those species which have evolved extra flight agility (and thus had to decrease their reproductive potential) could have evolved convergent colour patterns to advertise the fact. Only tentative conclusions can be drawn from so few contrasts. However, where exceptions occur to the pattern, there are possible explanations. In females, the only occasion a decrease in reproductive potential is not associated with an occurrence of mimetic patterns is within the genus *Dasysyrphus*. The contrast is between the species *Dasysyrphus bilineatus*, classed as non-mimetic by the criteria used, and 2 'mimetic' species in the same genus. However, *D. bilineatus* does have yellow-and-black stripes, albeit different in appearance from most other imperfect mimics. Therefore it is perhaps an artefact of the arbitrary cut-off point that it has been adjudged as 'non-mimetic'.

For males, the signs of the contrasts partly vary between testis length and testis volume. Testis length has increased with the occurrence of mimicry within the genus *Helophilus/ Aemosyrphus* (considered congeneric by Rotheray & Gilbert (1999)). Testis volume, on the other hand, has decreased with the occurrence of mimicry. It is not clear why this should have happened, though the magnitude of the contrast between the two is particularly small in testis volume, and therefore possibly an artefact. The only case where an increase in both testis length and testis volume is associated with the occurrence of mimicry is upon further inspection not entirely unexpected. As mimicry evolved in the genera *Temnostoma* and *Spilomyia*, reproductive

potential in males also increased, and the contrast between other taxa and these genera is the largest in magnitude of the five contrasts considered. These genera are examples of 'perfect' mimicry, with much more faithful imitation of wasps than the common 'poor mimic' species. Not only do these genera have sophisticated imitation of colour patterns, but they are also the same size and shape as wasps, and imitate them behaviourally, both by having black forelegs, held to resemble hymenopteran antennae (Waldbauer 1970) and a slower flight pattern (pers. obs.). Unlike species advertising flight agility, they could therefore be expected to have low flight agility, and hence high reproductive potential. However, if this is the case it is unclear why higher reproductive potential has not also evolved in females in these genera.

The advertisement of escape ability is a poorly-researched area of aposematism. Several examples do exist of the association of warning colouration and flight agility rather than the more usual link with unpalatability. For example, butterflies in the *Adelpha-Doxocopa* complex (Nymphalidae) are sometimes warningly coloured but palatable (Aiello 1984; Chai 1986; Pinheiro 1996), and some of these are particularly agile flyers. *Morpho* butterfly species provide another example; brightly coloured *Morpho* species are virtually uncatchable by predators, whereas cryptically coloured species are much more easily captured (Young 1971; Pinheiro 1996). Aposematism can only operate if predators can learn to associate the unprofitability with the conspicuous colouration. This has frequently been shown with unpalatability (e.g. Gittleman & Harvey 1980; Mappes & Alatalo 1997b), but birds can also learn to avoid conspicuous prey which suddenly disappear (Gibson 1974, 1980).

If hoverflies are advertising their escape ability, they could be Müllerian mimics of each other and thus need a less perfect resemblance to each other than if they were Batesian mimics (e.g. Sheppard 1959; Huheey 1988). According to this argument, Müllerian mimics need less exact resemblance because they only need to remind the predator of previous encounters, rather than trying to deceive it. However, the data of Srygley (1994, 1999) suggest that in fact species within mimicry groups, whether Müllerian or Batesian, converge very closely on each other. Convergence in colour patterns could partly be an advantage in decreasing predator discrimination errors by having a reduced number of colour patterns to remember (MacDougall & Dawkins 1998). It is therefore debatable why there is such a wide range of imperfect wasp mimicry in hoverflies. Several genera do resemble each other quite closely, for example *Syrphus*, *Epistrophe*, *Dasysyrphus*, *Megasyrphus* and *Parasyrphus* spp.

The relationship between flight agility, mimicry, abundance and noxiousness is a complex one. Further study should establish whether the primary force behind the evolution of colour patterns in hoverflies has been mimicry of wasps, or their own protection against predators.

Chapter Seven

Are hoverflies really mimics?: Direct measurement of flight agility using centre-of-body-mass position

7.1 Introduction

Wasp-mimicking hoverflies (Diptera: Syrphidae) present an interesting example of Batesian mimicry because in many cases their mimicry is imperfect. ‘Classic’ Batesian mimicry complexes such as the viceroy, monarch and queen butterflies (Brower 1958a,b, but see Ritland & Brower 1991) show very high-fidelity mimicry. In the hoverflies, a wide range of colour patterns exist, including black flies, honeybee mimics, bumblebee mimics, solitary wasp mimics and social wasp mimics. Of the latter group, a few species (e.g. *Temnostoma* and *Spilomyia* spp.), very rare or absent in the UK, are extremely good mimics of wasps. Most common yellow-and-black hoverflies, however, have only simple yellow bands or lunules on their abdomens (e.g. *Syrphus* spp.), or other patterns not accurately mimicking wasps (e.g. *Episyrphus* spp.).

Mimicry theory predicts perfect mimicry because protection from predators increases with better quality of mimicry (Hetz & Slobodchikoff 1988; Mappes & Alatalo 1997a). However, imperfect mimics are increasingly protected as models become more frequent (Pilecki & O’Donald 1971; Lindström *et al* 1997) and more distasteful or unprofitable (Duncan & Sheppard 1965; Goodale & Sneddon 1977; Lindström *et al* 1997). Though wasps may indeed be particularly

noxious models, the existence of perfect wasp mimics suggests there is an advantage to increasing the perfection of mimicry. Furthermore, many imperfect mimics are very common relative to their wasp models (Owen 1991; Howarth 1998).

Hence there are problems with attributing the yellow-and-black patterns in many hoverfly species solely to Batesian mimicry. Alternative explanations include the possibility that predator perceptions of imperfect mimicry differ from human ones (Dittrich *et al* 1993; Howse & Allen 1994), or that the colour patterns are in a transitional phase towards the evolution of perfect mimicry (Sheppard 1959; Duncan & Sheppard 1965; Alcock 1971). Another possibility is that these hoverflies are aposematic in their own right, advertising either their unpalatability or flight agility to predators. Aposematism (see Mallet & Singer 1987; Guilford & Dawkins 1991) is most commonly thought of as a warning to predators of unpalatability. Several unpalatable chemicals have been identified in brightly-coloured insect species (Brower 1984). Hoverflies, however, are unlikely to be unpalatable (Mostler 1935). Though toxic cardiac glycosides have been found once in the aphidophagous hoverfly *Ischiodon aegyptius* (Malcolm 1976), the results could not be reproduced and the hypothesis that they had been transferred from plants via aphids was falsified (Malcolm 1981, 1992). Moreover, hoverflies form a proportion of the diet of many bird species (McAtee 1932; Krištín 1994; Torp 1994).

Bright colours can also advertise other forms of unprofitability (Rettenmeyer 1970; Baker & Parker 1979), for example escape ability from

predators (Gibson 1980; Mallet & Singer 1987; Srygley 1994,1999; Pinheiro 1996). Such escape ability (through flight agility) is a well-established alternative to unpalatability for escaping bird predators in butterflies (Kammer & Heinrich 1978; Srygley 1994; Srygley & Kingsolver 1998). Hoverflies are expert fliers, with excellent vision, and capable of high acceleration and sudden changes of direction (Ellington 1984; Gilbert 1986). They may therefore be likely candidates for this form of aposematism, which has been identified in two *Morpho* butterfly species (Pinheiro 1996).

This study attempts to clarify the function of the colour patterns of imperfect mimics by directly measuring flight agility and similarity to wasps, and examining the relationship between the two. A strong indicator of flight agility and manoeuvrability is the position of the centre-of-body-mass (CM_{body}) relative to the wing base (Ellington 1984; Srygley & Dudley 1993). This position affects an insect body's speed of response to pitching motions by the wings when a change in direction or speed is desired (Ellington 1984). In effect, when CM_{body} is positioned near the wing base, this speed of response is quicker, and manoeuvrability is therefore increased. This biomechanical hypothesis of Ellington (1984) has been tested using the divergent evolution of neotropical butterflies as a natural experiment (Srygley & Dudley 1993). The position of CM_{body} across 27 genera was correlated with natural flight speeds and ability to evade predators in a small cage, as predicted.

The positioning of CM_{body} near the wing base in butterflies is associated with an 'escape' strategy, in which flight agility is the most important defence

mechanism. This is in contrast to an 'aposematic' strategy, used by unpalatable butterflies which do not require good manoeuvrability and can thus position CM_{body} further from the wing base. This is an advantage to unpalatable butterflies as it saves them the energetic costs of the irregular flight path associated with a centre-of-body-mass close to the wing base (Dudley 1991), and also gives them a longer body shape which predators may then associate with unpalatability (Chai 1996). Their smoother flight path also increases the conspicuous effect of their colouration, decreasing the chance of mistaken attack (Turner 1984b; Guilford 1986; Chai & Srygley 1990).

Batesian mimics of unpalatable species will improve their mimicry if they mimic the coloration, flight path and body shape of their models. Therefore CM_{body} in Batesian mimics could be expected to be positioned far from the wing base, as in aposematic species. If mimicry is effective, predation pressure is reduced, decreasing the need for agile flight and again leading to a flight morphology similar to that of unpalatable species. However, selection may also favour retaining features that contribute to evasive flight, since, unlike truly unpalatable species, Batesian mimics will not be released if captured by predators. Hence it is difficult for a good Batesian mimic with the flight pattern of the model to evolve (Srygley & Chai 1990a; Srygley 1994; Chai 1996), and there are very few butterflies which have evolved a long abdomen without unpalatability (Chai 1996).

An example of a Batesian mimic which does not fully mimic its unpalatable models in terms of flight morphology is the neotropical butterfly

Consul fabius, a palatable mimic. This species has CM_{body} near the wing base like other palatable species, retaining manoeuvrability, but positions its centre-of-wing-mass (CM_{wing}) near to that of its models (further from the wing base), which is associated with poorer flight performance (Srygley 1994). This suggests that it has retained aspects of evasive flight over its models (though a change in CM_{body} position could follow later in its evolution) (Srygley 1994).

Müllerian mimics, on the other hand, reinforce each other's message by converging in colour patterns, abdomen shape and unpalatability. There is evidence that the positions of CM_{body} and CM_{wing} converge strongly within Müllerian mimicry complexes, independent of phylogenetic effects (Srygley 1994, 1999; Pinheiro 1996), leading to close mimicry of flight patterns as well as colour patterns (in contrast to the traditional view that Batesian mimics will evolve to appear more similar to their models than Müllerian mimics do).

This strong association of positions of CM_{body} and CM_{wing} within mimicry groups is not only found among unpalatable species (Srygley 1994, 1999; Pinheiro 1996). Two mimetic butterfly groups, the *Adelpha-Doxocopa* complex (Aiello 1984) and a green-and-black pattern group, are usually considered to contain Batesian mimics. No evidence has been found of any unpalatable models in these groups (Pinheiro 1996), but some species in both complexes exhibit a good ability to escape predators. If predators avoid these unprofitable species (as they do unpalatable species), their mimicry of each other could be purely for escape ability (what Srygley (1994) calls 'locomotor' mimicry).

If CM_{body} position can be measured in hoverflies, therefore, it could act as a surrogate for differences among species in flight agility, allowing a test of hypotheses about the function of the colour patterns of 'imperfect mimics'. Different patterns are predicted if these are mimics of wasps or if they are advertising their own flight agility (summarised in Figure 7.1 and Table 7.1). If they are Batesian mimics of wasps, they will experience reduced predation pressure, and thus be able to reduce their costly investment in flight agility. Their subsequent flight morphology would also be advantageous because it mimics that of unprofitable models, which have no need for agile flight. On the other hand, as discussed above, some mimics have retained features of palatable species that improve flight agility when detected by predators. Since hoverflies vary in their similarity to wasps, those species which most resemble wasps are predicted to

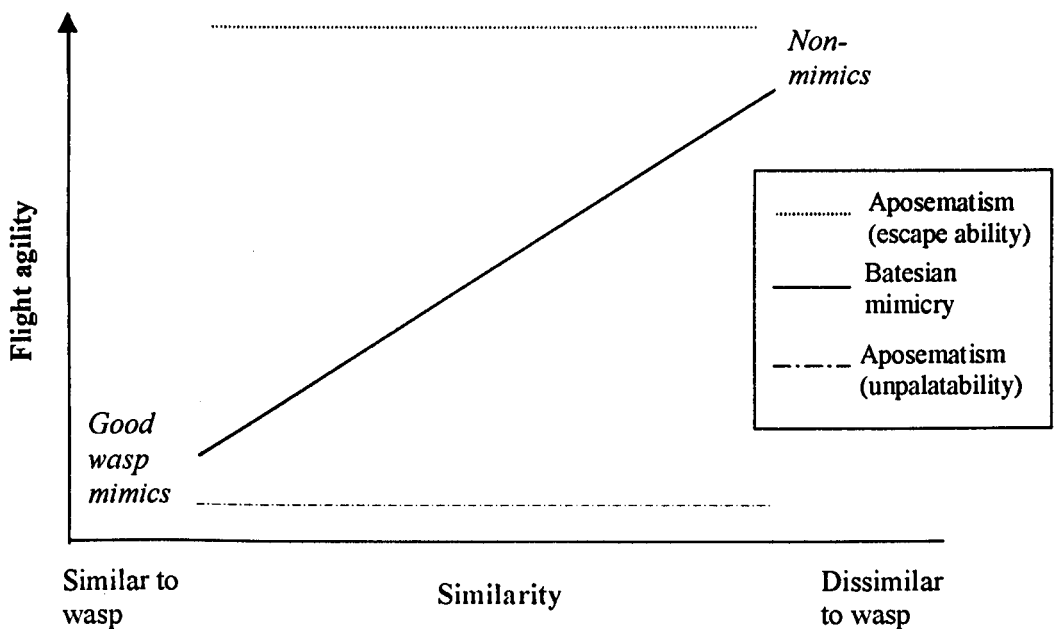


Figure 7.1. Predicted associations in 'imperfect wasp mimics' between similarity to wasps and flight agility under different hypotheses for their colour patterns.

have least need of retaining these features. The greater the similarity, the more ‘unpalatable’ features are likely to be retained (Figure 7.1). Hence the prediction is that increasing similarity to wasps is associated with decreasing flight agility (and thus CM_{body} further from the wing base).

If, in contrast, ‘imperfect mimics’ are aposematic, different flight morphologies are expected. Since in this case there is no mimetic relationship, no association is expected between decreasing flight agility and similarity to wasps among ‘imperfect mimics’. However, there could still be a contrast between ‘good mimics’ and ‘imperfect mimics’. There is little doubt that good mimics, such as *Temnostoma* spp., are mimicking wasps. If ‘imperfect mimics’ are aposematic for unprofitability via escape ability, the prediction is that greater

	Role of colour patterns in ‘imperfect’ mimics		
	<i>Mimicry</i>	<i>Aposematism (unpalatability)</i>	<i>Aposematism (escape ability)</i>
<i>Similarity/ flight agility relationship (excluding good mimics)</i>	Increasing similarity to model associated with decreasing flight agility	No relationship	No relationship
<i>Good mimics vs. imperfect mimics</i>	‘Imperfect mimics’ have better flight agility	Similar to each other	‘Imperfect mimics’ have better flight agility
<i>[‘Imperfect mimics vs. non mimics (not used in this study)]</i>	[Non-mimics have better flight agility]	[Non-mimics have better flight agility]	[‘Imperfect mimics’ have same or better flight agility]

Table 7.1. Predictions of relationships between similarity to wasps and flight agility. See text for details.

flight agility (and hence CM_{body} nearer the wing base) will be seen in imperfect wasp mimics than in good wasp mimics. In the unlikely case that ‘imperfect mimics’ are unpalatable, and are advertising this in the same way as butterflies, they are predicted to have CM_{body} placed similarly to good mimics, since both would be using ‘aposematism’ rather than ‘escape’ as their primary defence mechanism.

If hoverflies are aposematic, whichever type of unprofitability they are advertising, hoverfly species should be Müllerian mimics of each other, and strong convergence is predicted within mimicry groups for CM_{body} position and other features of flight morphology, as in neotropical butterflies (Srygley 1994, 1999). A trade-off between reproductive potential and flight agility is also predicted, as this has been recorded among species in several species of insect (e.g. Kaitala 1991), including neotropical butterflies (Marden & Chai 1991).

7.2 Methods

The role of flight agility in the evolution of hoverfly colour patterns was examined by comparing the position of the centre-of-body-mass with similarity to a wasp model between species, taking the phylogeny of the hoverflies into account.

7.2.1 Measuring centre of body mass position

Hoverflies were captured in the UK and the Russian Far East. The position of CM_{body} was measured on freshly captured hoverflies, killed immediately prior to measurement to minimise water loss and thus possible weight changes. The position of the centre-of-body-mass was then measured using the 'compound pendulum technique' (Ellington 1984; C.Ellington, pers. comm.). The wings were removed with a scalpel, and the body mounted on a pin through the thorax, entering and leaving the body through the wing bases. The pin was then balanced on two horizontal metal bars (Figure 7.2) and two photographs were taken from the side, perpendicular to the pin. A weighted black thread hung from the bars to indicate the angle the hoverfly hung at relative to the vertical. After taking the photograph, the pin was placed elsewhere on the hoverfly's body, taking care that it was perpendicular to the body, and parallel to the pin's previous position through the wing bases. This second position was usually also through the thorax, since this is a solid part of the body packed with muscle, and insertion does not distort the body shape. Again, the hoverfly was placed on the apparatus, but it hung at a different angle due to the different position of the pin. Two photographs were again taken from the side, parallel to the direction of the pin.

When developed, the clearest photograph of the body at each angle was scanned into a PC, and the images were manipulated using Adobe Photoshop, CorelDraw and CorelPhotoPaint. Background images were removed, such that only the outer edge of the body, the pin position, and the thread were visible. The thread image was then shifted laterally to coincide with the pin position, hence

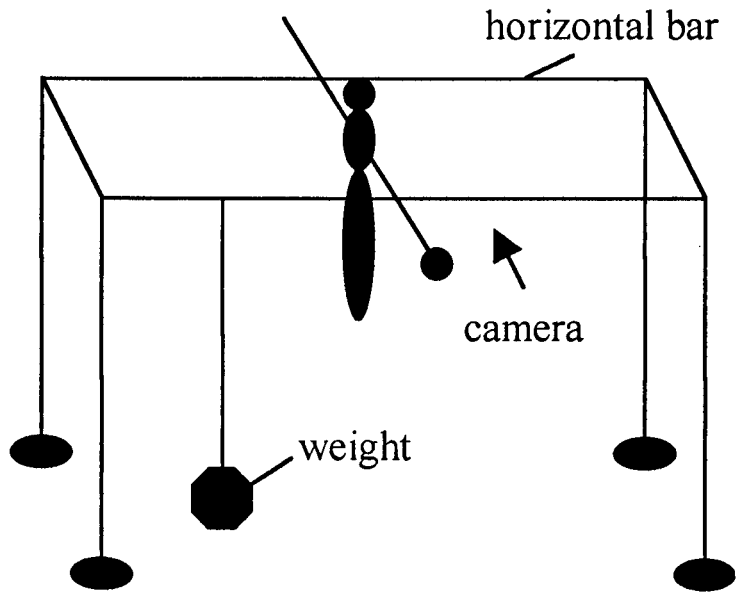


Figure 7.2. The compound pendulum technique for measuring position of CM_{body} . An entomological pin is stuck through the hoverfly in two different positions and the angle of the body relative to the vertical thread is recorded photographically parallel to the pin.

representing the position of the body relative to the vertical. The two images of each hoverfly were superimposed, and the point at which the two lines crossed is the position of the centre-of-body-mass (Ellington, pers. comm.). Its position from the head down the body was measured as a percentage of body length, and compared to the position of the wing base. CM_{body} positions were measured as:

CM_{body} position - wing base position.

7.2.2 Measuring similarity

Model-mimic similarity was measured using the method of Dittrich *et al* (1993). This directly compares two images pixel by pixel by measuring the

distance apart of each pair of corresponding pixels in Red-Green-Blue colour space (for details, see Dittrich *et al* 1993; Azmeh *et al* 1998). Pigeons have been shown to largely agree with the relative assessments of similarity generated by this method (Dittrich *et al* 1993; Green *et al* 1999). One difference from the method of Dittrich *et al* (1993) was introduced; any tergite which was entirely black was allocated a similarity value of zero. This avoided the situation where black species were given relatively high similarity values because of overlap with the black on the wasp's body.

The bitmaps compared by the similarity program are of equal size. To consider size differences between species the resulting similarity values were scaled by each species' size in relation to the model. *Vespula vulgaris* was used as the model, as it is the most ubiquitous social wasp in the UK, including at sites where hoverflies are abundant (Owen 1991).

Similarity values were not calculated for every species separately, but for colour-pattern groups. A group consisted of species whose abdominal patterns were identical or almost so, usually a genus or part of a genus. A similarity value was calculated for one species in the group and used for all species in the group. *Temnostoma*, *Xanthogramma* and *Chrysotoxum* spp were considered good mimics, and the remainder imperfect. This split between the similarity values was made subjectively, as *Temnostoma*, *Xanthogramma* and *Chrysotoxum* seem obvious mimics, with good mimicry of the abdominal patterns, antennae and shape of wasps, whereas there is ambiguity in the patterns of other hoverflies.

7.2.3 Comparative method

Comparative methods were used based on the logic of Felsenstein (1985), and implemented using CAIC (Comparative analysis by independent contrasts, Purvis & Rambaut 1995). Taxa in a branching phylogeny can not be considered independent points for purposes of statistical analysis (e.g. Harvey & Pagel 1991, Martins & Hansen 1996). Differences between taxa may be over-estimated if they are considered independent points, because traits might be shared by taxa due to common evolutionary descent, not independent evolution (Harvey & Pagel 1991, but see Ricklefs 1996). Thus computer simulations have shown that CAIC is a more valid method of comparing taxa than using species means, even where the phylogeny is poorly resolved or branch lengths are incorrect (Purvis & Rambaut 1995). Furthermore, simulations show that it is at least as valid as phylogenetic autocorrelation methods (Gittleman & Kot 1990), and a more powerful test provided the phylogeny is at least fairly resolved.

Independent comparisons methods remove the effect of phylogenetic relationships by specifying a set of independent contrasts between pairs of species or other taxa (Felsenstein 1985). Each contrast is standardised by scaling by its expected standard deviation. These standardised contrasts are then independent and normally distributed, and standard statistical analyses can be performed upon them.

7.2.4 Phylogeny

A genus-level phylogeny of the syrphids (Figure 7.3) was used (Rotheray & Gilbert 1999), based upon 187 larval morphological characters. The phylogeny consists of 85 genera, nearly all those in the Holarctic. It is completely independent of the adult characters used in this study, because it uses larval data. The branch lengths for the phylogeny are unknown, and therefore equal branch lengths were used, despite this assuming a strictly punctuational view of evolution (see e.g. Harvey & Pagel 1991). Computer simulations show that using inaccurate branch lengths still gives reasonably accurate results (Purvis *et al* 1994).

The data were considered at the species level even though the phylogeny is only generic; therefore all species within a genus simply branch from the same node (a 'soft' polytomy). This is taken into account by CAIC using the logic of Pagel (1992); the true phylogeny is assumed to be bifurcating, and the daughter taxa at a multiple node are arranged as such according to the closeness of their values of the independent variable.

7.2.5 Statistical analysis

Standardised contrasts were calculated for CM_{body} position (expressed as a proportion of body size) and similarity values. All data were log-transformed before calculating contrasts to ensure that the data conformed to Felsenstein's model of evolution of characters as a Brownian motion process, and that contrasts were thus suitable for regression analyses (Felsenstein 1981; Purvis & Rambaut 1995). To examine the relationship between CM_{body} position and similarity,



Figure 7.1. Genus-level phylogeny of the hoverflies, based on 187 morphological larval characters.

CM_{body} contrasts were regressed on similarity contrasts through the origin. The resulting slopes give the true relation between the variables in the absence of phylogenetic effects (Pagel 1993).

The relationship between CM_{body} position, batch size and testis length was also examined, to test for the presence of a trade-off between flight agility and reproductive potential. Clutch size and testis length measures were from a morphological dataset derived from fieldwork in the USA (Arizona, Oregon and Maine), Britain, Poland (Bialowieza forest), and the Russian Far East (for details, see Gilbert 1981, 1985, 1990; Gilbert *et al* 1994). Sample sizes of contrasts were too small for analysis ($n=3$ for testis length, $n=2$ for batch size), so logarithms of raw means were compared, not taking the phylogeny into account, though this is a less valid test than using the phylogeny (Harvey & Pagel 1991; Purvis & Rambaut 1995). Where reproductive data were not available for the correct species for which CM_{body} was determined, the mean value of other species in the genus was used, where available.

The effects of body size on testis and batch size were removed before comparison with flight agility, since there are allometric relationships between reproductive characters and body size [chapter 3]. This was done by regressing the reproductive traits on thorax volume. The residuals of these regressions were then regressed on CM_{body} position contrasts.

7.3 Results

Photographs were taken of 110 individual hoverflies. Of these, only 55 produced usable measures of the centre-of-body-mass position because of experimental errors, such as the camera not being perpendicular to the fly, or the two lines not crossing. The CM_{body} positions recorded are shown in Table 7.2.

Analysis of independent contrasts produced 11 contrasts from these 14 taxa. Analysis of imperfect mimics alone produced 7 contrasts from 9 species. A

	Position of CM_{body} (Mean \pm standard error)	Similarity value	Sample size for CM_{body} position
<i>Epistrophe diaphana</i>	0.2	43.8	1
<i>Episyrphus balteatus</i>	0.4 \pm 2.7	35.3	13
<i>Syrphus ribesii</i>	2.4 \pm 2.7	57.3	11
<i>Temnostoma bombylans</i>	4.2 \pm 4.4	79.9	3
<i>Helophilus pendulus</i>	6.2 \pm 1.7	57.8	5
<i>Temnostoma apiforme</i>	5.5 \pm 2.8	71.8	3
<i>Eupeodes luniger</i>	6.8 \pm 2.4	31.8	4
<i>Myathropa florea</i>	7.2 \pm 4.6	49.9	6
<i>Temnostoma vespiforme</i>	8.4 \pm 1.6	82.0	3
<i>Dasysyrphus venustus</i>	8.9	35.3	1
<i>Epistrophe melanostoma</i>	9.7	41.2	1
<i>Xanthogramma pedisiquium</i>	10.3 \pm 6.4	49.7	2
<i>Eupeodes nitens</i>	12.0	40.9	1
<i>Chrysotoxum arcuatum</i>	14.4	69.7	1

Table 7.2. Position of centre-of-body-mass (CM_{body}) relative to wing base position (percentage of body length) and similarity to wasp model. Species are in order of supposed flight agility (based on CM_{body} position).

regression of CM_{body} contrasts on similarity contrasts through the origin showed no relationship between them (Figure 7.4; $F_{1,10}=0.24$, $r^2=0.02$, $p=0.635$). There was also no relationship between ‘imperfect mimics’ alone, using independent contrasts (Figure 7.5; $F_{1,6}=0.04$, $r^2=0.01$, $p=0.847$.) Removing the outlier ‘a’ (the contrasts between two *Epistrophe* species; possibly spurious since $n=1$ for these species) in Figure 7.4 and Figure 7.5 results in an even weaker relationship in both cases. Among log-transformed means (not contrasts) of ‘imperfect mimics’, there was again no pattern (Figure 7.6; $F_{1,7}=0.00$, $r^2=0.00$, $p=0.985$).

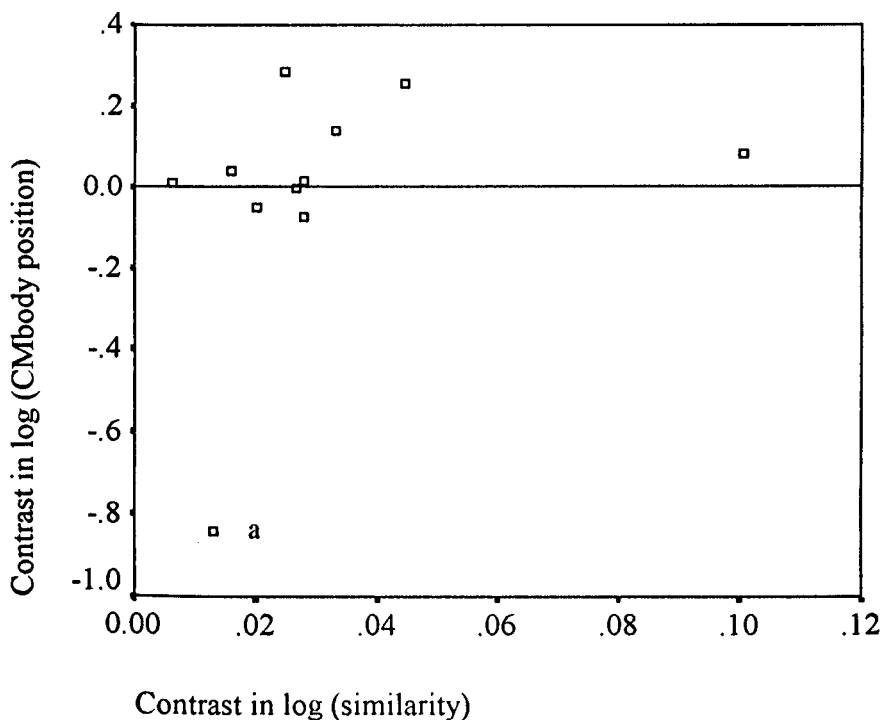


Figure 7.4. Similarity to a wasp model plotted against CM_{body} position (% of body length). All points are standardised independent contrasts between all fourteen species.

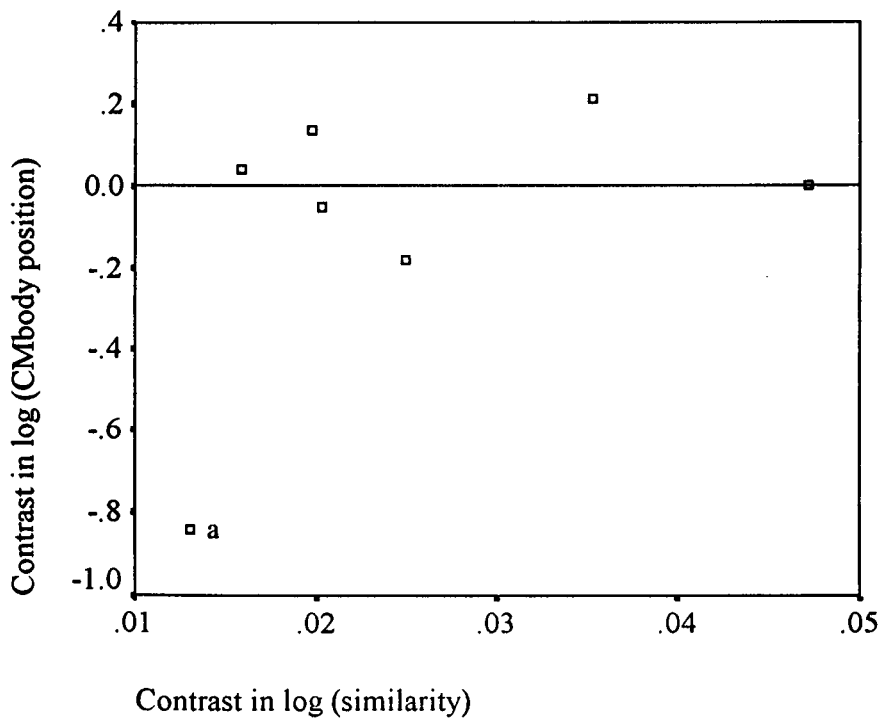


Figure 7.5. Similarity to a wasp model and position of CM_{body} in ‘imperfect wasp mimic’ species only. All points are standardised independent contrasts.

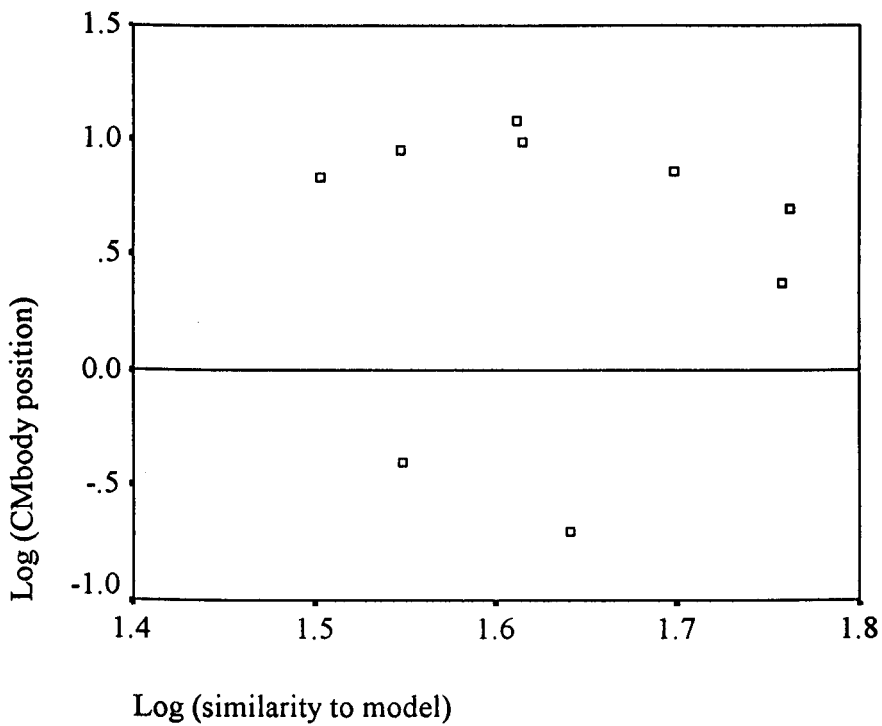


Figure 7.6. Phylogeny-free among-species relationship between similarity to the model and CM_{body} position relative to wing base (both log-transformed) in imperfect mimics.

The position of CM_{body} of good mimics (*Temnostoma*, *Chrysotoxum* and *Xanthogramma* spp.) was compared with that of 'imperfect mimics'. A one-way analysis of variance of species means (numbers of contrasts were too small for analysis) showed no difference between the two groups ($F_{1,12}=1.26$, $p=0.283$), though on average CM_{body} of good mimics (mean position= 8.6 ± 1.8 , $n=5$ species) was further from the wing base than in 'imperfect mimics' (mean= 6.0 ± 1.4 , $n=9$ species) (Figure 7.7).

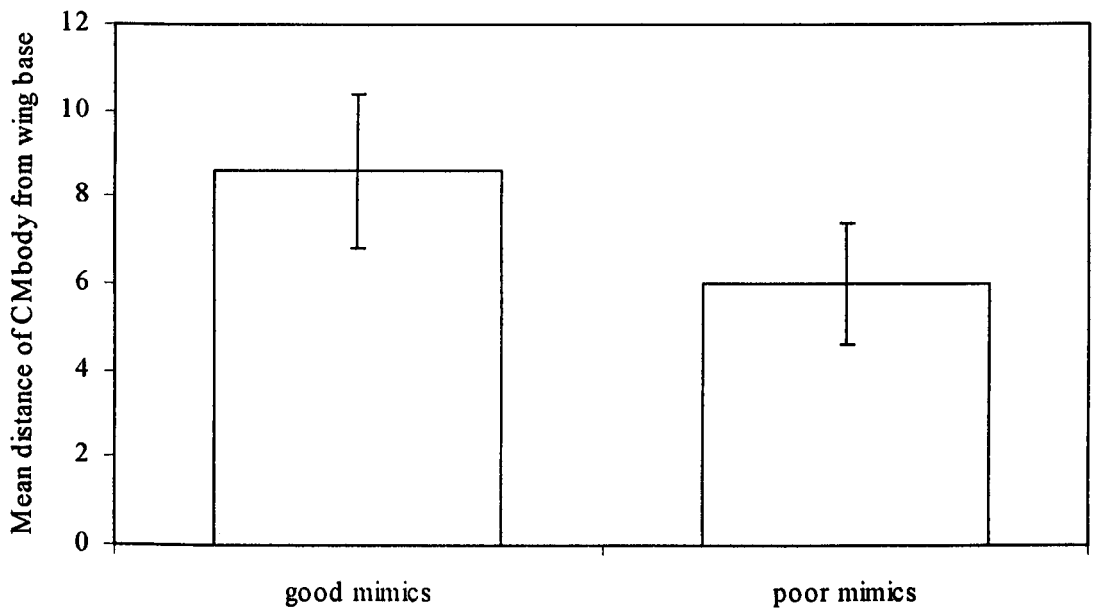


Figure 7.7. Mean and standard error of centre-of-body-mass distance posterior of wing bases. Good mimics $N=5$ species, 'imperfect mimics' $N=9$ species.

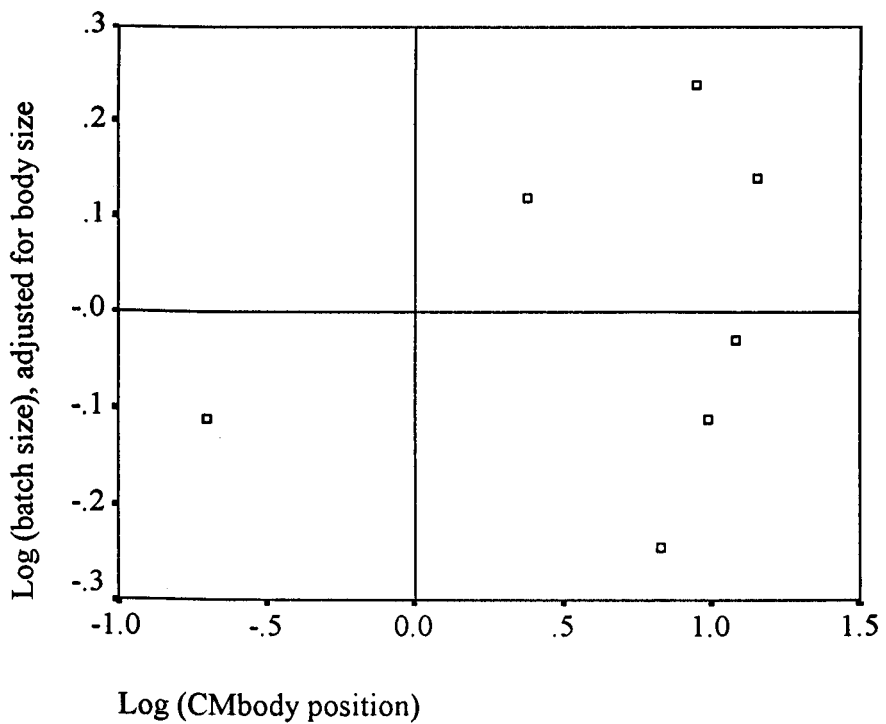
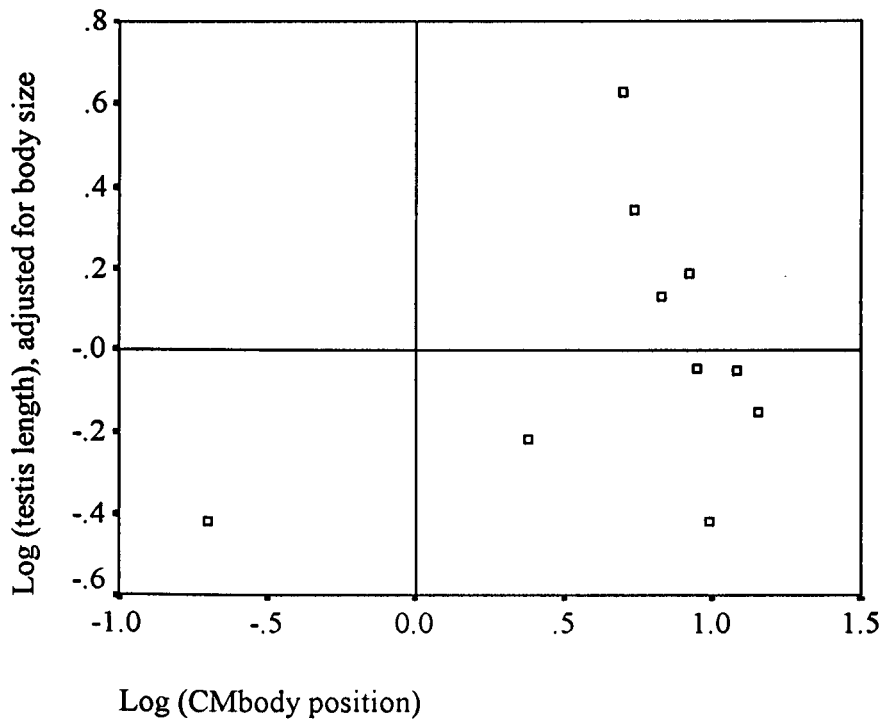


Figure 7.8. Log (centre-of-body-mass position) among species, related to (a) testis length in males and (b) batch size in females. Reproductive data were adjusted for body size by regressing against log (thorax volume) and using the residuals.

Testis length and batch size were both adjusted for body size by regressing them against thorax volume, and using the residuals of these regressions to regress against CM_{body} position (all log-transformed) (Figure 7.8a and 7.8b).

There was no significant relationship between reproductive potential and CM_{body} position, either for males ($F_{1,8}=0.89$, $r^2=0.10$, $p=0.374$) or females ($F_{1,5}=0.33$, $r^2=0.06$, $p=0.593$).

7.4 Discussion

In this study, a new approach to studying mimicry was explored by measuring the position of the centre-of-body-mass relative to the wing base. Smaller distance between the two enables better manoeuvrability, and hence better ability to escape from predators (Ellington 1984; Srygley & Dudley 1993). CM_{body} positions were measured for 15 species of hoverfly, with varying degrees of similarity to a wasp model, though all had yellow-and-black patterns.

The overall range of CM_{body} measurements concurs with the assumption that all hoverflies are relatively good fliers relative to other insects. In a study of neotropical butterflies, CM_{body} was positioned 0.10 of body length away from the wing base in the best fliers, and 0.356 in the worst (Dudley & Srygley 1993), whereas in this study of hoverflies the furthest CM_{body} position was 0.14 from the wing base.

The lack of any evidence of a relationship between CM_{body} contrasts and similarity contrasts in hoverflies, excluding obviously good mimics, suggests that

'imperfect mimics' are not Batesian mimics, since the evolution of better similarity was not linked with that of poorer flight agility (Table 7.1). The lack of such a pattern means increasing similarity (and hence probable quality of mimicry; Dittrich *et al* 1993) has not resulted in lower flight agility evolving through a lower attack rate by predators. The phylogeny-free log-transformed means also show no pattern (though this is likely to be a less valid test than using independent contrasts (Purvis & Rambaut 1995)). However, the lack of association is consistent with an alternative hypothesis, namely that the colour patterns in 'imperfect mimics' are in fact aposematic.

Separating the species into good and imperfect mimics showed that good mimics did position CM_{body} further away from the wing base than poorer mimics, though this difference was not significant. This is consistent with either a mimetic or an aposematic (for escape ability) function to the colour patterns of 'imperfect mimics' (Table 7.1). However, in combination with the lack of association between flight agility and similarity, this points towards an aposematic explanation (Table 7.1). Good manoeuvrability in 'imperfect mimics' could have evolved before their colour patterns, which could thus be a form of aposematism for escape ability (Gibson 1979; Srygley 1994). Advertisement of unpalatability also predicted no relationship between similarity and flight agility, but if 'imperfect mimics' have better flight agility than good mimics this is not supported, in accordance with the assumption that hoverflies are palatable (see introduction).

Unlike in butterflies (Srygley 1994, 1999), no particular convergence of positioning was seen within mimicry groups. For example, *Epistrophe*, *Eupeodes* and *Syrphus* species are broadly similar in appearance, but their positions of CM_{body} varied widely (Table 7.2). These species do differ in appearance, and perhaps should not be considered members of a mimetic group in the same way as butterflies (Srygley 1999). However, even *Temnostoma apiforme* and *T. vespiforme*, which resemble each other closely, were not similar in their positioning of CM_{body} (Table 7.2).

Ellington (1984) measured CM_{body} position of the hoverflies *Episyrphus balteatus* and *Eristalis tenax* using a graphical method. CM_{body} of these species was positioned significantly nearer the wing base than other flying insects measured, including Hymenoptera, Lepidoptera and other species of Diptera, indicating the superior agility of hoverflies compared to many other insect species. However, the difference between the two hoverfly species was small in comparison. It was these small differences that this study attempted to measure, but the high standard errors of the measurements indicate that the compound pendulum technique may not be precise enough to pick up these differences. For example, very small shifts in thread position when manipulating the image can lead to large differences in where the two lines cross and hence the calculated position. Therefore none of these conclusions can be considered definitive. The problem inherent in the method applied among hoverfly species is that they do not have great variety in body form, unlike butterfly species. This seems to have resulted in a smaller overall range of positions of CM_{body} than in butterflies. The

mean position of CM_{body} of the 15 species tested here ranged from 0.002-0.14 of body length (a difference of 0.138 of body length), whereas in 36 neotropical butterfly species (Dudley & Srygley 1993) the range was from 0.100-0.356 (a difference of 0.256).

Other methods of measuring flight agility include looking at the ratio of thoracic to abdominal mass (Marden & Chai 1991), though CM_{body} position proved a better predictor of escape tactics. Relative thoracic mass is easier to measure and may be a useful future direction. Comparison of the flight agility of non-mimics and mimics (Table 7.1) would also provide the opportunity of testing these hypotheses further.

Observation of hoverflies suggests that very good mimics like *Temnostoma* do fly more slowly and 'lazily' than poorer mimics. Although the capacity for flight agility may be retained, the flight pattern is used to mimic that of wasps and there may in fact be a low potential for manoeuvrability. Further measurements on these rare excellent mimics are needed to make the useful contrast with poorer mimics.

No trade-off was seen between flight agility and reproductive potential, unlike among butterflies (Srygley & Chai 1990a; Marden & Chai 1991) and other insects (Denno *et al* 1989; Groeters & Dingle 1989). Larger sample sizes and more consistency in the measurement of flight agility is needed before this can be confirmed.

Conclusions

As the review of mimicry research at the start of this thesis made clear, studies of Batesian mimicry in insects have historically been dominated by theoretical and laboratory studies because of the difficulties inherent in carrying out controlled practical work in the field. These have provided numerous valuable insights regarding the factors which influence the success of mimicry as a protection mechanism. However, most mathematical models remain untested, and laboratory studies where one type of predator is used, and one or two factors varied, are often difficult to apply to dynamic real life systems.

This thesis used new approaches to the study of mimicry, concentrating on the apparent paradox of abundance of imperfect mimics among wasp-mimicking hoverflies. I took advantage of the variety of mimetic patterns in this system to develop the image-comparison techniques devised by D.Grewcock and F.Gilbert, using the results to look at morphological patterns across many hoverfly taxa. Comparative studies like these are a new approach to the study of mimicry in hoverflies, inspired by studies of flight morphology, palatability and colour patterns in butterflies by R.Srygley, P.Chai, and others. The examination of long-term fluctuations in mimic and model numbers in one location was another novel approach, as was the attempted direct measurement of flight agility.

Many possible hypotheses exist for why wasp mimicry is imperfect in many hoverflies, and why imperfect mimics are so common relative to their models (Table 2), and this thesis has only been able to explore a few of these. It

has touched on the role of habitat disturbance in abundance of mimics, and the potential role of aposematism in the evolution of colour patterns. It also includes insights on alternative prey, the potential significance of wasp predation, the seasonality of models and mimics, and the probable selection pressures on reproductive characters in hoverflies, especially testis/ sperm characters in males.

In Chapter Two, the case of a suburban garden ecosystem in Leicester was examined in detail. The seasonal asynchrony between wasps and their imperfect mimics was confirmed, and possible reasons discussed. A high ratio of imperfect wasp mimics to their models was also found, particularly in July and August. In good wasp mimics, honeybee and bumblebee mimics, both synchrony and abundance were more in line with the expectations of Batesian mimics. Analysis of 23 years' worth of data showed no evidence of the influence of wasp abundance on numbers of imperfect mimics among years, contrasting with the effects of models numbers on good wasp mimic and bumblebee mimic abundance. The among-year comparisons also highlighted the role of wasps as potential major predators of non-mimetic and imperfectly mimetic hoverflies. Overall, the constraints expected on Batesian mimics if they are to be effectively protected by their colour patterns were much less evident in imperfect mimics than other mimics.

This ecosystem existed in a habitat that was highly influenced by human activity, and hence may not be applicable to hoverflies in general. Both the influence of predators on mimic numbers, and relative abundance of the insects themselves, may be distorted by the fact that conditions in this garden were very

different to those in which the colour patterns of hoverflies evolved. Chapter Five used part of the same dataset, taking advantage of the fact that the habitat is highly disturbed, to compare relative hoverfly abundances to those in less disturbed habitats. Substantial evidence was found for the influence of habitat disturbance on the relative abundance of hoverfly taxa, highly skewed in favour of poor mimics in disturbed habitats. This is a major contribution to the understanding of the paradox of poor wasp mimic abundance, and also has implications for the study of mimicry generally. Most habitat disturbance is recent in evolutionary time, so mimetic patterns in non-pristine areas may currently be in the process of changing in response to the resultant changes in selection pressures.

Chapter Five made use of image analysis techniques to rate hoverflies' similarity to wasps in an objective manner. These tools have now been refined and their mode of use validated and shown to be robust (Chapter Four), and potentially could be used for many further studies. In this thesis, as well as producing mimicry profiles, the image analysis programs were used to examine the other aspect of the paradox of imperfect mimicry in hoverflies, namely why mimicry of wasps is imperfect in so many species. Chapter Six tested several hypotheses, drawing on a large morphological dataset which was of interest in itself (Chapter Three). It revealed a huge amount of variation in reproductive characters among hoverfly species, in both males and females. In particular, the evolution of testis (and hence sperm) characters in males has not simply mirrored that of body size, compared to morphological characters such as tongue length. Of especial note were the huge testes present in some hoverfly species, leading to

speculation that these may have evolved sperm gigantism in a manner analogous to some *Drosophila* spp. Hence there may be a great deal of variation in mechanisms of dealing with sperm competition among hoverfly species, a topic hardly mentioned in the literature so far. The importance of taking the phylogeny into account when making comparisons among taxa was also stressed.

Reproductive morphology was again compared among hoverfly species in Chapter Six, on the premise that reproductive potential trades-off with flight agility. A variety of predictions were made about the relationship between flight agility and similarity to wasps under different evolutionary scenarios. The evolutionary associations predicted among species if the colour patterns have evolved through mimicry of wasps were not supported in females, and only weakly in males. The predictions made if the colour patterns co-evolved in association with flight agility, however, were supported (though the use of independent contrasts meant sample sizes were small). This raised the intriguing possibility that hoverflies may be advertising their own flight agility to predators, and may therefore be Müllerian mimics of each other.

In Chapter Seven, I tried to confirm these patterns by measuring flight agility directly, using the positioning of the centre-of-body-mass as an indicator of manoeuvrability. Definite conclusions could not be drawn because it was difficult to pick up the small differences between hoverfly species in body shape. However, within the limitations of this technique, the data did not support the predictions made if the colour patterns evolved through Batesian mimicry of wasps, and there was again some support for an aposematic role to the colour

patterns. The advertisement of flight agility is without doubt a subject worthy of further study, possibly using different techniques of measuring flight agility.

The questions ‘Why are wasp-mimicking hoverfly patterns imperfect?’ and ‘Are wasp-mimicking hoverflies really mimics?’ remain unanswered, since many hypotheses not examined in this thesis still remain to be investigated (Table 2). If, as the results presented here may imply, wasp-mimicking hoverflies are advertising their own unprofitability to predators, this does not preclude the possibility that their passing resemblance to wasps is also an advantage in defence against predators, or indeed that other factors have played a part in their evolution. The labelling of this system as ‘Batesian mimicry’ is a natural consequence of wishing to comprehend a very visible and well-known phenomenon in simple terms. Indeed, most undergraduate textbooks and teaching present Batesian mimicry generally as a well-understood paradigm of evolution by natural selection. The wasp-mimicking hoverflies are a particularly poorly understood system within mimicry, being somewhat unusual in their high level of variation in quality of mimicry. However, it is now doubtful that even ‘classic’ Batesian mimicry complexes (e.g. the queen-vice-roy-monarch complex) follow the ‘rules’ that Bates and Fisher thought shaped the dynamics of Batesian mimics (see Chapter One). The disparate selection pressures influencing the evolution of mimetic colour patterns in insects are likely to be much more complex than once thought.

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Appendix 1

Measurements of morphological characters

This appendix gives the raw means and standard errors for data on tongue length, ovariole number, egg volume, thorax volume, testis length and testis volume for 222 hoverfly species. The data are used in Chapters Three, Six and Seven. Details of how the characters were measured are given on pp. 127-128.

Appendix 1. Mean and standard error (s.e.) of measures of morphological characters in hoverfly species. n =sample size

Species	Tongue length		Ovariole number		Egg volume		Thorax volume		Testis length		Testis volume	
	Mean	± s.e.	Mean	± s.e.	Mean	± s.e.	Mean	± s.e.	Mean	± s.e.	Mean	± s.e.
<i>Allograpta micrura</i>	3.49	± 0.11	3	25 ± 2.38	4	0.06 ± 0.05	2	7.73 ± 0.64	4	0	0	0
<i>Anasimyia bilinearis</i>	4.16	± 0.11	2	35	1	0.12	1	20.95 ± 1.32	2	5.88	1	0.50
<i>A. lunulata</i>	4.48	± 0.19	6		0		0	18.96 ± 2.48	6	3.08 ± 0.35	4	0
<i>Arctophila harveyi</i>	5.72	± 0.18	2		0		0	79.00 ± 8.71	2	1.18 ± 0.13	2	0.27 ± 0.02
<i>Asemosyrphus mexicanus</i>	6.27		1		0	0.08	1	42.85	1	0	0	0
<i>A. polygrammus</i>	5.61	± 0.14	4	100 ± 3	2		0	41.78 ± 3.51	4	1.66	1	0.56
<i>Baccha elongata</i>	1.75	± 0.05	2		0		0	4.07 ± 1.29	2	0.44	1	0.01
<i>Betasyrphus nipponicus</i>	2.52		1	39	1	0.06	1	25.46	1	0	0	0
<i>Blera analis</i>	3.94	± 0.14	2		0		0	45.34 ± 6.08	2	4.80 ± 0.18	2	1.06 ± 0.29
<i>B. armillata</i>	4.40	± 0.09	3	46 ± 21	2	0.06 ± 0.01	2	46.06 ± 1.71	3	3.30	1	0.84
<i>B. badia</i>	3.63	± 0.29	2		0		0	35.84 ± 12.23	2	3.13 ± 0.22	2	0.68 ± 0.29
<i>B. confusa</i>	4.24	± 0.05	2	140	1		0	35.66 ± 0.07	2	3.18	1	0.66
<i>B. flukei</i>	4.75	± 0.08	3		0		0	56.21 ± 2.26	3	4.22 ± 0.22	3	0.81 ± 0.11
<i>B. humeralis</i>	3.85	± 0.11	6	85 ± 7	2		0	60.22 ± 1.88	6	10.50 ± 0.58	3	1.93 ± 0.16
<i>B. nigra</i>	2.82	± 0.13	2		0		0	15.44 ± 3.39	2	2.33 ± 0.01	2	0.18 ± 0
<i>B. scitula</i>	4.43	± 0.13	6	110.5 ± 29.5	2	0.11	1	62.76 ± 5.86	6	7.50 ± 0.58	3	1.49 ± 0.06
<i>B. umbratilis</i>	4.80		1		0		0	70.82	1	4.10	1	0.45
<i>Brachyopa dorsata</i>	2.81		1		0		0	24.21	1	1.59	1	0.28
<i>B. media</i>	4.30		1		0		0	43.90	1	3.40	1	0.54
<i>B. perplexa</i>	3.98	± 0.20	3		0		0	42.25 ± 2.65	3	2.90 ± 0.11	3	0.46 ± 0.04
<i>B. pivanica</i>	2.52		1	20	1	0.07	1	11.79	1	0	0	0
<i>Brachypalpus femorata</i>	6.18	± 0.10	5	150 ± 13.1	3	0.06 ± 0.01	3	94.12 ± 5.55	6	5.08 ± 0.08	2	0.93 ± 0.28
<i>B. oarus</i>	3.65		1		0		0	48.69	1	3.06	1	0.27
<i>Callicera aenea</i>	3.6	± 0.13	3	45	1	0.24	1	90.50 ± 4.93	3	0.70 ± 0.03	2	0.08 ± 0.00
<i>Ceriana conopsoidea</i>	3.12		1	53	1		0	24.28	1		0	
<i>Chalcosyrphus anthreas</i>	2.64		1		0		0	26.47	1	2.84	1	0.42
<i>C. curvaria</i>	3.18		1		0		0	43.65	1	3.69	1	0.54

Appendix 1 (continued)

Species	Tongue length		Ovariole number		Egg volume		Thorax volume		Testis length		Testis volume	
	Mean	± s.e.	n	Mean	± s.e.	n	Mean	± s.e.	n	Mean	± s.e.	n
<i>Chalcosyrphus flexus</i>	2.37		1	97		0	12.65		1			0
<i>C. interruptus</i>	2.29 ± 0.16		5	98 ± 15		0	16.92 ± 3.93		5	2.84 ± 0.57		3
<i>C. libo</i>	2.76 ± 0.08		2			0	30.88 ± 0.47		2	2.16		1
<i>C. nemorum</i>	2.57		1			0	19.00		1	2.40		1
<i>C. nigromaculatus</i>	3.43 ± 0.22		3	104 ± 5		1	30.22 ± 3.82		3			0
<i>C. nitidus</i>	2.06 ± 0.12		2	90		1	23.87 ± 3.76		2			0
<i>C. piger</i>	3.27 ± 0.10		3			0	36.61 ± 2.43		3	2.05 ± 0.07		3
<i>C. plesia</i>	2.56		1	140		1	26.39		1			0
<i>C. snecica</i>	1.65		1			0	20.66		1	4.69		1
<i>C. vecors</i>	3.28 ± 0.06		4	74		1	30.21 ± 1.17		4	4.91 ± 1.55		3
<i>Chrysogaster antitheus</i>	3.14		1	37		1	9.30		1			0
<i>C. solstitialis</i>	2.24		1	54		0	10.58		1			0
<i>Chrysotoxum bicinctum</i>	3.04 ± 0.16		2	66 ± 13		1	26.76 ± 0.96		2			0
<i>C. biguttatum</i>	3.49		1			0	55.59		1	0.69		1
<i>C. chinook</i>	3.35		1			0	31.16		1	0.66		1
<i>C. laterale</i>	4.56 ± 0.11		7	62.25 ± 6.14		2	73.89 ± 4.00		7	1.20		1
<i>C. plumeum</i>	3.50 ± 0.07		9	42 ± 1		0	35.16 ± 3.34		9	0.65 ± 0.11		5
<i>C. ventricosum</i>	3.80		1			0	35.68		1			0
<i>Copestylum avidum</i>	7.69 ± 0.25		3	223		0	80.13 ± 4.4		3	0.93 ± 0.08		2
<i>C. marginatum</i>	5.66 ± 0.19		5	90 ± 2		1	33.18 ± 4.79		5	0.78 ± 0.06		3
<i>C. satur</i>	5.73 ± 0.51		3	78 ± 4		2	25.25 ± 2.75		3	0.60		1
<i>Criorhina assuriensis</i>	4.90		1	115		1	68.85		1			0
<i>C. brevipilosa</i>	4.39 ± 0.22		2			0	41.75 ± 5.05		2	5.52		1
<i>C. caudata</i>	9.80 ± 0.10		2	301.5 ± 41.5		2	230.02 ± 25.54		2			0
<i>C. coquilletti</i>	6.01 ± 0.23		4	180		0	89.14 ± 12.94		4	13.63 ± 1.05		3
<i>C. kincaidii</i>	8.46 ± 0.3		5	263.5 ± 18.5		0	242.67 ± 27.45		6	24.83 ± 3.03		3
<i>C. nigriventris</i>	6.69 ± 0.61		2			0	134.75 ± 38.87		2	16.38 ± 1.56		2

Appendix 1 (continued)

Species	Tongue length		Ovariole number		Egg volume		Thorax volume		Testis length		Testis volume	
	Mean ± s.e.	n	Mean ± s.e.	n	Mean ± s.e.	n	Mean ± s.e.	n	Mean ± s.e.	n	Mean ± s.e.	n
<i>Criorhina quadriboscis</i>	9.59 ± 0.03	6	202.67 ± 6.57	3	0.13 ± 0.01	3	254.6 ± 20.14	8	23.33 ± 0.88	3	1.79 ± 0.32	3
<i>C. tricolor</i>	5.90 ± 0.13	3		0		0	80.00 ± 10.84	3	10.80 ± 0.75	3	1.47 ± 0.12	3
<i>Cynorhinella bella</i>	4.53 ± 0.27	4	70	1	0.06	1	31.42 ± 4.48	4	2.23 ± 0.24	3	0.40 ± 0.10	3
<i>C. sp.</i>	4.25	1	36	1	0.06	1	19.61	1		0		0
<i>Dasydyrphus bilineatus</i>	3.49	1	60	1	0.09	1	58.40	1		0		0
<i>D. pauxillus</i>	2.44 ± 0.07	4	12	1	0.18	1	11.00 ± 0.99	4	0.41 ± 0.01	3	0.02 ± 0.00	2
<i>D. venustus</i>	3.17 ± 0.13	10	17.80 ± 2.20	5	0.21 ± 0.03	3	25.25 ± 3.67	10	0.49 ± 0.04	4	0.03 ± 0.01	4
<i>Didea fuscipes</i>	2.75	1	24	1	0.11	1	31.16	1		0		0
<i>Doros aequalis</i>	2.91 ± 0.12	2	36	1	0.11	1	48.38 ± 0.47	2	0.59	1	0.02	1
<i>Epistrophe grossulariae</i>	3.89	1	44	1	0.11	1	56.59	1		0		0
<i>E. xanthostoma</i>	4.19	1		0		0	55.15	1	0.61	1	0.05	1
<i>Epistrophebella emarginata</i>	2.13 ± 0.04	2	18 ± 7	2	0.04	1	8.42 ± 0.60	2		0		0
<i>Eristalinus aeneus</i>	4.51	1	86 ±	1		0	30.69	1		0		0
<i>Eristalis anthophorina</i>	5.42 ± 0.22	8	79.33 ± 18.70	3	0.19	1	54.75 ± 6.23	8	0.96 ± 0.14	5	0.04 ± 0.01	5
<i>E. arbustorum</i>	4.89 ± 0.24	3	103	1	0.08	1	49.60 ± 2.21	3	0.86 ± 0.15	2	0.06 ± 0.03	2
<i>E. cerealis</i>	4.65	1		0		0	62.73	1	0.87	1	0.08	1
<i>E. dimidiata</i>	5.30 ± 0.1	13		0		0	65.08 ± 4.18	13	0.92 ± 0.07	6	0.05 ± 0.00	5
<i>E. flavipes</i>	6.28 ± 0.23	3	137 ± 21.01	3		0	105.87 ± 14.27	3		0		0
<i>E. hirta</i>	6.08 ± 0.31	4	74 ± 5.86	3		0	78.21 ± 11.62	4	0.88	1	0.07	1
<i>E. interrupta</i>	5.48 ± 0.19	3		0		0	54.92 ± 3.23	3	0.73 ± 0.01	2	0.02	1
<i>E. intricarius</i>	5.83 ±	1	92	1		0	77.38	1		0		0
<i>E. obscura</i>	5.71 ± 0.30	6	59.67 ± 22.21	3	0.30	1	63.43 ± 8.08	6	1.00 ± 0.02	2	0.03 ± 0.01	2
<i>E. rossica</i>	6.40	1		0		0	95.67	1	1.17	1	0.10	1
<i>E. rupium</i>	5.14 ± 0.58	2	23	1		0	74.79 ± 31.62	2	0.79	1	0.03	1
<i>E. tenax</i>	7.21 ± 0.12	9	156.33 ± 12.17	3		0	107.26 ± 3.30	9	1.04 ± 0.05	3	0.09 ± 0.00	3
<i>E. transversa</i>	5.4 ± 0.41	3		0		0	42.96 ± 7.21	3		0		0
<i>E. vitripennis</i>	5.89 ± 0.07	2		0		0	86.98 ± 1.28	2	0.39	1	0.01	1

Appendix 1 (continued)

Species	Tongue length		Ovariole number		Egg volume		Thorax volume		Testis length		Testis volume	
	Mean	\pm s.e.	n	Mean	\pm s.e.	n	Mean	\pm s.e.	n	Mean	\pm s.e.	n
<i>Eumerus strigatus</i>	1.95		1	64	0.02	1	13.68		1			0
<i>E. tuberculatus</i>	1.88		1			0	6.28		1			0
<i>Eupeodes fumipennis</i>	3.13 \pm 0.16		5	42 \pm 5	0.05	1	27.56 \pm 4.06		5	0.46 \pm 0.01	0.04 \pm 0.01	3
<i>E. lapponicus</i>	3.53 \pm 0.20		7	39.25 \pm 4.03	0.09 \pm 0.01	3	38.04 \pm 4.59		7	0.45 \pm 0.03	0.03 \pm 0.00	3
<i>E. latifasciatus</i>	3.25		1			0	26.14		1			0
<i>E. luniger</i>	3.30 \pm 0.04		2	16.5 \pm 4.50	0.05 \pm 0.00	2	19.89 \pm 1.35		2			0
<i>E. perplexus</i>	3.62 \pm 0.04		3	42.33 \pm 3.71	0.06 \pm 0.01	2	35.21 \pm 1.89		4	0.57	0.05	1
<i>E. pomus</i>	2.97 \pm 0.18		2	49	0.04	1	23.73 \pm 0.52		2	0.50	0.05	1
<i>E. volucris</i>	2.98 \pm 0.10		7	39.85 \pm 2.25	0.04 \pm 1.61	10	17.47 \pm 0.93		15	0.67 \pm 0.07	0.07 \pm 0.01	2
<i>Eurymia lineata</i>	5.09		1	153		0	12.74		1			0
<i>Ferdinandea cuprea</i>	4.00		1	49	0.10	1	52.05		1			0
<i>Hadromyia crawfordi</i>	3.58 \pm 0.12		4	120		0	57.48 \pm 3.30		4	3.83 \pm 0.25	0.57 \pm 0.07	3
<i>H. opaca</i>	4.25		1	182	0.07	1	87.21		1			0
<i>H. pulcher</i>	4.20		1			0	108.99		1	5.75	1.16	1
<i>Helophilus fasciatus</i>	5.07 \pm 0.15		4			0	56.33 \pm 4.78		4	4.25	0.58	1
<i>H. latifrons</i>	5.47 \pm 0.04		2	157		0	61.10 \pm 5.62		2			0
<i>H. obscurus</i>	5.00 \pm 0.24		5	71.33 \pm 8.19		0	44.49 \pm 5.87		5	3.65 \pm 0.58	0.52 \pm 0.02	2
<i>H. pendulus</i>	5.00		1			0	37.20		1			0
<i>H. sapporensis</i>	4.36 \pm 0.29		2	86		0	39.42 \pm 10.21		2	3.86	0.20	1
<i>Heringia californica</i>	1.37 \pm 0.04		2	13.5 \pm 0.50	0.05 \pm 0.01	2	4.01 \pm 0.58		2			0
<i>H. coxalis</i>	1.33 \pm 0.05		7	28 \pm 8	0.03 \pm 0.01	2	4.47 \pm 0.54		7	0.36 \pm 0.02	0.01 \pm 0.00	3
<i>H. elongata</i>	1.40		1			0	6.98		1	0.35	0.00	1
<i>H. heringii</i>	1.04		1			0	5.30		1	0.42	0.01	1
<i>H. placida</i>	1.40 \pm 0.06		3	19 \pm 4.58	0.05 \pm 0	2	5.13 \pm 0.77		3			0
<i>H. rita</i>	1.37 \pm 0.02		2			0	4.26 \pm 0.04		2	0.38 \pm 0.01	0.01 \pm 0.00	2
<i>H. sinuosa</i>	1.45		1	22		0	5.32		1			0
<i>H. squamulae</i>	1.63		1			0	3.81		1	0.35	0.01	1

Appendix 1 (continued)

Species	Tongue length		Ovariole number		Egg volume		Thorax volume		Testis length		Testis volume	
	Mean ± s.e.	n	Mean ± s.e.	n	Mean ± s.e.	n	Mean ± s.e.	n	Mean ± s.e.	n	Mean ± s.e.	n
<i>Heringia unicolor</i>	1.82	1		0	10.36	1		0		0		0
<i>Ischyrosyrphus beibienkoi</i>	4.02	1		0	70.12	1		0		0		0
<i>I. velutinus</i>	3.90 ± 0.10	2		0	20.62 ± 1.72	2		2	0.43 ± 0.06	2	0.03 ± 0.00	2
<i>Leucozona lucorum</i>	5.40	1	52	1	48.39	1		0		0		0
<i>Mallota auricoma</i>	5.24	1		0	131.35	1		1	1.14	1	0.10	1
<i>M. bautius</i>	5.75 ± 0.24	7	75.5 ± 0.50	2	120.80 ± 15.66	7		5	2.85 ± 0.10	5	0.56 ± 0.15	5
<i>M. megilliformis</i>	4.27 ± 0.49	2	40	1	53.32 ± 16.03	2		2	2.62	1	0.14	1
<i>M. posticata</i>	5.34 ± 0.20	5	37 ± 7	2	99.61 ± 7.40	5		3	8.02 ± 0.54	3	1.91 ± 0.11	3
<i>M. sackeni</i>	4.93 ± 0.08	2		0	47.48 ± 3.13	2		1	2.30	1	0.20	1
<i>Megasyrphus annulipes</i>	3.64 ± 0.37	5	42	1	56.66 ± 8.63	5		4	0.39 ± 0.01	4	0.05 ± 0.01	4
<i>Melangyna arctica</i>	1.78	1		0	3.89	1		1	0.45	1	0.02	1
<i>M. lasiophthalma</i>	2.64 ± 0.11	9	26 ± 4.98	4	14.37 ± 1.42	9		3	0.39 ± 0.02	3	0.01 ± 0.00	3
<i>M. umbellatarum</i>	2.61 ± 0.24	4	19	1	14.94 ± 3.46	4		2	0.42 ± 0.03	2	0.01 ± 0.00	2
<i>Melanostoma mellinum</i>	1.93 ± 0.08	6	7.5 ± 0.50	2	5.41 ± 0.51	6		6	0.48 ± 0.04	2	0.04 ± 0.01	2
<i>M. scalare</i>	2.40 ± 0.09	5	12 ± 0.58	3	9.38 ± 0.93	5		5	0.43	1	0.02	1
<i>Meliscaeva cinctella</i>	2.88 ± 0.10	3	13.67 ± 5.67	3	14.62 ± 1.26	4		4	0.44	1	0.02	1
<i>Merodon equestris</i>	5.84 ± 0.20	4	33	1	111.34 ± 4.77	4		4	4.50 ± 0.25	2	0.51 ± 0.08	2
<i>Microdon cothurnatus</i>	2.09	1	16	1	21.61	1		1		0		0
<i>M. piperi</i>	2.50	1	50	1	55.71	1		1	7.60	0	11.63	0
<i>M. sp.</i>	2.05	1		0	27.78	1		1	8.26	1	1.10	1
<i>M. tristic</i>	2.73 ± 0.52	3	44	1	30.03 ± 3.20	3		3		1		1
<i>Neoscasia amurensis</i>	1.75	1	16	1	2.45	1		1		0		0
<i>N. distincta</i>	1.56 ± 0.05	2		0	2.22 ± 0.53	2		2	0.78	1	0.04	1
<i>Ocyptamus diversifasciatus</i>	2.81 ± 0.06	4	29.33 ± 4.33	3	15.82 ± 1.14	4		4	0.58	1	0.04	1
<i>O. fascipennis</i>	2.17 ± 0.00	2	17 ± 1	2	9.00 ± 0.60	2		2		0		0
<i>Orthonevra pictipennis</i>	2.33	1		0	5.73	1		1	1.47	1	0.14	1
<i>O. pulchella</i>	2.08 ± 0.05	5		0	5.97 ± 0.52	5		5	1.71 ± 0.10	3	0.14 ± 0.02	3

Appendix 1 (continued)

Species	Tongue length		Ovariole number		Egg volume		Thorax volume		Testis length		Testis volume	
	Mean	± s.e.	n	Mean	± s.e.	n	Mean	± s.e.	n	Mean	± s.e.	n
<i>Orthonевра robusta</i>	2.40		1			0	5.98		1	1.58		1
<i>Paragus bicolor</i>	2.47	± 0.09	4	12	±	1	4.61	± 0.36	4	1.53	± 0.14	3
<i>P. haemorrhous</i>	2.43	± 0.01	2			0	3.10	± 0.99	2	0.61		1
<i>P. sp</i>	2.40		1			0	5.22		1	1.60		1
<i>Parasyrphus genualis</i>	1.83	± 0.08	3	17.67	± 5.17	3	7.47	± 1.00	3			0
<i>P. insolitus</i>	1.93	± 0.11	4	29	± 6	0	8.93	± 1.16	4	0.35		1
<i>P. lineolus</i>	1.88		1			0	9.99		1	0.38		1
<i>P. nigrirtarsis</i>	3.80	± 0.15	2			0	28.38	± 2.15	2	0.46	± 0.02	2
<i>P. relictus</i>	2.69	± 0.19	5	14	± 2	2	25.20	± 4.61	5	0.49	± 0.02	3
<i>P. tarsatus</i>	3.98	± 0.03	2			0	31.76	± 0.67	2	0.40	± 0.05	2
<i>Parhelophilus porcus</i>	4.97		1			0	23.61		1			0
<i>P. rex</i>	4.46		1	63		0	23.93		1			0
<i>Pipiza crassipes</i>	1.67		1	19		0	7.92		1			0
<i>P. femoralis</i>	1.98		1	42		1	18.58		1			0
<i>P. oregona</i>	2.40		1			0	27.37		1			0
<i>Platycheirus albimanus</i>	3.36	± 0.16	4	20		1	9.42	± 0.82	4	0.61		1
<i>P. ciliatus</i>	3.03		1			0	6.73		1	0.43	± 0.18	2
<i>P. clypeatus</i>	1.76	± 0.17	3	32		1	6.78	± 1.02	3	0.36		1
<i>P. confusus</i>	4.08	± 0.27	5	15	± 1.58	4	9.48	± 1.63	5			0
<i>P. discimanus</i>	4.34		1			0	12.23		1	0.37		1
<i>P. granditarsis</i>	2.73	± 0.12	3	39.5	± 0.5	2	8.40	± 0.12	3	0.32		1
<i>P. obscurus</i>	4.20	± 0.13	4	19.67	± 5.78	3	11.02	± 1.13	4	0.43		1
<i>P. peltaoides</i>	4.93	± 0.13	2			0	18.06	± 1.80	3	0.42	± 0.02	3
<i>P. quadratus</i>	2.27		1			0	12.95		1			0
<i>P. rufigaster</i>	1.97		1			0	5.83		1	0.50		1
<i>P. scutatus</i>	3.10		1			0	9.27		1	0.46		1
<i>P. sp</i>	2.48	± 0.42	2	11		1	5.48	± 0.39	2	0.47		1

Appendix 1 (continued)

Species	Tongue length Mean ± s.e.	Ovariole number Mean ± s.e.	Egg volume Mean ± s.e.	Thorax volume Mean ± s.e.	Testis length Mean ± s.e.	Testis volume Mean ± s.e.	n
<i>Platycheirus stegus</i>	3.62 ± 0.18	32.5 ± 0.5	0.05	13.73 ± 0.54	0.43 ± 0.03	0.03 ± 0.00	2
<i>Psilota sibirica</i>	2.04	38	0.05	6.70			0
<i>P. thatuna</i>	3.55	65		15.95			0
<i>Rhingia nasica</i>				23.39 ± 3.74	0.55 ± 0.03	0.04 ± 0.01	3
<i>Scavea pyrastris</i>	3.82 ± 0.07	59 ± 8	0.08 ± 0.01	50.75 ± 2.31	0.78	0.06	1
<i>S. selenitica</i>				41.69			0
<i>Sericomyia bifasciata</i>	5.75	70		65.60			0
<i>S. chalcopyga</i>	5.83 ± 0.16	85 ± 14		97.80 ± 10.33	1.22 ± 0.07	0.13 ± 0.06	2
<i>S. chrysoxoides</i>	4.46 ± 0.10	92 ± 5	0.12	49.88 ± 5.71	1.12	0.07	1
<i>S. lata</i>	4.53 ± 0.17	45		78.57 ± 9.09	4.23 ± 0.43	0.70 ± 0.19	2
<i>S. militaris</i>	5.06 ± 0.12	63.67 ± 12.24	0.30	99.33 ± 7.21	2.13	0.43	1
<i>Sphaerophoria abbreviata</i>	2.92 ± 0.08	13	0.04	6.03 ± 0.32			0
<i>S. asymmetrica</i>	2.87 ± 0.11	20.67 ± 7.06	0.04 ± 0.00	5.76 ± 0.58	1.61 ± 0.08	0.16 ± 0.01	5
<i>S. bifurcata</i>	2.83 ± 0.04	19	0.03	5.93 ± 1.84			0
<i>S. contigua</i>	3.35			7.26	1.80	0.16	1
<i>S. novae-angliae</i>	2.70 ± 0.08	17.5 ± 7.5		4.86 ± 0.14	1.57 ± 0.18	0.20 ± 0.10	2
<i>S. philanithus</i>	3.17 ± 0.12	16		7.38 ± 0.86	1.82 ± 0.04	0.22 ± 0.03	5
<i>S. species</i>				8.80			0
<i>S. sulphuripes</i>	3.20 ± 0.07	23.75 ± 0.85	0.04 ± 0.00	6.38 ± 0.44	1.50 ± 0.14	0.15 ± 0.02	3
<i>Sphegina californica</i>	2.36 ± 0.09			3.07 ± 0.09	0.90 ± 0.08	0.04 ± 0.00	2
<i>S. flavimana</i>	1.78			2.44	1.00	0.06	1
<i>S. infuscata</i>	2.63 ± 0.00			9.25 ± 0.30	0.52 ± 0.02	0.02 ± 0.00	2
<i>S. keeniana</i>	1.65 ± 0.09	23.5 ± 0.5	0.02	3.82 ± 0.29			0
<i>S. lobulifera</i>	1.93 ± 0.03			3.91 ± 0.41	1.30	0.10	1
<i>S. petiolata</i>	1.65 ± 0.06	34.33 ± 2.40		2.08 ± 0.34	1.50	0.08	1
<i>S. punctata</i>	1.95			3.30	1.18	0.09	1
<i>S. rufiventris</i>	1.92 ± 0.09			2.63 ± 0.26	0.76 ± 0.03	0.02 ± 0.00	4

Appendix 1 (continued)

Species	Tongue length		Ovariole number		Egg volume		Thorax volume		Testis length		Testis volume	
	Mean	± s.e.	n	Mean	± s.e.	n	Mean	± s.e.	n	Mean	± s.e.	n
<i>Sphegina sp</i>	2.03	± 0.18	2	39		1	6.13	± 1.02	2			0
<i>Spilomyia citima</i>	3.80		1	36		1	46.09	± 15.52	2			0
<i>S.fusca</i>	5.14	± 0.11	6	66	± 3.79	3	141.11	± 13.13	6	17.63		1
<i>S.longicornis</i>	4.19		1	38		1	61.17		1			0
<i>S.sayi</i>	4.42	± 0.09	2	49.5	± 1.5	2	64.49	± 5.46	2	2.95	± 0.08	2
<i>Syrpita pipiens</i>	3.10	± 0.17	5	120.5	± 6.5	2	7.34	± 1.70	5	0.46	± 0.02	4
<i>Syrphus opinator</i>	3.10	± 0.16	9	32	± 3.54	5	33.67	± 3.20	10	0.47		4
<i>S.rectus</i>	2.60	± 0.07	8	29.25	± 2.69	4	22.90	± 2.14	8	0.47		2
<i>S.ribesii</i>	3.35	± 0.15	11	44.14	± 8.7	7	37.44	± 3.38	11	0.56	± 0.02	3
<i>S.sp</i>	3.00		1			0	29.49		1	0.50		1
<i>S.torvus</i>	3.42	± 0.06	9	40	± 1.53	3	37.28	± 1.62	9	0.49	± 0.05	3
<i>Temnostoma alternans</i>	4.07	± 0.11	13	40.5	± 8.5	2	92.27	± 9.11	13	4.71	± 0.14	9
<i>T.apiforme</i>	3.59	± 0.29	2	39		1	73.42	± 16.45	2	5.10		1
<i>T.balyras</i>	2.91	± 0.25	3	40		1	31.03	± 8.21	3	2.88	± 0.42	2
<i>T.barberi</i>	3.26		1			0	28.10		1	3.10		1
<i>T.bombylans</i>	2.33		1			0	26.10		1			0
<i>T.meridionale</i>	3.40		1	38		1	72.96		1			0
<i>T.vespiforme</i>	4.01	± 0.12	8	43	± 10.41	3	95.53	± 3.83	8	5.10	± 0.61	4
<i>Toxomerus geminatus</i>	2.77		1			0	4.84		1	2.22		1
<i>T.marginatus</i>	2.48	± 0.12	6	15	± 0.71	4	3.40	± 0.34	6	1.37	± 0.11	2
<i>T.occidentalis</i>	2.99	± 0.07	8	27.6	± 2.8	5	6.30	± 0.37	8	2.42	± 0.08	3
<i>T.politus</i>	2.87		1	24		1	6.18		1			0
<i>Trichopsomyia apisaon</i>	1.46	± 0.15	2	8		0	4.25	± 0.47	2	0.40		1
<i>Tropidia quadrata</i>	5.02		1			0	46.44		1	4.94		1
<i>Volucella bombylans</i>	7.17		1	25		1	63.88		1			0
<i>V.pellucens</i>	6.83		1	56		1	123.09		1			0
<i>Xanthandrus comptus</i>	2.54	± 0.14	2	45		1	25.19	± 2.17	2	0.38		1

Appendix 1 (continued)

Species	Tongue length		Ovariole number		Egg volume		Thorax volume		Testis length		Testis volume	
	Mean	± s.e.	n	Mean	± s.e.	n	Mean	± s.e.	n	Mean	± s.e.	n
<i>Xanthogramma laetus</i>	2.33		1	24		1	29.61		1			0
<i>Xylota annulifera</i>	2.18	± 0.12	2	114		1	13.14	± 1.49	2			0
<i>X. barbata</i>	2.90	± 0.15	5	124		1	44.58	± 7.64	5	4.82	± 0.35	3
<i>X. confusa</i>	2.27	± 0.09	7	118	± 3.21	3	20.93	± 2.49	7	2.46	± 1.19	2
<i>X. flavifrons</i>	3.53		1			0	54.41		1	5.08		1
<i>X. hinei</i>	2.28	± 0.08	5	139		1	20.60	± 0.33	5	3.13	± 0.34	4
<i>X. lovetti</i>	2.70		1	170		1	28.86		1			0
<i>X. naknek</i>	2.15	± 0.07	3	100	± 6	2	14.34	± 2.33	3	3.18		1
<i>X. quadrimaculata</i>	2.06	± 0.11	5	106	± 32	2	16.32	± 2.60	5	4.59	± 2.31	2
<i>X. raineri</i>	2.61	± 0.20	3	172	± 23	2	30.16	± 5.14	3			0
<i>X. segnis</i>	2.02		1			0	15.56		1			0
<i>X. sp</i>	2.23	± 0.02	2			0	20.43	± 2.30	2	3.01	± 0.22	2
<i>X. subfasciata</i>	2.04	± 0.17	3	176		1	15.81	± 2.91	3	2.78	± 0.37	2
<i>X. tuberculata</i>	2.21		1			0	16.00		1			0

Appendix 2

Image analysis programs

This appendix contains the source code (written for QBASIC™ by F.Gilbert) for the image analysis programs BITMAP, SHIFT and SEGMENT, which are described in some detail in Chapter Four. Essentially, the method converts two-dimensional images to colour bitmaps, and then generates a single-value description of the similarity between them. An ASCII text file is produced listing the reference (model) filename (.bmp) and the files to be compared with it. BITMAP converts the bitmaps into a string of digits representing the colour patterns in each image, resulting in an ASCII file (with the extension .col) for each image. The .col files consist of a header which gives the size of the image (number of columns, number of rows and number of columns) and then the Red-Green-Blue values of the colours in order of their numerical representation in the bitmap.

In the second stage, either SHIFT or SEGMENT compares the .col files to produce a similarity value. SHIFT lines up the images in their bottom left corner (0,0), and shifts them vertically and horizontally to maximise the matching of pixels. SEGMENT uses bitmaps split into four sections (corresponding to tergites on an insect's abdomen) using vertical lines of single white pixels, and tests each tergite by overlaying the midlines of the reference and test tergite, and shifting them in the y-axis only to produce the maximal match.

A2-1. BITMAP source code

```
DECLARE SUB sword ()  
DECLARE SUB dword ()  
DECLARE SUB twodigit (I$)
```

This program converts standard-format bitmap files (.BMP) arising from WINDOWS programs such as BITEDIT, into a string of digits representing the colours of the bitmap. No more than 16 colours must be used, but these do not have to be the standard 16. The two main subroutine called read WORDs (2 bytes) and DWORDs (4 bytes) in the bitmap header, interpreting them so as to read the resulting bitmap. It produces a straight ASCII file for comparison of bitmap images using SHIFT or SEGMENT.

open reading files in turn

```
DIM COLOR$(16), F$(60)  
COMMON SHARED word$
```

read in the file names

```
INPUT ; "File for names of bitmaps = ", name$  
OPEN name$ FOR INPUT AS #1  
PRINT : PRINT "Opening picture files: "  
INPUT #1, NPIC%  
PRINT "Number of files = "; NPIC%  
FOR I% = 1 TO NPIC%  
    INPUT #1, F$(I%)  
    PRINT "file "; F$(I%)  
NEXT I%  
CLOSE  
  
FOR II% = 1 TO NPIC%  
  
    FF$ = F$(II%) + ".BMP"  
    OPEN "I", 1, FF$
```

output files, all named F\$(I%) with .COL as identifier

```
F2$ = F$(I%) + ".COL"
OPEN "o", 2, F2$
PRINT "Reading file "; FF$, ", writing file "; F2$

CALL sword:                                ' read BM, the bitmap ID code
CALL dword:                                ' read size of file
CALL sword: CALL sword:                    ' read reserved bytes
CALL dword: OFFSET% = VAL(word$):          ' bitmap offset
CALL dword: HEADER% = VAL(word$):          ' size of header
CALL dword: X% = VAL(word$):                ' width of bitmap in pixels
wid% = X%                                  ' save original width in wid%
CALL dword: Y% = VAL(word$):                ' height of bitmap in pixels
CALL sword: Z% = VAL(word$):                ' set to 1
IF (Z% <> 1) THEN PRINT " biPlanes not = 1": CLOSE : GOTO 9
CALL sword: BITCOL% = VAL(word$)            ' set to 8 for a 256-color bitmap
                                           ' to 4 for a 16-color bitmap
CALL dword: Z% = VAL(word$)                 ' = 0 for uncompressed bitmap
IF (Z% <> 0) THEN PRINT " NOT an uncompressed bitmap": CLOSE : GOTO 9
CALL dword                                  ' size of padded image in bytes
CALL dword: CALL dword:                    ' pixels per m, not used here
CALL dword: NCOL% = VAL(word$)              ' no of colours used in bitmap
CALL dword: Z% = VAL(word$)                 ' no of important colours

FOR I% = 1 TO NCOL%
CALL dword: COLOR$(I%) = word$             ' read the RGB values of colours used
NEXT I%
```

find the padding factor. For 256-colour bitmaps each represents one pixel, and the image is padded so that the number of pixels is divisible by 4.

This is different for 16-colour bitmaps since each byte represents 2 pixels, and the image is padded so that the number of BYTES is divisible by 4


```

extra% = 0
IF (BITCOL% = 4) THEN
  IF ((X% MOD 2) = 1) THEN X% = X% + 1: extra% = 1
  AD% = (X% / 2) MOD 4
  IF AD% = 0 THEN ADD% = 0: GOTO 1
  ADD% = (4 - AD%) * 2
1  X% = X% + ADD%:                ' add the padding factor
  XLIM% = X% / 2
  XWID% = 35
ELSEIF (BITCOL% = 8) THEN
  AD% = X% MOD 4
  IF AD% = 0 THEN ADD% = 0: GOTO 22
  ADD% = (4 - AD%)
22  X% = X% + ADD%
  XLIM% = X%
  XWID% = 70
ELSE
  PRINT "Strange format: Bitmap not 16 or 256 colours": CLOSE : GOTO 9
END IF

```

print out the characteristics of the file

```

PRINT #2, USING "####"; X%; Y%; NCOL%; X% - wid%
FOR I% = 1 TO NCOL%
  PRINT #2, COLOR$(I%)
NEXT I%

PRINT " size is"; wid%; "+"; extra%; "+"; ADD%; "="; X%; " by "; Y%
PRINT " bits per pixel = "; BITCOL%; " no. of colours used = "; NCOL%

```

read in the bit map, one line at a time

```

L$ = "": I$ = ""
FOR I% = 1 TO Y%
  FOR J% = 1 TO XLIM%
    I$ = HEX$(ASC(INPUT$(1, #1)))

```

```
IF (BITCOL% = 4) THEN CALL twodigit(I$)
```

```
L$ = L$ + I$
```

if 16-colour bitmap, need to write only 35 rather than 70 per line

```
IF J% MOD XWID% = 0 THEN PRINT #2, L$: L$ = ""
```

```
NEXT J%
```

```
PRINT #2, L$: L$ = ""
```

```
NEXT I%
```

```
,
```

```
CLOSE
```

```
PRINT "Closing down files "; FF$; " and "; F2$
```

loop to the next file

```
,
```

```
NEXT II%
```

```
,
```

9 END

```
SUB dword
```

```
word$ = ""
```

```
I1$ = HEX$(ASC(INPUT$(1, #1)))
```

```
I2$ = HEX$(ASC(INPUT$(1, #1)))
```

```
I3$ = HEX$(ASC(INPUT$(1, #1)))
```

```
I4$ = HEX$(ASC(INPUT$(1, #1)))
```

```
IF LEN(I1$) < 2 THEN I1$ = "0" + I1$
```

```
IF LEN(I2$) < 2 THEN I2$ = "0" + I2$
```

```
IF LEN(I3$) < 2 THEN I3$ = "0" + I3$
```

```
IF LEN(I4$) < 2 THEN I4$ = "0" + I4$
```

```
IF I4$ = "00" THEN I4$ = "" ELSE 810
```

```
IF I3$ = "00" THEN I3$ = "" ELSE 810
```

```
IF I2$ = "00" THEN I2$ = "" ELSE 810
```

```
810 I5$ = I4$ + I3$ + I2$ + I1$
```

```
word$ = "&H" + I5$
```

```
END SUB
```

```

SUB sword
word$ = ""
I1$ = HEX$(ASC(INPUT$(1, #1)))
I2$ = HEX$(ASC(INPUT$(1, #1)))
word$ = "&H" + I2$ + I1$
END SUB

```

```

SUB twodigit (I$)

```

subroutine to restore number < 10 to two digits

```

IF LEN(I$) > 1 THEN GOTO 2

```

```

I$ = "0" + I$

```

```

2 END SUB

```

A2-2. SHIFT source code

```

DECLARE SUB ColourMatch ()
DECLARE SUB ShiftPic (rj1%, rk1%, pj1%, pk1%, limj%, limk%)
DECLARE SUB getdata (PIC%())
DECLARE SUB pixel (R%, P%, match, mism)

```

This program uses picture files imported into a bitmap via a program such as BITEDIT and converted into fewer colours, suitably edited to represent the pattern of colours of the original.

Bitmaps are then converted by FSG's QBASIC program BITMAP.BAS into a series of digits representing the colours. The header to these files gives the size of the picture (no. of columns, no. of rows, no. of colours) and then the RGB values of each colour in order of their numerical representation in the bitmap. 0 is always BLACK, and the largest number is always WHITE (the background colour).

This program then matches pictures of patterns to one reference picture. The patterns come from picture files of pixel colours, all named fname.COL The reference picture is then shifted in the x-axis to maximise the number of matches

made with the test picture. This is to allow for slight orientation and pattern differences.

```
DIM SHARED PIC%(100, 100), REF%(100, 100), F$(50)
DIM SHARED RGB$(50, 16), NCOL%(50), CLR(16, 16)
COMMON SHARED ii%, match, mism, mj%, mk%, fmatch, fmism
COMMON SHARED RX%, RY%, X%, Y%, jshift%, kshift%, background%
```

read in the names of the picture files

```
CLS
INPUT ; "Picture file list in ", name$
PRINT
OPEN name$ FOR INPUT AS #1
INPUT #1, NPIC%
FOR I% = 1 TO NPIC%
    INPUT #1, F$(I%)
NEXT I%
CLOSE #1
```

read the reference image (always in first named file in 'name\$') into REF%

```
F2$ = F$(1) + ".COL"
OPEN F2$ FOR INPUT AS #1
PRINT "Opening "; F$(1); " for reference picture"
ii% = 1
CALL getdata(REF%())
CLOSE #1
```

```
OPEN "RESULT" FOR OUTPUT AS #2
PRINT #2, "Comparison of images: reference = ", F$(1)
PRINT #2, ""
```

```
RX% = X%: RY% = Y%
```

loop through the pictures

FOR ii% = 2 TO NPIC%

read the test picture into PIC%

F2\$ = F\$(ii%) + ".COL"

OPEN F2\$ FOR INPUT AS #1

PRINT "Opening "; F\$(ii%); " for comparison"

CALL getdata(PIC%())

CLOSE #1

create the lookup matrix of the degree of matching of the available colours

CALL ColourMatch

Start the shifting of the pictures in both x and y directions. Shifting is of the test picture relative to the reference, and runs from - 10% of pixels to + 10% in the x direction, and from corresponding edge to corresponding edge in the y direction.

The shift that generates the maximal similarity is remembered in mj%, mk%

fmatch = 0: fmism = 0: background% = NCOL%(ii%) - 1

initshiftj% = INT(Y% / 20)

endj% = 2 * initshiftj%

initshiftk% = INT(X% / 20)

endk% = 2 * initshiftk%

FOR jshift% = 0 TO endj%

 rj1% = (RY% / 2) - (Y% / 2) - initshiftj% + jshift%

 IF (rj1% > 1) THEN rj1% = 1

 rj2% = (RY% / 2) + (Y% / 2) - initshiftj% + jshift%

 IF (rj2% < RY%) THEN rj2% = RY%

 pj1% = (Y% / 2) - (RY% / 2) + initshiftj% - jshift%

 IF (pj1% > 1) THEN pj1% = 1

 pj2% = (Y% / 2) + (RY% / 2) + initshiftj% - jshift%

 IF (pj2% < Y%) THEN pj2% = Y%

```

IF ((rj2% - rj1%) < (pj2% - pj1%)) THEN
    limj% = rj2% - rj1%
    pj2% = pj1% + limj%
ELSE
    limj% = pj2% - pj1%
    rj2% = rj1% + limj%
END IF

FOR kshift% = 0 TO endk%
    match = 0: mism = 0
    PRINT ; ". ";
    rk1% = (RX% / 2) - (X% / 2) - initshtk% + kshift%
    IF (rk1% > 1) THEN rk1% = 1
    rk2% = (RX% / 2) + (X% / 2) - initshtk% + kshift%
    IF (rk2% < RX%) THEN rk2% = RX%
    pk1% = (X% / 2) - (RX% / 2) + initshtk% - kshift%
    IF (pk1% > 1) THEN pk1% = 1
    pk2% = (X% / 2) + (RX% / 2) + initshtk% - kshift%
    IF (pk2% < X%) THEN pk2% = X%

    IF ((rk2% - rk1%) < (pk2% - pk1%)) THEN
        limk% = rk2% - rk1%
        pk2% = pk1% + limk%
    ELSE
        limk% = pk2% - pk1%
        rk2% = rk1% + limk%
    END IF

    CALL ShiftPic(rj1%, rk1%, pj1%, pk1%, limj%, limk%)

NEXT kshift%
PRINT
NEXT jshift%
simil = (fmatch / (fmatch + fmism)) * 100: PRINT
PRINT "Finished "; F$(ii%); " similarity "; simil; "at shift "; mj%; ". "; mk%
PRINT #2, F$(ii%); " similarity =";

```

```
PRINT #2, USING "###.##"; simil;
PRINT #2, " at shift "; mj%; ", "; mk%
```

```
NEXT ii%
CLOSE #2
END
```

SUB ColourMatch

This subroutine creates a lookup matrix for colour matches look for approximate matches, allowing for colour differences and store them in CLR. White (always the last colour, NCOL%-1) is ignored because it is the background colour

```
FOR I% = 1 TO NCOL%(1) - 1
  FOR J% = 1 TO NCOL%(ii%) - 1
```

black-black corresponding pixels = a match, but black with any other colour is a mismatch

```
IF ((I% = 1) AND (J% = 1)) THEN
  CLR(I%, J%) = 1: GOTO 20
ELSEIF ((I% = 1) OR (J% = 1)) THEN CLR(I%, J%) = 0: GOTO 20
END IF
```

other combinations get a calculation of the match, using a Euclidean distance apart in trichromatic space of the RGB values

```
c1% = VAL("&H" + MID$(RGB$(1, I%), 3, 2))
c2% = VAL("&H" + MID$(RGB$(ii%, J%), 3, 2))
diffr = (c1% - c2%) / 10
c1% = VAL("&H" + MID$(RGB$(1, I%), 5, 2))
c2% = VAL("&H" + MID$(RGB$(ii%, J%), 5, 2))
diffg = (c1% - c2%) / 10
c1% = VAL("&H" + MID$(RGB$(1, I%), 7, 2))
c2% = VAL("&H" + MID$(RGB$(ii%, J%), 7, 2))
diffb = (c1% - c2%) / 10
prop = SQR((diffr * diffr) + (diffg * diffg) + (diffb * diffb))
```

this euclidean distance, p, is then expressed relative to the distance between black (0,0,0) and white (255,255,255). The degree of match is then (1 - p), and stored in CLR

```
        prop = prop * 10 / (SQR(3) * 255)
        prop = (1 - prop)
        CLR(I%, J%) = prop
20    NEXT J%
    NEXT I%
END SUB
```

```
SUB getdata (ARR%())
```

this takes the hex data put out from BITMAP.BAS and reads it into the array ARR%, converting the hex numbers 0 - F into the integer numbers 0 - 15

```
INPUT #1, X%, Y%, NCOL%(ii%), pad%
FOR I% = 1 TO NCOL%(ii%)
    INPUT #1, RGB$(ii%, I%)
NEXT I%
LINEX% = 70
FOR I% = 1 TO Y%
    k% = X% \ LINEX%
    FOR L% = 1 TO k%
        INPUT #1, HOLD$
        FOR J% = 1 TO LINEX%
            IF ASC(MID$(HOLD$, J%, 1)) < 58 THEN
                ARR%(I%, (L% - 1) * LINEX% + J%) = ASC(MID$(HOLD$, J%, 1)) - 48
            ELSE
                ARR%(I%, (L% - 1) * LINEX% + J%) = ASC(MID$(HOLD$, J%, 1)) - 55
            END IF
        NEXT J%
    NEXT L%

L% = X% MOD LINEX%: IF L% = 0 THEN GOTO 1
INPUT #1, HOLD$
```



```

FOR J% = 1 TO L%
  IF ASC(MID$(HOLD$, J%, 1)) < 58 THEN
    ARR%(I%, (k% * LINEX%) + J%) = ASC(MID$(HOLD$, J%, 1)) - 48
  ELSE
    ARR%(I%, (k% * LINEX%) + J%) = ASC(MID$(HOLD$, J%, 1)) - 55
  END IF
NEXT J%

NEXT I%

1  X% = X% - pad%
END SUB

```

SUB pixel (R%, P%, match, mism)

reject if both are background pixels: these are WHITE and their ascii code is NCOL% - 1 since colours are represented by the numbers 0 - F and the syrphid palette has no more than 8 colours

```
IF ((R% = background%) AND (P% = background%)) THEN GOTO 11
```

if one is background and the other not, is a complete mismatch

```
IF ((R% = background%) OR (P% = background%)) THEN mism = mism + 1: GOTO 11
```

count matches of same colour

```
IF (R% = P%) THEN match = match + 1: GOTO 11
```

if different colours, then lookup in CLR to find match

```
clmtch = CLR(R% + 1, P% + 1)
```

```
match = match + clmtch: mism = mism + (1 - clmtch)
```

```
11  END SUB
```

```

SUB ShiftPic (rj1%, rk1%, pj1%, pk1%, limj%, limk%)

  FOR sj% = 0 TO limj%
    FOR sk% = 0 TO limk%
      IF (((rj1% + sj%) < 1) OR ((rj1% + sj%) > RY%)) THEN
        R% = background%
      ELSEIF (((rk1% + sk%) < 1) OR ((rk1% + sk%) > RX%)) THEN R% =
background%
      ELSE
        R% = REF%(rj1% + sj%, rk1% + sk%)
      END IF
      IF (((pj1% + sj%) < 1) OR ((pj1% + sj%) > Y%)) THEN
        P% = background%
      ELSEIF (((pk1% + sk%) < 1) OR ((pk1% + sk%) > X%)) THEN P% =
background%
      ELSE
        P% = PIC%(pj1% + sj%, pk1% + sk%)
      END IF

      CALL pixel(R%, P%, match, mism)
    NEXT sk%
  NEXT sj%

  IF (fmatch < match) THEN
    fmatch = match
    fmism = mism
    mk% = kshift%
    mj% = jshift%
  END IF

END SUB

```

A2-3. SEGMENT source code

```

DECLARE SUB CheckIfBlack (ARR%(), arrwid%, arrht%, yes%)

```

```

DECLARE SUB tergite (ARR%(), bkgrd%, NX%, NY%, NCOL%, AT1%(), nt1%, AT2%(),
nt2%, AT3%(), nt3%)
DECLARE SUB ColourMatch ()
DECLARE SUB ShiftPic (REFARR%(), TESTARR%(), rj1%, rk1%, pj1%, pk1%, limj%,
limk%)
DECLARE SUB getdata (PIC%())
DECLARE SUB pixel (R%, P%, match, mism)

```

This program uses picture files imported into a bitmap via a program such as BITEDIT and converted into fewer colours, suitably edited to represent the pattern of colours of the original.

The separate tergites of the wasp and hoverfly patterns are indicated by a vertical line of single white (background) pixels. There should be three lines separating tergites 2, 3 and 4+ on the hoverfly, and three similar segments on the wasp.

Bitmaps are then converted by FSG's QBASIC program BITMAP.BAS into a series of digits representing the colours. The header to these files gives the size of the picture (no. of columns, no. of rows, no. of colours) and then the RGB values of each colour in order of their numerical representation in the bitmap. 0 is always BLACK, and the largest number is always WHITE (the background colour).

This program then matches pictures of patterns to one reference picture. The patterns come from picture files of pixel colours, all named fname.COL

When both corresponding pixels are WHITE, it is ignored. When only one is WHITE it counts as a mismatch. If any picture is more than 100 pixels wide or high, the dimensions of the arrays of this program will need to be altered. The dimensions need to be slightly larger than the image size because bitmaps are padded with extra bytes to ensure the widths and heights are divisible by 4

The test tergite is then shifted in the x-axis to maximise the number of matches made with the reference picture. This is to allow for slight orientation and pattern differences. SEGMENT.BAS splits the wasp and test images into separate tergites, recognised by vertical lines of single white pixels, and tests each tergite separately, shifting vertically but not horizontally.

```
COMMON SHARED ii%, match, mism, mj%, fmatch, fmism
COMMON SHARED RX%, RY%, X%, Y%, jshift%, black%
COMMON SHARED Pbackground%, Rbackground%
```

set size of bitmap

```
bmlen% = 105: bmwid% = 105
```

This sets the maximum length (i.e. horizontally) of each tergite It may need altering if tergites are very thick

```
tlen% = INT(bmlen% / 2)
```

```
DIM SHARED PIC%(bmwid%, bmlen%), REF%(bmwid%, bmlen%), F$(50)
DIM RT1%(bmwid%, tlen%), RT2%(bmwid%, tlen%), RT3%(bmwid%, tlen%)
DIM TT1%(bmwid%, tlen%), TT2%(bmwid%, tlen%), TT3%(bmwid%, tlen%)
DIM SHARED RGB$(50, 16), NCOL%(50), CLR(16, 16)
```

read in the names of the picture files

```
CLS
INPUT ; "Picture file list in ", name$
PRINT
OPEN name$ FOR INPUT AS #1
INPUT #1, NPIC%
FOR i% = 1 TO NPIC%
    INPUT #1, F$(i%)
NEXT i%
CLOSE #1
```

read the reference image (always in first named file in 'name\$') into REF% as a sequence of pixel colours REF%(RY% vertically, RX% horizontally)

```
F2$ = F$(1) + ".COL"
OPEN F2$ FOR INPUT AS #1
PRINT
```

```
PRINT "Opening "; F$(1); " for reference picture"
```

```
ii% = 1
```

```
CALL getdata(REF%())
```

```
CLOSE #1
```

```
INPUT "Output file = "; f3$
```

```
OPEN f3$ FOR OUTPUT AS #2
```

```
PRINT #2, "Comparison of images: reference = "; F$(1)
```

```
PRINT #2, ""
```

```
PRINT #2, " limits are "; Y%; " vertically, "; X%; " horizontally"
```

```
PRINT
```

```
PRINT "Comparison of images: reference = "; F$(1)
```

```
PRINT
```

```
PRINT " limits are "; Y%; " vertically, "; X%; " horizontally"
```

```
RX% = X%: RY% = Y%
```

find out the code for 'white' (background) in the reference image

```
Rbackground% = -1
```

```
FOR i% = 1 TO NCOL%(1)
```

```
IF RGB$(1, i%) = "&HFFFFFF" THEN
```

```
    Rbackground% = i% - 1
```

```
END IF
```

```
NEXT i%
```

```
IF Rbackground% = -1 THEN
```

```
PRINT
```

```
PRINT "Failure to discover code for white"
```

```
PRINT
```

```
PRINT "Press Esc for exit ....."
```

```
DO
```

```
LOOP UNTIL INKEY$ = CHR$(27)
```

```
CLOSE
```

```
STOP
```

```
END IF
```

identify the separate tergites of the wasp pattern

```
CALL tergite(REF%), Rbackground%, RX%, RY%, NCOL%(1), RT1%(), rnt1%,
RT2%(), rnt2%, RT3%(), rnt3%)
```

```
PRINT #2, " 3 tergites"; RY%; " by "; rnt1%; ", "; rnt2%; " & "; rnt3%
```

loop through the pictures

```
FOR ii% = 2 TO NPIC%
```

read the test picture into PIC%

```
F2$ = F$(ii%) + ".COL"
```

```
OPEN F2$ FOR INPUT AS #1
```

```
PRINT
```

```
PRINT "Opening "; F$(ii%); " for comparison"
```

```
CALL getdata(PIC%())
```

```
CLOSE #1
```

```
PRINT #2, ""
```

```
PRINT
```

```
PRINT ii% - 1; " Test image = "; F$(ii%)
```

```
PRINT "*****"
```

```
PRINT #2, USING "##"; ii% - 1;
```

```
PRINT #2, " Test image = "; F$(ii%)
```

```
PRINT #2, "*****"
```

```
PRINT " limits are "; Y%; " vertically, "; X%; " horizontally"
```

```
PRINT #2, " limits are "; Y%; " vertically, "; X%; " horizontally"
```

find out the code for white in this picture

```
Pbackground% = -1
```

```
FOR i% = 1 TO NCOL%(ii%)
```

```
IF RGB$(ii%, i%) = "&HFFFFFF" THEN
```

```
Pbackground% = i% - 1
```

```
END IF
```

```
NEXT i%
```

```
IF Pbackground% = -1 THEN
```

```
PRINT
```

```
PRINT "Failure to discover code for white"
```

```

PRINT
PRINT "Press Esc for exit ....."
DO
LOOP UNTIL INKEY$ = CHR$(27)
CLOSE
STOP
END IF

```

******* assumes here that black colour is always the first colour**

```
black% = 0
```

create the lookup matrix of the degree of matching of the available colours

```
CALL ColourMatch
```

Identify the separate main tergites T2, T3 & T4 in the test picture

```
CALL tergite(PIC%, Pbackground%, X%, Y%, NCOL%(ii%), TT1%(), tnt1%,
TT2%(), tnt2%, TT3%(), tnt3%)
```

```
PRINT "3 tergites"; Y%; " by "; tnt1%; ", "; tnt2%; " & "; tnt3%
```

```
PRINT #2, " 3 tergites"; Y%; " by "; tnt1%; ", "; tnt2%; " & "; tnt3%
```

```
CALL CheckIfBlack(TT1%(), Y%, tnt1%, black1%)
```

```
CALL CheckIfBlack(TT2%(), Y%, tnt2%, black2%)
```

```
CALL CheckIfBlack(TT3%(), Y%, tnt3%, black3%)
```

Start the shifting of the tergites in the vertical direction only. The tergites are placed together on their midlines, and shifted relative to that position. Shifting is of the test picture relative to the reference, and runs from -initshift% pixels to +initshift%

The shift that generates the maximal similarity is remembered in mj%

```
f1match = 0: f1mism = 0
```

f2match = 0: f2mism = 0

f3match = 0: f3mism = 0

the degree of shifting is set here, vertically:

initshiftj% = INT(Y% / 10)

endj% = 2 * initshiftj%

now determine the limits of overlap of the two image from rj1% on the reference image, pj1% on the test image and extending to limj% vertically

FOR jshift% = 0 TO endj%

limits on the reference image

rj1% = (RY% / 2) - (Y% / 2) - initshiftj% + jshift%

IF rj1% < 1 THEN rj1% = 1

rj2% = (RY% / 2) + (Y% / 2) - initshiftj% + jshift%

IF rj2% > RY% THEN rj2% = RY%

limits on the test image

pj1% = (Y% / 2) - (RY% / 2) + initshiftj% - jshift%

IF pj1% < 1 THEN pj1% = 1

pj2% = (Y% / 2) + (RY% / 2) + initshiftj% + jshift%

IF pj2% > Y% THEN pj2% = Y%

IF (rj2% - rj1%) < (pj2% - pj1%) THEN

 limj% = (rj2% - rj1%)

ELSE

 limj% = (pj2% - pj1%)

END IF

now calculate the similarity for this overlap for each tergite

tergite 1


```

IF rnt1% < tnt1% THEN
    limk% = rnt1%
ELSE
    limk% = tnt1%
END IF
match = 0: mism = 0
CALL ShiftPic(RT1%(), TT1%(), rj1%, 1, pj1%, 1, limj% - 1, limk%)
IF (f1match < match) THEN
    f1match = match
    f1mism = mism
    m1j% = jshift%
END IF

```

tergite 2

```

IF rnt2% < tnt2% THEN
    limk% = rnt2%
ELSE
    limk% = tnt2%
END IF
match = 0: mism = 0
CALL ShiftPic(RT2%(), TT2%(), rj1%, 1, pj1%, 1, limj% - 1, limk%)
IF (f2match < match) THEN
    f2match = match
    f2mism = mism
    m2j% = jshift%
END IF

```

tergite 3

```

IF rnt3% < tnt3% THEN
    limk% = rnt3%
ELSE
    limk% = tnt3%
END IF
match = 0: mism = 0
CALL ShiftPic(RT3%(), TT3%(), rj1%, 1, pj1%, 1, limj% - 1, limk%)

```

```

IF (f3match < match) THEN
    f3match = match
    f3mism = mism
    m3j% = jshift%
END IF

NEXT jshift%

IF black1% = 1 THEN
    f1mism = f1mism + f1match
    f1match = 0
END IF
IF black2% = 1 THEN
    f2mism = f2mism + f2match
    f2match = 0
END IF
IF black3% = 1 THEN
    f3mism = f3mism + f3match
    f3match = 0
END IF
fmatch = f1match + f2match + f3match
fmism = f1mism + f2mism + f3mism
simil = 100 * (fmatch / (fmatch + fmism))
PRINT
PRINT "Finished "; F$(ii%); " match/mismatch, similarity of"
PRINT "   tergit 1 = ";
PRINT USING "####.#"; f1match;
PRINT "/";
PRINT USING "####.#"; f1mism;
PRINT ", ";
PRINT USING "###.##"; (f1match / (f1match + f1mism)) * 100;
PRINT " at shift "; m1j% - initsj%
PRINT "   tergit 2 = ";
PRINT USING "####.#"; f2match;
PRINT "/";
PRINT USING "####.#"; f2mism;
PRINT ", ";

```

```

PRINT USING "###.##"; (f2match / (f2match + f2mism)) * 100;
PRINT " at shift "; m2j% - initshiftj%
PRINT "   tergite 3 = ";
PRINT USING "####.#"; f3match;
PRINT "/";
PRINT USING "####.#"; f3mism;
PRINT ", ";
PRINT USING "###.##"; (f3match / (f3match + f3mism)) * 100;
PRINT " at shift "; m3j% - initshiftj%
PRINT "overall = ";
PRINT USING "####.#"; fmatch;
PRINT "/";
PRINT USING "####.#"; fmism;
PRINT ", ";
PRINT USING "###.##"; simil
PRINT

PRINT #2, ""
PRINT #2, "Finished "; F$(ii%); " match/mismatch, similarity of"
PRINT #2, "   tergite 1 = ";
PRINT #2, USING "####.#"; f1match;
PRINT #2, "/";
PRINT #2, USING "####.#"; f1mism;
PRINT #2, ", ";
PRINT #2, USING "###.##"; (f1match / (f1match + f1mism)) * 100;
PRINT #2, " at shift "; m1j% - initshiftj%
PRINT #2, "   tergite 2 = ";
PRINT #2, USING "####.#"; f2match;
PRINT #2, "/";
PRINT #2, USING "####.#"; f2mism;
PRINT #2, ", ";
PRINT #2, USING "###.##"; (f2match / (f2match + f2mism)) * 100;
PRINT #2, " at shift "; m2j% - initshiftj%
PRINT #2, "   tergite 3 = ";
PRINT #2, USING "####.#"; f3match;
PRINT #2, "/";
PRINT #2, USING "####.#"; f3mism;

```

```

PRINT #2, ", ";
PRINT #2, USING "###.##"; (f3match / (f3match + f3mism)) * 100;
PRINT #2, " at shift "; m3j% - initshiftj%
PRINT #2, "overall = ";
PRINT #2, USING "####.#"; fmatch;
PRINT #2, "/";
PRINT #2, USING "####.#"; fmism;
PRINT #2, ", ";
PRINT #2, USING "###.##"; simil
PRINT #2, ""

NEXT ii%
CLOSE #2
END

```

```

SUB CheckIfBlack (ARR%(), arrht%, arrlen%, yes%)

```

```

    yes% = 1
    pixels% = 0
    FOR i% = 1 TO arrht%
        FOR j% = 1 TO arrlen%
            IF ARR%(i%, j%) <> Pbackground% THEN
                IF ARR%(i%, j%) <> black% THEN yes% = 0
            END IF
        NEXT j%
    NEXT i%

```

```

END SUB

```

```

SUB ColourMatch

```

This subroutine creates a lookup matrix for colour matches look for approximate matches, allowing for colour differences and store them in CLR. White (always the last colour, NCOL%-1) is ignored because it is the background colour

```

    FOR i% = 1 TO NCOL%(1) - 1
        FOR j% = 1 TO NCOL%(ii%) - 1

```

black-black corresponding pixels = a match, but black with any other colour is a mismatch

```
IF ((i% = 1) AND (j% = 1)) THEN
  CLR(i%, j%) = 1: GOTO 20
ELSEIF ((i% = 1) OR (j% = 1)) THEN CLR(i%, j%) = 0: GOTO 20
END IF
```

other combinations get a calculation of the match, using a Euclidean distance apart in trichromatic space of the RGB values

```
c1% = VAL("&H" + MID$(RGB$(1, i%), 3, 2))
c2% = VAL("&H" + MID$(RGB$(ii%, j%), 3, 2))
diffr = (c1% - c2%) / 10
c1% = VAL("&H" + MID$(RGB$(1, i%), 5, 2))
c2% = VAL("&H" + MID$(RGB$(ii%, j%), 5, 2))
diffg = (c1% - c2%) / 10
c1% = VAL("&H" + MID$(RGB$(1, i%), 7, 2))
c2% = VAL("&H" + MID$(RGB$(ii%, j%), 7, 2))
diffb = (c1% - c2%) / 10
prop = SQR((diffr * diffr) + (diffg * diffg) + (diffb * diffb))
```

this euclidean distance, p, is then expressed relative to the distance between black (0,0,0) and white (255,255,255). The degree of match is then (1 - p), and stored in CLR

```
prop = prop * 10 / (SQR(3) * 255)
prop = (1 - prop)
CLR(i%, j%) = prop
20 NEXT j%
NEXT i%
END SUB
```

```
SUB getdata (ARR%())
```

**this takes the hex data put out from BITMAP.BAS and reads it into the array
ARR%, converting the hex numbers 0 - F into the integer numbers 0 - 15**

```
INPUT #1, X%, Y%, NCOL%(ii%), pad%
FOR i% = 1 TO NCOL%(ii%)
  INPUT #1, RGB$(ii%, i%)
NEXT i%
LINEX% = 70
FOR i% = 1 TO Y%
  K% = X% \ LINEX%
  FOR L% = 1 TO K%
    INPUT #1, HOLD$
    FOR j% = 1 TO LINEX%
      IF ASC(MID$(HOLD$, j%, 1)) < 58 THEN
        ARR%(i%, (L% - 1) * LINEX% + j%) = ASC(MID$(HOLD$, j%, 1)) - 48
      ELSE
        ARR%(i%, (L% - 1) * LINEX% + j%) = ASC(MID$(HOLD$, j%, 1)) - 55
      END IF
    NEXT j%
  NEXT L%

  L% = X% MOD LINEX%: IF L% = 0 THEN GOTO 1
  INPUT #1, HOLD$
  FOR j% = 1 TO L%
    IF ASC(MID$(HOLD$, j%, 1)) < 58 THEN
      ARR%(i%, (K% * LINEX%) + j%) = ASC(MID$(HOLD$, j%, 1)) - 48
    ELSE
      ARR%(i%, (K% * LINEX%) + j%) = ASC(MID$(HOLD$, j%, 1)) - 55
    END IF
  NEXT j%

NEXT i%

1 X% = X% - pad%
END SUB

SUB pixel (R%, P%, match, mism)
```

**reject if both are background pixels:these are WHITE and their ascii code is
NCOL% - 1 since colours are represented by the numbers 0 - F and the syrphid
palette has no more than 8 colours**

```
IF ((R% = Rbackground%) AND (P% = Pbackground%)) THEN GOTO 11
```

if one is background and the other not, it's a complete mismatch

```
IF ((R% = Rbackground%) OR (P% = Pbackground%)) THEN mism = mism + 1:  
GOTO 11
```

other combinations, lookup in CLR to find match

```
clrmitch = CLR(R% + 1, P% + 1)
```

```
match = match + clrmitch: mism = mism + (1 - clrmitch)
```

```
11 END SUB
```

```
SUB ptergite (ARR%(), nt%, RY%)  
FOR i% = 1 TO RY%  
FOR j% = 1 TO nt%  
PRINT USING "#"; ARR%(i%, j%);  
NEXT j%  
PRINT  
IF i% MOD 20 = 0 THEN  
DO  
LOOP UNTIL INKEY$ = CHR$(27)  
END IF  
NEXT i%  
PRINT "end of tergite"  
DO  
LOOP UNTIL INKEY$ = CHR$(27)
```

```
END SUB
```

SUB ShiftPic (REFARR%(), TESTARR%(), rj1%, rk1%, pj1%, pk1%, limj%, limk%)

FOR sj% = 0 TO limj%

FOR sk% = 0 TO limk%

IF (((rj1% + sj%) < 1) OR ((rj1% + sj%) > RY%)) THEN

R% = Rbackground%

ELSEIF (((rk1% + sk%) < 1) OR ((rk1% + sk%) > RX%)) THEN R% =

Rbackground%

ELSE

R% = REFARR%(rj1% + sj%, rk1% + sk%)

END IF

IF (((pj1% + sj%) < 1) OR ((pj1% + sj%) > Y%)) THEN

P% = Pbackground%

ELSEIF (((pk1% + sk%) < 1) OR ((pk1% + sk%) > X%)) THEN P% =

Pbackground%

ELSE

P% = TESTARR%(pj1% + sj%, pk1% + sk%)

END IF

CALL pixel(R%, P%, match, mism)

NEXT sk%

NEXT sj%

END SUB

SUB tergite (ARR%(), bkgrd%, NX%, NY%, NCOL%, AT1%(), nt1%, AT2%(), nt2%,
AT3%(), nt3%)

white% = 0: nt% = 0: nj% = 1

FOR j% = 1 TO NX%

check to see if this vertical line of pixels is all white

white% = 1

FOR i% = 1 TO NY%

IF ARR%(i%, j%) <> bkgrd% THEN


```
white% = 0
END IF
NEXT i%
```

if this is the white divider, reset the horizontal pixel counter and increment the tergite counter

```
IF (white% = 1) AND (nt% < 4) THEN
  SELECT CASE nt%
    CASE 1
      nt1% = nj% - 1
    CASE 2
      nt2% = nj% - 1
    CASE 3
      nt3% = nj% - 1
  END SELECT
  nt% = nt% + 1
  nj% = 1
END IF
```

read in non-white columns

```
IF (white% = 0) AND (nt% < 4) THEN
  FOR i% = 1 TO NY%
    SELECT CASE nt%
      CASE 1
        AT1%(i%, nj%) = ARR%(i%, j%)
      CASE 2
        AT2%(i%, nj%) = ARR%(i%, j%)
      CASE 3
        AT3%(i%, nj%) = ARR%(i%, j%)
    END SELECT
  NEXT i%
  nj% = nj% + 1
END IF
NEXT j%
IF nt% = 3 THEN
```

```
    nt3% = nj% - 1
END IF

IF nt% < 3 THEN
    PRINT
    PRINT "Error: three tergites not found"
    PRINT
    PRINT "Press Esc for exit ....."
    DO
    LOOP UNTIL INKEY$ = CHR$(27)

    CLOSE
    STOP
END IF

END SUB
```