
9 The Evolution of Imperfect Mimicry

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1. Ideas about mimicry

Apart from some notable exceptions, mimicry and brightly coloured aposematic patterns have been discussed by biologists mainly from three very different points of view, each making unrealistic assumptions about aspects of the other two (Mallet and Joron, 1999). The most obvious in the voluminous literature (see Komarek, 1998) is the insect natural history approach, used by both naturalists and professional biologists, which has simplistic ideas about the ways in which predators behave and of their evolutionary impact on their prey. The second is a modelling approach, that of evolutionary dynamics: this virtually ignores predator behaviour and any details of the interactions between predators and their prey. The final viewpoint is centred on the details of predator behaviour, but this is often simplistic about the evolutionary dynamics, and can make unrealistic assumptions about the psychological processes of learning and forgetting. A gradual synthesis is taking place between these viewpoints, partly in response to the inadequacy of older theory to explain the phenomenon of imperfect mimicry.

In this chapter, I outline the basic ideas of mimicry theory, and show how they fail to account for the commonly imperfectly mimetic patterns of the main taxonomic group in the Holarctic that contains mimics; the hoverflies (Diptera, Syrphidae). I review the relevant information about this group, and assess a variety of new theories of imperfect mimicry, which have been put forward largely to account for the evolution of their colour patterns. I conclude that only one of these recent ideas – Sherratt's (2002) multiple-model theory – accounts for all the facts.

1.1 Basics

Traditionally the main forms of mimicry are Batesian and Müllerian, formulated in 1862 and 1878, respectively, and still thought to provide some of the most

easily understandable examples of the way in which natural selection operates (Poulton, 1890; Carpenter and Ford, 1933; Malcolm, 1990; Joron and Mallet, 1998; Mallet and Joron, 1999). In this chapter, the word 'mimic' without any qualifying adjective refers to Batesian mimics only: the word 'model' includes Müllerian mimics and Müllerian mimicry rings.

Batesian mimicry is thought to occur when a rare harmless species evolves to resemble closely an abundant 'unprofitable' model. A Batesian mimic gains protection from predators which cannot tell the difference between model and mimic and, since they tend to encounter models rather than mimics when searching for food, they associate the colour pattern of the model with a nasty experience, and tend to avoid it in future. Since the more closely a mimic resembles its model, the more protection it gets, there is constant selection for mimetic perfection, which results in mimics evolving to be indistinguishable from models to their predators. The basis of the unprofitability is usually assumed to be unpalatability, or more generally noxiousness; however, there is no reason why other bases might not be important, such as difficulty of capture ('escape' mimicry: van Someren and Jackson, 1959; Hespeneheide, 1973).

Müllerian mimicry occurs when several noxious species evolve to resemble each other, and hence they all benefit by a reduction in predation: Nicholson's (1927) analysis of Australian insects is a very clear example of this for an entire fauna. Since predators need only recognize resemblance rather than identity, there is no reason to suppose that protection is proportional to similarity, and Müllerian mimics are therefore not indistinguishable from one another: they are 'imperfect mimics'.

In Batesian mimicry a new mimetic form will be advantageous since it is rare, but at a high frequency it loses mimetic protection and is selected against. This frequency dependence generates 'diversifying' (i.e. disruptive) selection for different morphs, and hence for polymorphism. In contrast, there is no such diversifying selection on models (Nur, 1970). Different morphs of a model will be disadvantageous, because they will not be identified as inedible; this 'purifying' (i.e. stabilizing) selection maintains a single colour pattern in the population of the model (and in a group of Müllerian mimics).

The study of Batesian mimicry has traditionally involved imagining a one-to-one correspondence between model and mimic species (e.g. Howarth *et al.*, 2000), but this may be incorrect as a general rule. Many insect models are bound up in Müllerian complexes, and typically many harmless insects mimic each complex (see Nicholson, 1927). European work has rarely acknowledged this aspect of mimicry, preferring to identify a single model species for each apparent mimic. Because each mimic usually resembles a Müllerian mimicry ring, a whole suite of models, this has resulted in different models being cited in different studies, generating a great deal of confusion. The situation may be different in the tropics, where models are usually much more diverse (M. Edmunds, personal communication), but knowledge about tropical mimetic relationships outside the Lepidoptera is very scarce.

1.2 What maintains imperfect mimicry?

With some notable exceptions (Schmidt, 1960; Duncan and Sheppard, 1965; Holling, 1965; Ford, 1971; Pilecki and O'Donald, 1971; Dill, 1975; Goodale and Sneddon, 1977; Schuler, 1980; Greenwood, 1986; Hetz and Slobodchikoff, 1988; Lindström *et al.*, 1997; Rowe *et al.*, 2004), consideration of the evolution of mimicry has been mostly confined to the evolution of good mimics. However, these views ignore the obvious fact that most mimicry is of rather poor quality (Getty, 1985), and such imperfect mimicry is widespread in many Batesian mimetic systems (e.g. salticid spiders mimicking ants: Edmunds, 1993, 2000). 'Imperfect mimicry' in a Batesian mimic is defined here as being obviously different (to us) from its putative model, usually visually.

The prevailing opinion was (and still is) that since individuals with closer resemblance to the model gain more protection, Batesian mimics should be under constant selection to improve their mimetic resemblance, and hence eventually only good mimics would exist. Some models are very noxious, and others less so. The degree of protection afforded to mimics will depend upon just how noxious a model is, and predators will generalize more widely to poorer and poorer mimics as the noxiousness of the model increases (Duncan and Sheppard, 1965; Goodale and Sneddon, 1977). This effect is measurable in experiments (e.g. Lindström *et al.*, 1997). However, there would still be selection, however slight, for improvement of mimetic resemblance and thus there would still be constant selection for perfect mimicry.

Very few, and only recent, authors have considered what kind of resistance there might be to directional selection for improving mimicry (apart from the usual 'genetic constraints' possibility). If we view the current colour patterns of models and their mimics as existing in some kind of equilibrium state, then for poor mimicry to be stable, such opposing or balancing forces must exist (Grewcock, 1992; Sherratt, 2002). What might such forces be? Only the costs of producing mimetic colours (Grewcock, 1992), kin selection opposing natural selection (Johnstone, 2002), and the existence of multiple models (Sherratt, 2002) have been suggested. These ideas are described in detail in Section 6.9.

Of course, it is possible that the colour patterns are not at equilibrium, but are constantly evolving. Models do suffer extra mortality when a mimic is present, because by chance some predators encounter mimics rather than models, learn that the pattern is edible, and consequently attack models in error. This generates 'advergence' (Brower and Brower, 1972), i.e. where the colour pattern of a Batesian mimic evolves towards that of its model, but the model evolves away: this is the 'coevolutionary chase' process of Turner (1987). However, selection is always stronger on the mimic, which always catches the model in this evolutionary process, resulting in stability. Simulations of multispecies systems (Franks and Noble, 2004) show that Müllerian mimicry only evolves if there is some initial resemblance among models; however, the additional presence of Batesian mimics strongly promotes the formation of Müllerian mimicry rings by causing models to move in colour space, and hence converge. Despite this, the end result is stasis once again, and an equilibrium state. Thus I do not think there is any empirical or theoretical evidence for a non-equilibrium view of the evolution of mimetic colour patterns.

1.3 Other elements of mimicry theory: relative abundance and predator behaviour

Traditional mimicry theory suggests that mimics should be rarer than models, so that predators tend to meet unprofitable rather than profitable examples, and hence associate the pattern with the unprofitability. The rarity of mimics relative to models has been a constantly repeated feature of the way in which Batesian mimicry has been described. Protection can extend to commoner mimics when their models are also common, and the close correlation between model and mimic abundances was shown in butterflies by Sheppard (1959). It also may be that it is not that mimics are rare, but that models are common, since abundant warningly coloured models will gain more mimics than rare ones (Turner, 1984). More sophisticated models and thinking have altered this viewpoint considerably: mimics can still be protected even when more abundant than their model (e.g. Brower, 1960), when that model is really nasty, or if the mimic has low nutritional value, or if distributions are clumped. This is also true when profitable alternative prey are present (which encourage the predator to drop both model and mimic from its diet). Holling (1965) reached this conclusion explicitly almost 30 years ago:

The greater the proportion of distasteful models to mimics the greater is the protection in each of the four cases simulated, although some protection is afforded even if the distasteful models are very rare. [...] Thus the often expressed belief that the advantages of mimicry collapse when the palatable mimic outnumbers its model is no longer tenable, if it ever was.

Furthermore, what matters is the relative abundances as perceived by predators, and these are very difficult to measure realistically (see below for an example).

The recognition, discrimination and generalization of prey by predators are features hardly considered in the early theoretical treatment of mimicry. Errors (real or apparent) must be made in order for the whole system to work, since mimics must be avoided in case they turn out to be models. Most of the discussions in the literature focus only upon perfect mimics, and therefore assume that predators are unable to distinguish them from the models. We now know more, but still not enough, about the way in which predators generalize from a colour pattern associated with unprofitability to other similar, but not identical, colour patterns (see Rowe *et al.*, 2004). The few experiments done on this actually show clearly that even a vague resemblance can be protective: just a bit of black or red is often good enough (e.g. Schmidt, 1960). Many factors probably affect the extent of generalization, the degree of noxiousness of the model being the most obvious: the more dangerous or toxic the model, the more likely it is that even a partial resemblance will afford protection to a mimic. This interacts with model–mimic relative frequencies, as was shown by a clever experiment using birds feeding on mealworm larvae experimentally modified to form models with two levels of nastiness (Lindström *et al.*, 1997; Mappes and Alatalo, 1997). Mimics survived best when the model was relatively common and highly distasteful. When the model was highly distasteful, the birds clearly did not bother to discriminate, whatever the relative

abundances, and poor mimics gained while models suffered slightly reduced protection. However, when the model was only slightly distasteful, birds discriminated between model and mimic when models were common, but did not bother when models were rare: the mimics still gained some protection, but not as much (see also Alcock, 1970). The results of these experiments show that discrimination is often perfectly possible, but when correct decisions are less beneficial (prey less profitable), or mistakes are more likely (relative frequencies) or more costly (noxiousness), birds may prefer not to risk it (see Dill, 1975). It seems logical that this decision may also depend on how hungry the bird is in relation to its perception of the availability of prey (including alternatives to the model and mimic). In a marvellous early work of computer-based modelling, Holling (1965) included all of these features in a simulation predicting that even vague resemblances would be protective; thus, he concluded, mimicry should be a very pervasive feature of natural communities.

The perceptual problem of an experienced predator encountering a mimic is one of signal detection. Psychologists have developed signal detection theory for measuring the way in which decisions are made between a desired objective and undesirable 'noise'. It quantifies the fundamental trade-off between making correct choices sufficiently often while keeping the cost of making mistakes to a minimum (Shettleworth, 1998: 61–69). The appearance of the insect is often the only information the predator has in order to make the discrimination, and the more similar the model and mimic are, the more likely it is that the predator will make a mistake. The probabilities of making a correct decision and making a mistake cannot be varied independently, since mimics are by definition sometimes or always confused with models. All the predator can do is to set a threshold value of prey 'appearance', using whatever clues can be obtained at reasonable cost (usually time). Exceeding this threshold determines whether the predator attacks or not (see below, and Fig. 9.3). A predator with a low threshold attacks more often, is correct more often, but also makes more mistakes. A conservative predator makes fewer mistakes, but also makes fewer correct decisions. Despite its obvious applicability, only Oaten *et al.* (1975), Getty (1985), Greenwood (1986), Sherratt (2002) and Johnstone (2002) have used this approach to analyse the way in which predators affect model–mimic complexes.

Holling (1965) argued that because the distance of perception is so large in visual vertebrate predators (i.e. those that can learn associations), the potential for regulating even low-density populations is present, and the evolution of mimicry results in an increase in the equilibrial population density (cf. Sherratt, 2002). However, current ecological opinion today considers it very unlikely that populations of insects in general, let alone mimics, are regulated by visually based predators of adults.

The ways in which the evolution of aposematism and mimicry affect other aspects of the life history are only just beginning to be explored. The evolution of effective defence is costly, and these costs should be measurable in terms of fitness components. As with Bates' original observations that led to the idea of mimicry, such studies have involved the South-American heliconiid butterflies. Marden and Chai (1991) and Srygley (1999) found a real dichotomy between

palatable, non-mimetic versus unpalatable or mimetic species: palatable non-mimics maintained higher body temperatures, and had larger flight muscles, allowing them to accelerate faster in flight, and had smaller digestive tracts (in males) and smaller ovaries (in females). Thus there were measurable reproductive costs to the need to evade predators effectively, some of which mimics could avoid paying. However, there are also measurable aerodynamic costs to evolving a mimetic flight pattern (Srygley, 2004).

1.4 Variation in noxiousness/unprofitability at all levels

The clear and simple distinction between Batesian and Müllerian mimicry is currently under scrutiny, using theories of the psychological processes of predators. These 'receiver psychology' models make a variety of assumptions about the processes of learning, forgetting and extinction (a learned erasing of a previously memorized association), and can lead to a great variety in different forms of mimicry (see Speed and Turner, 1999). In particular, where Müllerian mimics differ in the degree of noxiousness, the existence of a more palatable one can result in an increase in attack rate on the less palatable, leading to a parasitic form of Müllerian mimicry called 'quasi-Batesian' (Speed, 1993, 2001). This kind of Müllerian mimicry would allow the evolution of polymorphism, which we know occurs in heliconiine butterflies (although there are other explanations: see Mallet and Gilbert, 1995).

In this context it is interesting that the classic case of Batesian mimicry, between monarch and queen butterfly models (*Danaus* spp.) and the viceroy mimic (*Limenitis archippus*) is now known to be much more complex (Brower, 1988; Mallet, 1999). Some, but not all, individuals in monarch populations sequester poisons (cardenolides, cardiac glycosides) from their larval food plants, the milkweeds (Asclepiadaceae – whose members vary in their glycoside content), which render the butterfly distasteful and cause vomiting in a number of bird predators. Evidently a great deal of variation in palatability exists within and among populations of monarch butterflies, a veritable palatability spectrum. Whilst initial experiments mainly appeared to show that the viceroy was palatable, we know now that this butterfly can be just as unpalatable as the monarch (Ritland and Brower, 1991).

2. What phenomena does theory need to explain?

I have outlined some of the more traditional ideas of mimicry theory, and some of their deficiencies: I shall introduce the two newest theories later on, when I have described what it is they are trying to explain. Thus I turn now to the question of whether traditional theory can account for the data. In order to do this manageably, I concentrate on a single taxonomic group that contains a very large proportion of the Holarctic Batesian mimics: the hoverflies (Diptera, Syrphidae). If theory cannot explain the colour patterns of these insects, then it is clearly deficient. I consider hoverfly colour patterns, ecology and behaviour

in detail to show that classical mimicry theory copes poorly in explaining them, as do most of the more recent additions. In my opinion, only one very recent theory (Sherratt, 2002: described below) based on predator signal detection in a world of multiple models has the potential to explain all the characteristics of hoverfly mimicry.

3. Mimicry complexes in the Holarctic

There are few general overviews of mimetic relationships in particular faunas, except for Australia (Nicholson, 1927) and the UK (Brown, 1951). Most models have conspicuous aposematic patterns, often involving sharp contrasts of two or more different colours. In Britain the following aposematic patterns occur amongst models: yellow and black (wasps, hornets, many bumblebees), red and black (many beetles, some bugs, moths, and a few bumblebees), red (beetles), black (beetles) and metallic shining colours (beetles). There are some non-aposematic mimics, for example of honeybees, and ants (e.g. spiders). Not all possible models are made use of by Batesian mimics: for example, the red-and-black burnet moths and other similar distasteful insects have not been copied. Two sets of models and their Batesian mimics make up significant proportions of the fauna: hymenopteran models with dipteran mimics, and unpalatable coleopteran models with palatable coleopteran mimics. Numerically the Hymenoptera form the most important group of models, and the Diptera the largest group of mimics. Diptera are exclusively mimics of Hymenoptera, and most of the mimics belong to one family, the hoverflies (Syrphidae). This is one of the largest and most diverse of all dipteran families, with a worldwide distribution and more than 5600 species described (see Rotheray, 1993; Rotheray and Gilbert, 1999). The literature contains information about the mimetic status of some 279 species of hoverfly (F. Gilbert, unpublished), an astonishingly high proportion relative to other insect groups: clearly mimicry is a dominant theme of the evolution of this group of flies. Especially in Europe, most of the models for hoverfly mimics appear to be social insects: the bumblebees, honeybees and social wasps.

4. The models of hoverfly mimics

4.1 Bumblebees

Bumblebees are well-known both taxonomically (Williams, 1998) and biologically (Prys-Jones and Corbet, 1991; Goulson, 2003), occurring largely in boreal or high-altitude habitats. Most of the 239 recognized species are Holarctic, but some extend down the Andes into South America. While morphologically very uniform, some species of bumblebee can be extraordinarily variable in the colour patterns of their body hairs, with several different morphs and broad geographic trends within a single species (see Williams, 1991; von Hagen and Aichhorn, 2003); different judgements about the significance of this variation have resulted in more than 2800 names (Williams, 1998). However, the colour patterns are not 'all

possible combinations' (as Drees, 1997, thought), but unrelated species have converged in the colour patterns of their morphs into just a few Müllerian mimicry rings (Nicholson, 1927; Vane-Wright, 1978; Plowright and Owen, 1980; Williams, 1991). Thus virtually all eastern Nearctic bumblebees have broad bands of yellow and black, often with a black spot in the middle of the yellow thorax (see Table 9.1: group G); western Nearctic species are predominantly black with narrow yellow bands (group B); in between in the Rocky Mountains there are two mimicry groups, yellow-and-black banded (group D), and yellow-and-black banded with an extensively red abdomen (group H) (Gabritschevsky, 1924, 1926). In Europe they are more diverse, forming four main Müllerian mimicry rings (groups A, E, F and J: see Prys-Jones and Corbet, 1991). These groupings are inevitably not always clear-cut. For example, some individual workers of *Bombus pascuorum* have dense tawny hairs all over the thorax and abdomen, whereas in others the abdominal hairs are thin and do not obscure the dark cuticle beneath, creating the appearance of a dark abdomen. The former pattern would be classified into group J of Table 9.1, whereas the latter would fall either into group G (which are virtually all Nearctic bumblebees) or even into the honeybee group (M), where there are many species with the pattern of a hairy thorax and bare dark abdomen.

Why is there more than one Müllerian ring? Why have all models not converged into one massive Müllerian complex? Holling (1965) suggested the evidence implied a limit to the number of species within a ring, but could not think of a mechanism other than a vague recourse to other general density-dependent features of their biology. It is possible that there are subtle differences in habitat segregation in heliconiine mimicry rings (Mallet and Gilbert, 1995), but this is unlikely in bumblebees. Mallet (1999) suggested that while it might theoretically be because of quasi-Batesian processes caused by different degrees of noxiousness, the evidence is very weak (really just the fact that some species are polymorphic, with each morph belonging to a different mimicry ring, and some emerge later than others). This deserves detailed study in bumblebees, where a huge amount of information is available, especially in Europe. A fascinating recent simulation (Franks and Noble, 2004) suggests that it is the presence of Batesian mimics and the 'coevolutionary chase' that causes models to converge into a smaller number (typically three) of Müllerian mimicry rings than would otherwise form. However, too many Batesian mimetic forms break up Müllerian mimicry rings or prevent them from evolving.

How noxious are bumblebees to their predators? With the exception of the specialist red-backed shrike (*Lanius collurio*), adults of the 19 species of birds in Mostler's (1935) amazingly comprehensive trials only ate 2% of the 646 bumblebees that were presented to them, rejecting all the rest without even attempting to attack, whatever the species involved (mainly *Bombus terrestris*, *B. lapidarius*, *B. hortorum* and *B. ruderarius*). The question arises as to what may be the source of the aversion, and most authors (e.g. Stiles, 1979; Plowright and Owen, 1980) assume that it is their sting. However, the evidence is only convincing in one case: naqve toads ate *Bombus pennsylvanicus* that had had their stings removed, but having attempted to eat an intact bumblebee, from then on strongly avoided them (Brower *et al.*, 1960), a pattern repeated with honeybees (Brower and Brower, 1962, 1965). The evidence that birds are

Table 9.1. Holarctic mimicry rings from assessments in the literature (full data of all the hoverfly species and their morphs are provided in F. Gilbert (unpublished). Some species have both good and poor morphs, and hence only summary numbers of each are given).

Ring	Colour pattern	Species	Number of hoverfly mimics			Species with sex-linked morphs
			Good	Poor	Polymorphic species	
Bumblebees						
A	All black with a variable-sized red or orange tip to the abdomen		12	2		
B	Black with a yellow collar and thin yellow posterior band		2	0		
C	Black with a yellow collar and white or whitish tail		1	1		
D	Broad yellow-and-black bands with a black tail		7	0		
E	Broad yellow-and-black bands with a white tail		5	2		
F	Broad yellow-and-black bands with a red/orange/yellow/brown tail;		18	3		
G	Yellow/brown anterior (± a central black spot on the thorax), dark brown-black posterior		5	2		
H	Yellow thorax with a black central band, and yellow/orange abdomen		13	0		
J	All tawny		14	3		
K	Broad white-and-black bands with a red/orange/yellow tail		3	1		
L	All black		2	0		
	Total		82	14	25	14
Honeybee						
M	Light-haired thorax, dark abdomen with ± orange anterior and thin whitish bands total		16	12	0	6?
Wasps						
I	'Eumenids': black with 1–3 narrow, widely spaced bright yellow bands on the abdomen		22	2		
II	Mainly polistines: alternating, more or less equal-sized bright yellow and black bands		6	26		
III	Small <i>Vespa</i> : black with paired yellow spots or lunules on each segment		1	15		
IV	Large <i>Vespa</i> : mostly bright yellow with narrow black triangular bands ± spots		19	12		
V	Hornets: large, mostly dull yellow with reddish brown to blackish markings		4	0		
VI	<i>Dolichovespula</i> : large, mostly dark with white bands at the abdomen tip		2	0		
VII	Larger solitary wasps: strongly 'waisted', brown/orange with poorly defined yellow markings		0	0		
VIII	Small to medium, black with a red/orange abdomen and black tip		5	2		
IX	Small to medium, narrow abdomen with small whitish/yellow/orange/red side spots/bands		9	32		
	Total		68	89	0	4?
			157			

also deterred by the sting is weak and unconvincing. Mostler (1935) recorded no stings suffered by experienced adult birds, and of 70 prolonged contacts between bumblebees and young naive birds trying to eat them, there were only three stings. He found that bumblebee tissues were highly palatable, never evoking any of the unpalatability reactions that were so typical of contact with wasp and honeybee abdominal tissues. He attributed the noxiousness of bumblebees to the difficulty of handling: a hand-reared young female Whitethroat (*Sylvia communis*), feeding independently for the first time, took 18 min to kill, dismember and eat a bumblebee, after which it was completely exhausted. The equivalent handling time for houseflies, mealworms or beetles was a fraction of a minute, even for young birds. Mostler suggested three reasons why bumblebees were aversive: these were, in order of importance: (i) the tough chitin and hairy bodies of these insects made it necessary for birds to have to expend great efforts in subduing, dismembering and swallowing them; (ii) bumblebee tissues were not easily digestible; and (iii) the sting. Likewise Evans and Waldbauer (1982) thought that the sting of *Bombus pennsylvanicus americanorum* was not the main protection against birds. Only two of their birds were stung; the others avoided eating bumblebees only after having eaten the 'middle segments of the abdomen', presumably with the venom sac. In this case unpalatability may be due to distasteful venom.

Different bumblebee species are not equally noxious, partly because they vary a lot in aggressiveness, although nothing systematic seems to have been studied about this: the subgenus *Fervidobombus* is supposed to be particularly aggressive (Kearns and Thomson, 2001: 70). Such differences should have an impact on the effectiveness of Batesian mimicry, and the occurrence of quasi-Batesian processes. Rupp (1989) noted differences in attack readiness among the German and Swiss bumblebees with which he worked – the workers of *B. terrestris* and *B. lucorum* reacted with particularly fierce attacks to irritation of the nest, whilst he could dig out the nests of *B. pascuorum* and *B. wurfleini mastrucatus* without any special protection being required. He found an unexpectedly low proportion of the black-red *bombylans* morph of the mimetic syrphid *Volucella bombylans* in Switzerland, and attributed this to the fact that the relevant model in the lowlands (*B. lapidarius*) was replaced by a far less aggressive visual counterpart (*B. wurfleini mastrucatus*) in the mountains, which therefore provided less protection. Alford (1975) too mentions the different levels of aggressiveness amongst species of bumblebee: most species in the UK are benign and easy to handle, and their nests are simple to collect, but *B. terrestris* and *B. muscorum* are noticeably much more aggressive and difficult to deal with.

4.2 Honeybees

Honeybees are one of the best known of all insects (Seeley, 1985). *Apis mellifera* probably originally had an African distribution, together with all but northernmost Europe and western Asia. Whilst all individuals have an obviously tawny-haired thorax, most workers either have a dark-brown/black abdomen or carry transverse orange bands on the abdominal tergites. The extent of the

banding is mainly a racial difference, but is also sensitive to temperature, and hence varies seasonally. A wide variety of solitary bees and some other Hymenoptera also belong to this mimicry ring.

Mostler (1935) conducted about 480 feeding trials on honeybees with his insectivorous birds. Spotted flycatchers (*Muscicapa striata*) were perfectly willing to take honeybees as prey. There was individual variation in two species: pied flycatchers (*Ficedula hypoleuca*) (where one individual regularly fed on honeybees), and redstarts (*Phoenicurus phoenicurus*) (where females, but not males, were willing to feed on honeybees). In the other birds, the insects were scarcely even looked at in most trials. When tasted or eaten, honeybees induced the same unpalatability reactions as for wasps (see below), but these were more limited in degree, and appeared less frequently. Using mealworms smeared with abdominal tissues, Mostler showed that unpalatability was the main cause of the rejection response. As in the case of wasps, Liepelt (1963) demonstrated that the bad taste of the abdomen derived from the venom. The removal of the entire sting apparatus, including the venom sac, rendered honeybees completely palatable, and all were eaten.

Do honeybees sting predators more or less readily than wasps do? It has been reported that 25–100% of toads were stung during feeding attempts (Cott, 1940; Brower and Brower, 1965), but birds appear to be rarely, if ever, stung (Mostler, 1935; Liepelt, 1963), and probably the sting is not a significant deterrent (Liepelt, 1963). Unpalatability arising from the taste of the venom must be the main cause of avoidance by birds. It is probable that the beak of an insectivorous bird is a useful defence against stings, since it is hard and non-living, but the fleshy mouths of toads offer no protection. In some birds their feeding method exposes them to multiple stings, and they must be immune (e.g. swifts: M.F. Johannsmeier, personal communication).

There are substantial differences in noxiousness among honeybee races (Seeley, 1985: 139–149). A European beekeeper is astonished at the defensive ferocity of African bees, receiving 6–10 times more stings for the same hive manipulation. This is probably a consequence of the much greater level and longer history of nest predation in Africa, especially by humans. We might predict from mimicry theory that these highly noxious bees would therefore be used more frequently as models for palatable insects than other races: although hardly studied at all, honeybee mimicry is said to be a dominant theme of the Diptera of southern Africa (B. Stuckenberg, personal communication), much more so than in Europe.

Given that they are noxious, and birds learn to avoid them, why is the honeybee complex not aposematically coloured (Holloway, 1976)? Perhaps their high abundance and gregarious foraging render bright colours unnecessary in promoting memorability (J. Mallet, personal communication).

4.3 'Wasps'

The 'wasps' as models for hoverflies contain three main groups: social wasps (Vespidae) and two groups of solitary wasps, the potter (Eumenidae) and digger

wasps (Sphecidae). It is probable that other related taxa can also serve as models, including spider wasps (Pompilidae) and sawflies (Tenthredinidae), although little is known of their noxiousness. Many different species have been identified as possible models for mimetic syrphids. Whether birds really differentiate among these species is the critical point. Workers in North America have grouped models into a few Müllerian complexes (e.g. Evans and Eberhard, 1970: 245; Waldbauer, 1988), but this sort of classification of wasp colour patterns has hardly ever been done by European workers, although the existence of Müllerian pattern groups has been mentioned occasionally (e.g. Heal, 1979).

Females of all species have a sting, but the sting of the social vespids is often thought to be much more painful. Like the other model groups, the basis of the noxiousness of these models has generally been assumed to be their sting (e.g. Edmunds, 1974: 62, 82). It comes as rather a surprise, therefore, to read the work of those (Mostler, 1935; Steiniger, 1937a,b; Liepelt, 1963) who actually offered wasps experimentally to birds, and who discovered that, as with honeybees, the stings are only rarely used against birds, and that the taste of the venom sac is responsible for their noxiousness. Adults of these birds attacked fewer than 10% of the wasps, eating fewer than 3% of them. Hand-reared naive young birds ate a somewhat higher proportion overall, but this average masked an initial willingness to attack, followed by rapid learned avoidance. There was no sign of any innate avoidance of black-and-yellow colour patterns in these studies. Mostler (1935) only recorded four birds being stung by wasps in the 1082 presentations in his extensive experiments, and Liepelt (1963) states definitively that 'no wasp stings occurred' during his 99 wasp presentations, although during another series of experiments, two redstarts were stung. Although not fatal, the redstarts spent 6–7 h recovering from their experience, which in nature might easily have been critical to their chances of surviving the night (Birkhead, 1974). From these studies it seems clear that, although having a dramatic effect when used, birds only rarely get stung by wasps, and therefore the sting cannot be the primary source of wasp noxiousness. This seems to be a classic case of risk versus hazard: the risk is low but the hazard great (C.J. Barnard, personal communication). Mostler considered the unpalatability of the abdomen to be the major source of noxiousness for wasps, and the sting being only secondary: subsequently Liepelt (1963) found that venom-free abdominal tissue evoked none of the typical unpalatability reactions. It is the terrible taste that the venom imparts to the abdomen that is the main deterrent for birds.

4.4 Comparison among models

Based upon the data available at present, I conclude therefore that all three main Holarctic groups of aposematic insects form Müllerian mimicry rings, one of them (bumblebees) consisting of subsets of Müllerian rings based on particular colour patterns, and involving some polymorphic species whose morphs are members of different rings. Any theory that predicts that such polymorphic mimicry rings should be rare cannot therefore be correct. For most bird predators, wasps are the most noxious models, and bumblebees are the

least noxious: bumblebees seem to be classified as unprofitable food by small insectivorous birds, whereas honeybees and especially wasps are categorized as noxious food.

5. The hoverfly mimics

5.1 Resemblance

Hoverfly colour patterns have often been labelled as mimetic, but only some species resemble their models closely, whereas others resemble their supposed models only vaguely, so are at best rather poor mimics (see, for example, the assessments in Howarth *et al.*, 2000). There is a clear distinction in the literature between bumblebee mimics, which are usually accepted as such without question, and honeybee and wasp mimics, where a large proportion are generalized or imperfect to the human eye. Furthermore, there have been many conflicts among writers about the supposed models of particular species. For example, *Criorhina asilica* was labelled as a bumblebee mimic by Verrall (1901), but as a perfect or almost perfect honeybee mimic by most authors (e.g. Dlusskii, 1984; Röder, 1990), although Drees (1997) called it 'cryptic'.

Table 9.1 counts all the Holarctic hoverfly species that have been named as mimics in the literature, organized by mimicry ring (F. Gilbert, unpublished). The striking thing is their sheer number, 256 species from a total of 2334 Holarctic species (11%). The world totals cited above (279 from 5600) demonstrate that outside Europe the available information is very fragmentary and unsystematic, hence these numbers are almost certainly an underestimate. European insects have been studied much more intensively, and in Europe there are 138 mimics out of a total of about 630 species (22%).

Virtually all the model identifications made by the authors concerned were purely on the basis of visual similarity according to our own human perception, with no experimental or any other kind of evidence. Of course, in natural circumstances predators are required to deal with potential prey in a wide variety of circumstances, including as fast-moving evasive insects, and some potential prey represent a significant threat to well-being. Identifications based upon our own perceptions may not correspond to the perceptual confusions between models and mimics generated by the eyes of predators, and this might distort our view of biological reality. One element that has been highlighted is the UV-component of colour patterns (Cuthill and Bennett, 1993; Church *et al.*, 2004), invisible to mammalian predators, but possibly conspicuous to UV-sensitive birds or insects. *A priori* an unsuspected and different UV-component to the colour pattern is unlikely in Diptera, since their black colours are indole-based eumelanins: melanins strongly absorb in the UV, and therefore syrphids are unlikely to have UV patterns superimposed on any black part of their body. Photographs of social wasps and some of their hoverfly mimics in both visible and UV light have no UV patterns evident in either, nor in non-mimetic *Sarcophaga* flies (L. Gentle, personal communication). Similarly, Nickol (1994) took photographs of the hoverflies *Volucella inanis*, *V. zonaria* and their models

(social wasps and hornets), and also found both models and mimics to appear entirely black under UV light. Thus the ability of birds but not humans to see UV light does not seem to be a serious problem in assessing the model–mimic relationships of hoverflies. In principle, if they did exist, these kinds of distortions are simple to remove, providing that we have realistic predator-based assessments of the degree of model–mimic confusion (see Green *et al.*, 1999); in practice, such assessments are difficult to obtain. The fact that we are able to classify some mimics as ‘extremely accurate’ probably implies that our perception is probably rather similar to that of at least some other predators.

Amongst the hoverfly mimics of bumblebees, most model identifications are reasonably obvious, and the lists of bumblebee models generated from the various suggestions by different authors are generally very similar in their colour patterns. Usually there is little ambiguity, since the quality of the mimicry is very high. The distribution of mimics among the various Müllerian complexes is very different between the Nearctic and the Palaearctic. No form seems to mimic the black bumblebees with thin yellow bands (complex B) in the western Nearctic, and this complex is absent from the Palaearctic. A large proportion of Palaearctic mimics are either black with red tails like *B. lapidarius* (complex A), or all tawny-coloured like *B. pascuorum* (complex I), or yellow-banded with a white tail like *B. lucorum* (complex E); all of these complexes and their mimics are largely absent from the Nearctic. In contrast, the Nearctic complex of syrphid mimics with a pattern of a yellow anterior and a black posterior, like *B. impatiens* (complex G), is absent from the Palaearctic, although the inconspicuous white tail of *Criorhina berberina berberina* and possibly one morph of *Cheilosia illustrata* are rather similar (and which therefore lack a closely corresponding model pattern in the Palaearctic). The white-patterned bumblebees of the Caucasus are paralleled by the white-patterned mimetic Diptera there. These distributional correspondences themselves constitute powerful corroborative evidence for the reality of mimetic relationships.

Only four Palaearctic hoverfly species have a quality of bumblebee mimicry that can be regarded as poor or unclear. In the Nearctic, very little work on models and their mimics has been done, except for the series of papers by Waldbauer and colleagues (see Waldbauer, 1988). In all their work, Waldbauer *et al.* decided to consider all bumblebees as members of a single Müllerian complex, and hence clearly regarded the differences among their colour patterns as irrelevant. Mimetic flies were labelled merely as generalized bumblebee mimics, without noting any closer resemblance to particular species. The authors were then able to assume that *Mallota bautias* was a general mimic of bumblebees, although in fact it resembles a particular group of eastern Nearctic bumblebee species rather closely. The context dependency of mimicry is highlighted, however, by the fact that *M. bautias* was for decades regarded as conspecific with the Palaearctic *M. cimbiciformis*, so closely do they resemble one another morphologically. However, *M. cimbiciformis* is uniformly interpreted as ‘a particularly fine mimic of the honeybee’ (Stubbs and Falk, 1983), and to my knowledge has never been identified as a mimic of any Palaearctic bumblebee. In the Nearctic, where honeybees were only introduced in the 19th century, the identical colour pattern can operate as a

bumblebee mimic: there are even some good experimental data showing that this bumblebee mimicry is effective in protecting the fly from predation (Evans and Waldbauer, 1982).

The mimicry of honeybees by some hoverflies (mostly *Eristalis* species, commonly called droneflies) has been commented upon for a very long time (Osten-Sacken, 1894), and even experts can be fooled. Benton (1903) exhibited a photograph published in an apicultural journal of 'Bees working on Chrysanthemums' which were in fact *Eristalis tenax*. He also recounted his role in 'the famous Utter trial' (whatever that was!), where the prosecution could not distinguish between honeybees and droneflies, and therefore were unable to prove positively that bees were the cause of some alleged damage. Even experienced beekeepers were unable to make the same discrimination. However, other entomologists have been less impressed with the match between the honeybee model and *Eristalis* species, and Mostler (1935) attributed their lower protection in his experiments to their lesser resemblance to the model. Nicholson (1927) agreed that *E. tenax* was 'somewhat like the common hive-bee', but insisted that it was 'one of the least convincing cases of mimicry I know'. I suspect that most entomologists would agree with Mostler (1935). There is a range of different mimics that correspond to the colour variants of honeybees: for example, *Eristalis tenax* and female *E. arbustorum* are like the darker varieties, and male *E. arbustorum* resemble the lighter varieties. There are also a number of bee-like *Eristalis* species in North America, but honeybees are not native to the New World and we have little idea about which of the native bee fauna might have led to the evolution of mimetic colour patterns amongst Nearctic *Eristalis* species.

It is the apparently wasp-mimetic syrphids that cause the greatest difficulties in assessing the extent of mimicry among the Syrphidae. They are freely quoted as examples of mimicry, but are often unsatisfactory under critical consideration. The resemblance is often not particularly close, and the quality of mimicry varies from good to bad: many authors have made this point (e.g. Brown, 1951; Dlusskii, 1984; Waldbauer, 1988; Dittrich *et al.*, 1993). Such problems led Waldbauer to define wasp mimicry to include only specialists that also mimic the long antennae and folded wings of vespoid wasps. However, this still does not mean that there is a one-to-one correspondence between species of models and these mimics, since often there is no particular exact replica of the mimic among available models. Some of the morphological adaptations for mimicry in this group are truly remarkable. For example, there are at least ten independently evolved solutions to the problem of mimicking wasp antennae (Waldbauer, 1970), three of which involve using the front legs. Species of the genera *Spilomyia*, *Temnostoma* and *Volucella bombylans* have only the normal short cyclorrhaphan type of antennae, but instead the anterior half of the forelegs is darkened, and the flies hold them up and wave them about in front of the head to create an amazingly good illusion of wasp-like antennae. Interestingly, not one bumblebee mimic has evolved elongated antennae, and only *V. bombylans* uses behaviour to mimic having them (although only females do this, in their final stealthy approach to the bumblebee nest in which they oviposit: Fincher, 1951; Rupp, 1989). This difference must tell us something about the salience of

such features to predators; presumably long antennae are important features of identifying wasps, but the coat of hairs dominates when identifying bumblebees. Wasps do indeed wave their antennae about conspicuously, and bumblebees do not.

One characteristic of aposematic models and their mimics is that they often have harder, more durable bodies than other insects, toughened to withstand attack by predators so that the predators taste them but the prey still survive (Rettenmeyer, 1970: 58). The abdomen of many syrphine species is 'emarginate', i.e. each tergite is compressed just before the lateral margin, creating a narrow ridge or beading along the edge: this feature may have arisen in order to toughen the abdomen, since it occurs only in mimics. Specialized mimics have gone much further, and have the entire abdomen arched and convex, or cylindrical; the cuticle is punctate and hence greatly strengthened; and the joints between the overlapping tergites are very strong. If possession of an abdomen of this type is taken to define which of the black-and-yellow syrphids are truly wasp mimics, then rather few temperate species pass the test – in the northern hemisphere, only those of the genera *Ceriana*, *Chrysotoxum*, *Sphecomyia*, *Spilomya* and *Temnostoma*. There are, however, many genera with this type of abdomen in the tropics, perhaps an indication of a longer period of evolution among models and mimics there compared with the Holarctic.

The possibility that large Müllerian complexes of many wasp species together constitute a single model for Batesian mimics has hardly been addressed by anyone since Nicholson's (1927) largely uncited paper, except by Waldbauer and his colleagues in the eastern USA; this is an especially surprising omission among Palaearctic workers. Only Nickol (1994) has really identified this property clearly in his discussion of mimicry in *Volucella zonaria*, although it was also implicit in Dlusskii's (1984) important paper. Despite this omission, many such complexes appear to exist amongst black-and-yellow noxious insects and their mimics. The Müllerian complexes themselves are much less homogeneous than those of bumblebees, and overlap so that the boundaries are less distinct; presumably this is a consequence of their noxiousness.

5.2 Overall features of resemblance

Two patterns are very striking across these major model–mimic groups. The first is the great difference in the incidence of polymorphism among the groups (Table 9.1). There are 71 species of bumblebee mimics, at least 25 of which are polymorphic (35%), with each morph mimicking a different bumblebee species. This number of polymorphic species may in fact be even higher, since several species are only represented by a few specimens, or are poorly known taxonomically (e.g. some of the magnificent *Criorhina* species from western North America): there may still be multiple instances of 'species' which in fact represent different colour morphs of a single species. Among the better-known European species, more than 50% are polymorphic (18 of 35 species). Many of the polymorphisms are different between the sexes, either by each sex having a

different (overlapping or non-overlapping) range of morphs, or mimicry being limited to only one sex (there are 17 male-only and 11 female-only morphs recorded); this may indicate a role for apostatic (non-mimetic) mechanisms in these polymorphisms (B. Clarke, personal communication). In stark contrast, of all the other mimetic hoverfly species, there is not a single example of a truly polymorphic species. A few species have a small degree of sexual dimorphism in their patterns, which some authors have then interpreted as mimicking different models, but none is very convincing.

The second striking pattern is the difference in specificity of mimicry (Table 9.1), to which I have already alluded. Virtually all authors who describe bumblebee mimics comment on their amazing similarity to their models. In contrast, many of the supposed wasp mimics are not very similar at all to their models. Honeybee mimics are somewhat intermediate, with some species being described as very good mimics, but others as rather poor.

An obvious objection to the claim of differences in the specificity of mimicry is that human perception is not the same as that of predatory birds, and perhaps they perceive the 'poor' mimics differently. Dittrich *et al.* (1993) used operant conditioning to test whether a representative bird would make the same sort of mistakes that humans do when presented with models and their hoverfly mimics. They chose pigeons (*Columba livia*) to represent a generalized avian visual system. The birds were trained to discriminate between images of wasps and non-mimetic flies, and then tested to see how they would respond to images of wasp mimics. One group (fly⁺) were trained to peck at the images of non-mimetic flies for food, wasp images being unrewarded. A second group (wasp⁺) were trained to peck at wasp images for food, with the non-mimetic flies being unrewarded. Both the fly⁺ and wasp⁺ groups of pigeons learned to discriminate between the two sets of images equally quickly, after only two training sessions. During the 20-s projection time of a rewarding stimulus, the pigeons pecked 50–60 times, whereas they hardly pecked at all at non-rewarding images. This suggests that there is no inherent bias of the pigeon visual system against black-and-yellow wasp-like patterns (perhaps not surprisingly, since it is not insectivorous).

The pigeons were then tested using images of hoverflies chosen to represent a range of mimetic quality as perceived by humans. The pigeons were extremely consistent in their responses, ranking the hoverflies in more or less the same order as did the humans, with the fly⁺ group being more or less the mirror image of the wasp⁺ group. Thus the main conclusion from this work is that pigeons do appear to see hoverfly mimics in roughly the same way as we do: they seem to rank the images in the same way, and make the same sort of category mistakes. The result is not an artefact of the lack of UV in the photographic images used for the experiment, as claimed by Cuthill and Bennett (1993), since using real specimens produces the same result (Green *et al.*, 1999).

There were two interesting exceptions to this general pattern, which may contain pointers to some aspects of the evolution of mimicry. *Syrphus ribesii* was classified by the pigeons as the most wasp-like of all the images they looked at, and *Episyrphus balteatus* was also classified as extremely wasp-like:

these are not at all like the decisions made by humans, who are generally not impressed by their mimicry. Perhaps these species have exploited some peculiar aspect of the avian visual system or the psychology of learning so that they get classified as very wasp-like, even though to our eyes they are not; or pigeons use rather different features of insects than humans use in the classification process; or there may be some entirely different explanation.

5.3 Abundance

Considering how many people are interested in mimicry, it is amazing how little is known about mimic : model ratios in nature, even for butterflies. There are several hundred studies of syrphid communities, often using Malaise traps that also catch Hymenoptera, but not one presents any estimates of these ratios. Even vague estimates are very rare. Occasionally authors will comment on perceived ratios: for example, Heal (1982) stated that *Eristalis tenax* was more abundant than its honeybee model at many sites in the autumn, but he did not say what the actual ratios were. Heal did measure the relative abundance of light and dark morphs of *E. tenax* in relation to the light and dark forms of honeybees: over all his sites the light morph of the mimic was at a frequency of 44%, and of the model 45%, which is certainly consistent with mimicry maintaining the morph frequencies.

The quantitative data we do have to reconstruct these ratios consist of the extensive Malaise trap sampling from an urban garden in Leicester (Owen, 1991) and a similar but more restricted dataset from the ancient forest of Bernwood in Oxfordshire (Watts, 1983; Archer, 1988), and a set of observer censuses from the USA (Waldbauer and Sheldon, 1971; Waldbauer *et al.*, 1977; Waldbauer and LaBerge, 1985), UK (Grewcock, 1992; Howarth and Edmunds, 2000), European Russia (Dlusskii, 1984), and the Massane forest in the French Pyrenees (a fragment of the original wildwood of Europe: Grewcock, 1992). All methods of systematic sampling introduce some sort of bias (Southwood and Henderson, 2000), especially among species, and Malaise traps are poor at catching certain species, rendering the trapping data potentially misleading. In contrast, observer censuses could be considered to be a fairly close approximation of the hunting behaviour of predators (but see below).

Owen's (1991) data on a yearly basis show generally low mimic : model ratios, with mimics usually less or much less common than their models. This is always true for the bumblebee and honeybee mimicry complexes found in the garden, and for all the good wasp mimics; only the poor mimics of social wasps (complexes III and IV of Table 9.1) are much more abundant than their models. In Bernwood Forest the social wasps (43%) and bumblebees (39%) made up most of the hymenopteran catch, with solitary bees (10%), solitary wasps (6%) and honeybees (2%) being much less common. Poor wasp mimics were more than four times commoner than their models, and both good and poor honeybee mimics were also commoner than their models. In contrast, all the bumblebee mimics were rarer than their models, the commonest (complex J of Table 9.1, mainly *Criorhina berberina*) being only 32% as common as its model (*Bombus pratorum*).

From observer censuses of only good mimics in Illinois (USA), Waldbauer and colleagues found mimic : model ratios were all consistently at or below 1.00, meaning that mimics were always about as common, or more usually less common than their models. All the wasp complexes had higher ratios of mimics to models than the bumblebee complex, which had consistently low ratios in all areas. In ancient woodland sites in the UK, Grewcock and Howarth also showed that these ratios were low (<1) for the good bumblebee and wasp mimics, but poor wasp mimics were much more abundant than their models (by a factor of 4–19). In Massane, wasp mimics were more abundant than their models, but only by a factor of 2. Honeybee mimics were also much more abundant than their models in the UK (by a factor of up to 50), less so in Massane (4.5). Thus as in the Malaise-trap data, excess mimic : model ratios are a feature of poor wasp mimics, and also sometimes of honeybee mimics.

The relative abundance of models should also probably be an important feature of mimicry theory, especially if these vary in aversiveness (which could imply quasi-Batesian systems): What is the evidence from field studies? Among insects visiting flowers in dry grasslands of Germany (Kratochwil, 1983), bumblebee mimicry rings were very common (complex A of Table 9.1 – 90, E – 220, F – 188, J – 185), as were honeybee-like forms (222, but none of them *Apis*), but social wasps were rather rare (23). In Howarth's (1998) census walks in UK ancient woodlands the same pattern was evident, with bumblebee rings (complexes of Table 9.1: A – 61, F – 3271, J – 663) and honeybees (1475) being common relative to social (complexes II to IV of Table 9.1 – 880) or solitary wasps (I – 312). Waldbauer's group working in forests in the USA also found that bumblebee models were between 1.5 and 3.2 times as common as all the wasp models combined. Only in Bernwood (Archer, 1988) were social wasps (complexes II to IV of Table 9.1 – 1846) a bit commoner than bumblebees (complexes of Table 9.1: A – 1, E – 1021, F – 142, J – 549), and much more common than honeybees (224, including 74 *Apis*). The pattern seems very clear: the least noxious bumblebee models are also normally substantially more common than the most noxious wasp models.

It is possible that simultaneous model : mimic ratios are not what matters. In much-cited studies of Waldbauer and colleagues (see Waldbauer, 1988), the phenologies of mimics in Illinois showed a gap in the mid- to late-summer period, which the researchers concluded was timed to coincide with the period when young fledglings were learning about what was good and not good to eat. Furthermore, early-emerging mimics did not necessarily coincide with the appearance of their supposed models, whose flight period was much later in the season. Putting these phenological patterns together with the finding that some individual birds can, under some circumstances, remember aposematic colour patterns for long periods of time (months), they concluded that mimics must be protected by these memories, and therefore models and mimics do not have to coincide in space and time in order for mimicry to be effective. There are several problems with these conclusions. The first is that even non-mimetic hoverflies show the same mid-season lull in numbers, which seems to be more connected with the availability of aphids than with the number of fledgling birds. Many host-alternating aphids switch hosts in mid-season, creating a

mid-season gap in aphid numbers well known to applied entomologists (e.g. Bombosch, 1963). A second problem is that the predator education process is not simply one of the rates of learning and forgetting, but also that of extinction, the learned alteration of a previously established association (see Shettleworth, 1998). Very little is known about the rates of these three processes in birds in any realistic setting, but Holling's (1965) experiments with shrews and Mostler's (1935) with birds generally showed a much faster process of losing the association than Waldbauer envisaged. Although rather easy to test experimentally, the hypothesis has only been tested observationally by repeated phenological studies in different areas; more critical testing is needed before these ideas can be accepted as established. Most other natural history information indicates that mimicry is only effective when models and mimics can be experienced simultaneously by a predator.

Heal (1995) noted that the main model changes from month to month. In spring, the best model to copy is the honeybee, because workers start foraging in the very first days of spring, and indeed some of the common honeybee mimics are active at that time. The great increase in bumblebee workers from growing colonies occurs in June and July, and many bumblebee mimics are on the wing then. Wasps are most obvious in late summer, when wasp mimicry peaks. Thus there is a regular shape to the phenology of mimetic complexes in the UK. These speculations were broadly supported by the quantitative data of Howarth and Edmunds (2000).

Howarth *et al.* (2004) predicted further that there would be an hour-to-hour dependency between the numbers of models and their Batesian mimics because of behavioural convergence in responses to habitat and weather conditions. Testing for covariation among models and their mimics, over and above the effects of month, site, weather and other general conditions, they found some very striking patterns. There were nine significantly positive relationships out of the 17 model-mimic pairs tested, and furthermore all 17 (bar one) were positive, itself a highly non-random pattern. Only one relationship was significantly negative, between *Helophilus* and their poorly mimicked social wasp models. In four out of seven poor mimics, and five out of ten good mimics, there was a significant positive relationship with numbers of the presumed model: this pattern is not significantly different between good and poor mimics. Interestingly, though, six of the seven common or abundant species showed relationships with their models, whereas this was true for only three of the ten rarer species, a significantly non-random pattern; thus common mimics are more likely to co-vary with their models. This result is very different from Waldbauer's since it involves intimate simultaneous co-occurrences between models and mimics, rather than their phenologies being completely different because of long predator memories. Possibly predators require constant reminding of noxious patterns (Rothschild's, 1984, *aide-mémoire* mimicry), but we need much more study of predator behaviour so that realistic models of their learning processes can be used in mimicry theory.

We do not have to reject the idea that common syrphids have evolved to be mimics merely because they are common. This crucial point was made by Nicholson as long ago as 1927. He pointed out that mimicry evolves when some

individuals have a slightly higher probability of surviving than others because their variant of the colour pattern happens to provide some protection from predation via its greater resemblance to a noxious model. As long as that is true, then mimetic colour patterns will increase in the population relative to normal patterns. As alluded to in the introduction, ecologists would be very surprised if syrphid populations were regulated by birds feeding on the adult stages.

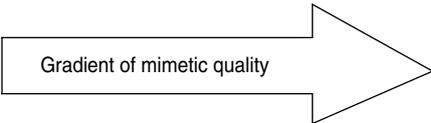
It is probably true that if the population is low, the selective advantage to mimicry will be greater, and hence there may be stronger selection to perfect the mimetic pattern. Thus, as Glumac (1962) suggested, low relative abundance may lead to mimicry, rather than the other way round. He pointed out also that many of the morphological and behavioural components of good mimics are also present in non-mimics, but acquire a new significance when selection acts to improve mimetic resemblance. Thus 'wasp-waisted' abdomens occur in *Baccha*, *Sphegina* and *Neoascia* without much or any mimetic coloration, but this morphology is particularly effective when combined with other morphological components of mimicry, such as elongated antennae and a darkened anterior sector of the wing. Glumac regarded only certain rare syrphids as mimetic; indeed, he really thought that mimicry was completely incidental in syrphid ecology. Most of the features normally interpreted as mimetic, he regarded as the result of convergent evolution, and his thinking was really part of the group-selectionist mind-set of biologists before the Darwinian revolution in behaviour and ecology.

5.4 Overall characteristics of hoverfly mimicry

Table 9.2 gives a picture of the range of mimetic quality within one of the major model types, mimics of social wasps. The hoverflies are ordered along a spectrum of mimetic quality, indicated by the arrow, as assessed by both

Table 9.2. Spectrum of mimetic quality among the hoverfly mimics of social wasps. Assessments of variability are from Holloway *et al.* (2002); mimetic quality estimates come partly from Dittich *et al.* (1993), Howarth *et al.* (2000); all other data are from F. Gilbert (unpublished).

	Model	Hoverfly mimics			Non-mimics
Palatability	Noxious				Palatable
Mimetic accuracy	n/a	Accurate	Less accurate	Poor quality	n/a
Pattern variability	Variable	Variable	Quite variable	Less variable	Variable
Abundance	Common	Rare	Common	Abundant	Common
Structure	Armoured	Often armoured	Rarely armoured	Not armoured	Not armoured
Behavioural mimicry	n/a	Absent	Present	Present	n/a



human and pigeon eyes (see Dittrich *et al.*, 1993). Other axes of variation correlated with this spectrum are pattern variability, relative abundance and the occurrence of behavioural mimicry. Like the models, good mimics have very variable colour patterns, consistent with a relaxation of selection pressure caused by their accurate mimetic appearance: poor-quality mimics have much less variable patterns, but non-mimics are just as variable as the models (Holloway *et al.*, 2002). Visually poor mimics are much commoner than their models, and may compensate for these factors by evolving behavioural mimicry such that they tend to co-occur much more frequently with the models at particular times and places where predators encounter them (Howarth *et al.*, 2004). In the model, the tergites of the abdomen are joined together extremely strongly with overlapping sclerites, making it very difficult for a predator to grasp hold and dismember it. This kind of structure is often also present in the rare, highly accurate mimics, but is absent in common poor mimics.

Across the major types of model (Table 9.3a) there are also some very strong patterns. I have ordered the groups along a gradient of increasing noxiousness (justified above). Unlike the other two groups, the bumblebees contain a diverse set of Müllerian complexes, and the overwhelming characteristics of its hoverfly mimics are: a matching diversity, including a very high degree of polymorphism in both models and mimics; relative rarity; and highly accurate visual mimicry. The contrast with the social wasp group is very clear. Their hoverfly mimics are not polymorphic, are often visually very poor matches to the model, and are often many times more abundant than their models.

Thus polymorphism in certain Müllerian models (bumblebees) is common, and polymorphism among their apparently Batesian mimics is also common. Where the model has racial colour variation (honeybees), its mimics match this. Finally, in the wasp complex where there is no polymorphism within any of the model species (even though variation among the colour patterns of its constituent species certainly exists), no polymorphism is seen in the mimics.

6. Can mimicry theory account for the spectrum of hoverfly mimicry?

The widespread occurrence of poor-quality mimicry has given rise to a variety of different hypotheses to try to account for the evolution of these 'mimetic' patterns, many of them based to some extent upon the consideration of syrphid colours. Many are not really part of standard mimicry theory, but are additions or alternatives to some of its postulates. I have listed the main elements of these ideas in Table 9.3b, with an indication of the way in which each idea accounts for the spectrum of mimicry identified in Table 9.3a. These ideas are not necessarily mutually exclusive, since in the main they involve different types of trade-offs, costs and benefits, and several are almost certainly operating at the same time.

Table 9.3. (a) Overall characteristics of hymenopteran-model : hoverfly-mimic complexes; and (b) their possible causes. The thick arrow indicates the gradient of model noxiousness (see text for justification), and the possible explanations each creates a spectrum correlated with this gradient.

	Bumblebees	Honeybees	Wasps
(a) Models			
Size	Large	Medium-sized	Medium-sized
Coloration	Aposematic	Non-aposematic	Aposematic
Number of Müllerian rings	Usually 1–4 in any one region	One	One large diffuse ring
Polymorphism	Present	Racial variation	Absent
Nature of defence	Heavily armoured Palatable Rarely sting	Armoured Unpalatable Rarely sting	Armoured Highly unpalatable Sometimes sting
			↑
Hoverfly mimics			
Size	Large	Medium-sized	Small to medium-sized
Physical defence	Often armoured	Rarely armoured	Rarely armoured
Abundance	Rare	Often common	Often abundant
Polymorphism	Polymorphic; often sex-linked	Variation matching model	Non-polymorphic
Visual similarity	Usually visually accurate	Reasonable quality	Occasionally good, usually poor
(b) Possible explanations			
1 Occurrence of mimicry	Mimics		Non-mimics
2 Nature of predator perception	Same as human		Different from human
	Birds		Invertebrates
3 Nature of mimicry	Batesian		Müllerian
4 Nature of model	Model only mildly noxious		Terribly noxious
5 Type of mimicry	Mainly visual		Mainly behavioural
6 Effect on predator	Deceived		Reminded/confused
7 Speed of evolution	Fast, complete		Slow, incomplete
8 Disturbance by man	Forest habitats, undisturbed		Habitats disturbed by man
9 Resistance to evolving perfection:			
(a) cost of mimetic pattern	High cost, high benefit		Low cost, low benefit
	Hair colour easily modified		Major changes to tergite colours not possible
(b) attack threshold + kin selection	Attack threshold low, no kin-structured distribution		Attack threshold high, kin-structured distribution
(c) number of models	Single model	Different races of model	Multiple models

6.1 The occurrence of mimicry: 'poor mimics' are not mimics at all

An obvious tack is to deny that mimicry can possibly be of poor quality, and hence to claim that poor 'mimics' simply are not mimics at all. Before the advent of more rigorous quantitative testing of mimicry theory by the Browers and others, there were several who claimed that because some mimics were eaten by some predators sometimes, this meant that mimicry did not 'work', and hence was invalid as a theory (Heikertinger, 1918, 1936, 1954; McAtee, 1932). It is a simple step then to accept perfect mimicry as a valid concept, but to deny any other kind of resemblance as mimetic: for example, Glumac (1962) and Drees (1997) thought there were no mimics among syrphids except for those with elongated antennae (even bumblebee mimics, which they attributed to convergent requirements of thermoregulation). Waldbauer and his colleagues (see Maier, 1978; Waldbauer, 1988) simply ignored poor mimics altogether because it was impossible to determine whether they were really mimics or not.

However, denial of the reality of mimicry in these syrphids has not been credible since Mostler's (1935) detailed and large-scale experiments on learning in naive and experienced insectivorous birds. Single, either hand-reared or experienced (wild-caught) birds were free to fly in a large windowed room with naturalistic perches, and models and mimics were released alive into the back of the room, usually to fly directly to the window: Mostler recorded the subsequent behaviour of the birds. He divided his study into two parts: the first was concerned with the beginning and the end points of the learning of birds, i.e. the responses of young naive birds and of old experienced birds to models and mimics; the second part investigated the learning process itself. Although he did not plot or hardly even analyse his data, the great value of his work is not just that it was the first well-designed large-scale experimental approach to testing the theory of mimicry, but also that he obtained comparable data on all three hymenopteran models and their hoverfly mimics. These established beyond doubt that the colour patterns of all the syrphids he used did give substantial protection from predation, and that the protective effect was proportional to mimetic similarity (Figs 9.1 and 9.2). Honeybees and their mimics were a less successful mimetic system than the wasp system, while the bumblebee system was the most successful of all. When mimics were offered soon after their models (within 50 min) in the wasp mimicry system, the wasp mimics were strongly protected (Fig. 9.2), fading with time, but this protection vanished when they were offered before models, and in fact the wasps suffered, since more wasps than normal were attacked. Assessment was easier when the birds could compare models and mimics at the same time, but when this could not be done, they were much more cautious, and the protective effect lasted much longer. Mostler also conducted some trials of wasps and wasp mimics where he gave insects in the sequence model – mimic – model, ensuring in each case that the mimic was eaten before the second model was presented. The proportion of models attacked after experiencing the mimic was much higher than those attacked beforehand, demonstrating very clearly the negative effect that mimics have on models.

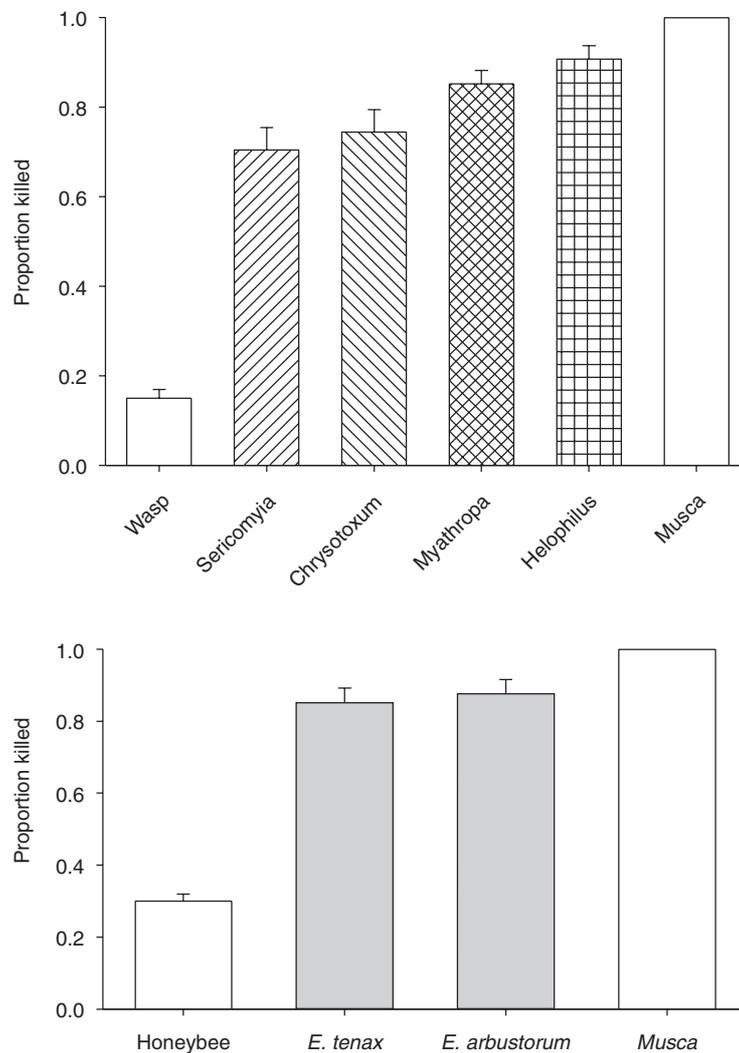


Fig. 9.1. The mean proportion (\pm SE) of offered model and mimetic insects that were attacked and killed by a set of insectivorous birds ($n = 48$) of various species. *Above*: wasps and their mimics, *Below*: honeybees and their mimics (two *Eristalis* species). In each case, mimics are ordered along a gradient of mimetic quality as assessed visually by the observer. Data from Mostler (1935).

A further and powerful argument about whether the colour patterns are mimetic is the observation that in New Zealand there are no native bumblebees or yellow-and-black noxious wasps, and uniquely there are no wasp- or bumblebee mimics either among native New Zealand syrphids (S.D. Wratten, personal communication).

The only field-based experiments on the protection afforded to syrphid mimics were done by Dlusskii (1984) in a forest close to Moscow. He undertook

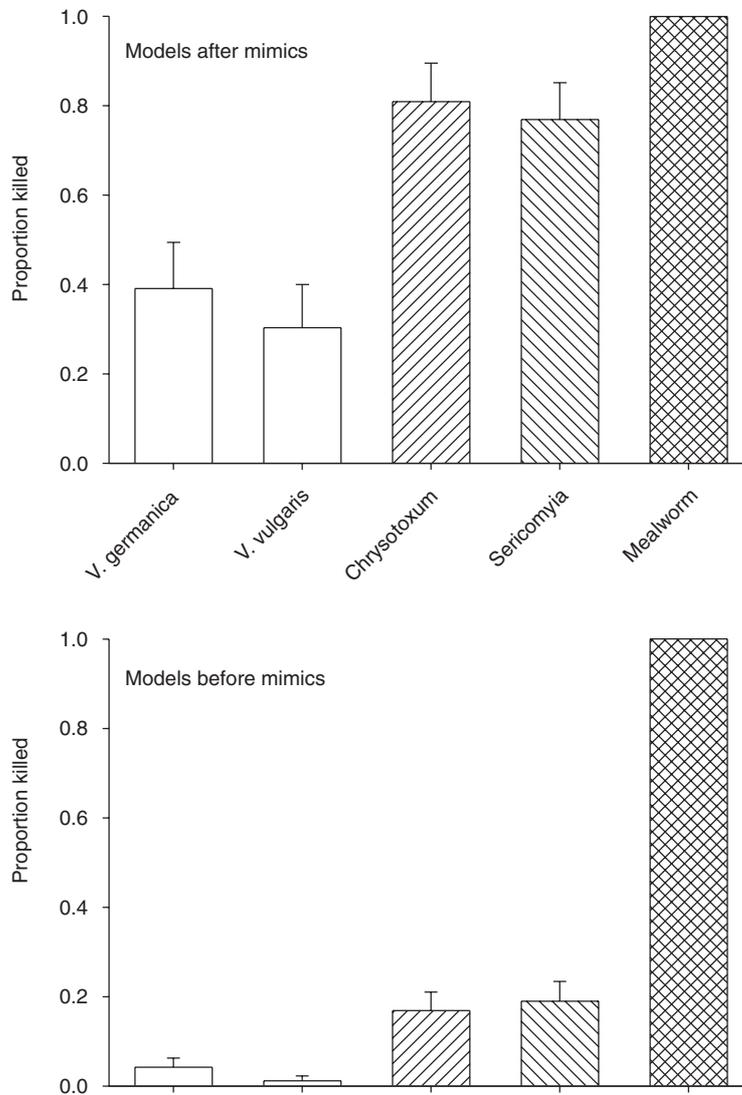


Fig. 9.2. The average proportion (\pm SE) of models (*Vespula germanica*, *V. vulgaris*) and mimics (*Sericomyia borealis*, *Chrysotoxum arcuatum*) from the wasp model–mimic complex, and mealworms (control) killed and eaten by birds when models were offered after mimics (*upper*) or before mimics (*lower*). Data from Mostler (1935)

a series of choice tests under natural conditions, by placing near nests a table on which were offered live insects tethered in pairs, able to move and even to start up flying. Dlusskii paired a series of different insect species with *Eristalis nemorum*, which he knew from earlier experiments to be acceptable, and he determined which of the two insects was taken first. If one insect appeared to be palatable and the other unpalatable, then the palatable insect was taken at least

90% of the time, and even if the unpalatable insect was taken, it was never delivered to the nest. If both seemed unpalatable because of prior experience, then the bird sat and looked at them, but flew away again without sampling either. If both seemed palatable, then the bird ate them both, but the most attractive one was eaten first, and usually this was the larger of the two alternatives. Thus it was possible to test whether insects were considered to be palatable or not to the birds being tested. The Hymenoptera were always considered to be unpalatable, even *Eucera longicornis*, which was rare in the area and therefore (Dlusskii thought) unlikely to have been encountered before by these birds. These observations (and pigeon experiments by W. Dittrich (unpublished data)) suggest that the birds had a polymorphous concept (see Lea and Harrison, 1978) of what a hymenopterous insect was, and could apply it effectively to identify the insects on offer even if they had never encountered them before. On the other hand, all the syrphids were considered to be palatable, and even the superb wasp mimic *Temnostoma vespiforme* was eaten by spotted flycatchers despite the fact that its model was rejected. Dlusskii concluded that these experienced birds usually distinguished between models and mimics, even the good ones, and thus mimicry was ineffective here. There were cases where prior experiences caused the birds to reject mimics, however, and thus on occasion even weak similarity to a model could protect mimics.

Apart from Mostler's and Dlusskii's work, there are really only fragments of information in the literature about the protective effects of syrphid mimicry (see Pocock, 1911; Lane, 1957; Steiniger, 1937a,b; Liepelt, 1963; Davies and Green, 1976; Evans and Waldbauer, 1982; Heal, 1982, 1995; Evans, 1984; Grewcock, 1992). I can summarize the available data no more clearly than Steiniger (1937b) did many years ago:

- Syrphids form part of the normal dipteran diet of many insectivorous birds such as robins (*Erithacus rubecula*), redstarts, and *Sylvia* and *Phylloscopus* warblers.
- Wasps are not normal food for these birds, which do not have any innate avoidance of wasps, and eventually come to try one; once tried, they are not eaten any more.
- Syrphids are also removed from the normal diet of these insectivores as soon as they become acquainted with wasps, since wasps and syrphids are apparently confused.
- The protective effects of this process are related to the similarity between model and mimic, but even poor-quality mimics benefit to some degree.

6.2 The nature of predator perception: 'poor mimics' appear perfect to their predators

It is possible that poor mimicry is an artefact of human perception, and that to the predators that generate the selection on the pattern, these mimics appear to be just as perfect as any other mimic. We have already seen that Dittrich *et al.* (1993) have suggested that the apparent imperfections of two very common

syrrhid mimics were only so for human eyes, because they appeared to be categorized as extremely good mimics by pigeons. Against this interpretation is the overall pattern of mimicry obtained from the pigeon experiment, which matched the ordering of mimetic quality of the human eye. It may well be true that certain species have managed to exploit some feature of bird perception in order to appear more perfect than they do to us, but in general this is not the case, and hence it is not a solution to the problem of imperfect mimicry. I have already shown above that the fact that birds can see UV does not seem to be an important feature of syrphid predation, and therefore is an invalid interpretation of the two anomalous patterns (cf. Cuthill and Bennett, 1993; Church *et al.*, 2004).

Alternatively, the fact that bumblebee mimics are on average substantially bigger than wasp mimics might cause them to have *different* predators, and this might underlie the observed differences in mimetic quality and relative abundance (Edmunds 2000). According to current thinking, however, this requirement for a visually selective agent restricts the potential candidates basically to birds, because it seems to rule out virtually all invertebrate predators. But is this true?

Kassarov (2003) tries to argue that not even birds are suitable candidates because even their visual abilities are inadequate for perceiving adequately the largest insect patterns (butterflies). He thinks that birds only see the flight movements of potential prey, relying on these to make decisions about whether to attack or not. He rejects the idea that birds can be the selective agents generating mimetic colour patterns. If true, then the patterns must have arisen by magic!

Dragonflies are perhaps the most obvious of insect predators that hunt visually, although their eyes seem to be adapted to detecting potential prey moving against the sky, rather than forming an image that would include the colour pattern (Corbet, 1999: 341). Most insect eyes appear to be primarily movement detectors, and the conventional wisdom is that they probably do not form an image sufficiently detailed to be able to generate selection for high quality mimicry. Some large aeshnids do take many bees (Corbet, 1999: 354, 379), but no-one has recorded them taking bee-mimics. While they may sometimes avoid certain prey types, such as wasps (Alonso-Mejia and Marquez, 1994; O'Donnell, 1996; Howarth, 1998: 16), unless this avoidance is visually based it is hard to imagine this contributing to the evolution of mimicry. Recent work (Kauppinen and Mappes, 2003; T. Sherratt, personal communication), however, shows that dragonflies are able to select between wasps and flies, and that this discrimination is largely visual: black-and-yellow stripes alone reduce rates of attack. Thus dragonflies may well have contributed to the evolution of mimicry in insect colour patterns.

The beewolves of the genus *Philanthus* (Sphecidae) are well-known bee predators (Osten-Sacken, 1894: 11). The European *P. triangulum* takes almost exclusively honeybees, mostly from flowers but also from the hive entrance; they never take any mimetic Diptera (Iwata, 1976: 150). Fabre (1913) tried to deceive one by offering it an *Eristalis tenax*, which it 'rejected with supreme contempt!' In the USA, *P. bicinctus* preys on bumblebees in Yellowstone

National Park, but is apparently never deceived by mimetic flies; it makes an interesting contrast with the sphecid *Bembix pruinoso*, a fly predator that feeds very often on *E. tenax* (Evans, 1966: 131). In neither case is there any evidence of any protection gained from the resemblance. This is not surprising, since *Philanthus* is well known to respond visually first to motion, and then when close odour becomes the crucial cue, stimulating the final pounce. This odour-directed prey capture explains why honeybee mimics are never captured. Similarly predators specializing on flies, such as *Bembix*, often take mimetic syrphids but do not take wasps, for the same reason (Evans and Eberhard, 1970: 52).

Robberflies (Diptera: Asilidae) are also voracious predators, but there is only a single study that suggests they can generate selection based on vision: a study of tiger beetles by Shelly and Pearson (1978) suggested that a robberfly may have been responsible for the evolution of both chemical and aposematic defences. However, the red pattern involved is just a block of colour, very crude in comparison to hoverflies. Brues (1946) suggested that asilids had a 'fondness' for worker honeybees, but this seems unlikely, given the evidence of all the prey records (listed at www.geller-grimm.de/catalog/lavigne.htm). He thought that because they frequently catch *E. tenax*, this meant that 'to the insect eye *Eristalis* really looks like a bee'. However, the appropriate null hypothesis of no ability to discriminate, that asilids merely catch both because they co-occur in the same habitats, has never been tested.

Sphecidae (Hymenoptera) are well-known insect predators, but members of only two of the subfamilies (Nyssoninae and Crabroninae) take syrphids (Bohart and Menke 1976; Iwata, 1976). *Bembix* (Nyssoninae) are large, very fast-flying wasps that deliberately target flies on flowers, or swarming males, and hence often take a large number of muscids, tabanids and syrphids. In Tsuneki's (1956) Japanese study, for example, *B. nipponica* took prey belonging 11 families of flies overall, but in some sites and years syrphids formed almost half the prey (47%), mainly *Eristalis cerealis*. A large number of the hoverflies caught were mimetic, such as the wasp-like *Takaomyia* and *Chrysotoxum*, and the bee-like *Eristalis*. Large flies took disproportionately longer to find, capture, subdue and bring back to the nest: although it took on average 0.7 s longer to catch a syrphid rather than a non-syrphid, this difference was not significant and there was no evidence that syrphids were harder to catch than other flies. The other subfamily, the Crabroninae, are virtually all dipteran specialists, and the Crabronini are especially significant as hoverfly predators. A number of genera are important, especially *Ectemnius*. At least one species, *E. cavifrons*, seems to be a syrphid specialist; it is the commonest species in the UK (Pickard, 1975). The great majority of the prey in Pickard's study consisted of poor mimics (*Syrphus* spp. and *Episyrphus balteatus*). There was some selectivity involved because small dark species were greatly underrepresented, and no *Eristalis* were taken at all: Pickard thought their resemblance to honeybees might have protected them. Thus discrimination on the basis of colour patterns is possible, with a preference for yellow-and-black species. Some other studies have suggested that visual mimicry may protect against solitary wasps (e.g. predation on salticid spiders: Edmunds, 1993)

Social wasps (Spradberry, 1973: 141) take a huge variety of prey, but they concentrate on adult Diptera: some colonies have been recorded as taking up to 84% flies. Hornets can certainly take a lot of honeybees. It is usually thought very unlikely that these predators identify their prey visually, but recently (Tibbetts, 2002) *Polistes* wasps have been shown to identify individual colony members via variation in facial markings. Such a sophisticated ability indicates the capability for social wasps to generate natural selection for visual mimicry: this needs testing.

It is also possible that spiders make the sort of visual mistakes that would select for mimetic colour patterns, even though Bristowe (1941, vol. 2: 319) states that 'the yellow and black wasp-like appearance of certain syrphids is of no avail against spiders'. In fact spiders treat social wasps and bees with great caution, and only the largest species can tackle them successfully. Pocock (cited in Osten-Sacken, 1894: 11) noticed that *Agelena labyrinthica* used special precautions before overpowering a honeybee enmeshed in the web, whilst they pounced immediately on normal prey: when offered *Eristalis*, spiders approached and finally killed them, but used the same precautions as for honeybees.

Spider webs are in general not very good at catching hoverflies (Nentwig, 1982) since these flies are too large, strong and active. Insects with kinetic energies of about 150 μJ are able to fly straight through a web, and those with energies greater than about 500 μJ always do. The weight and flight speeds of syrphids indicate kinetic energies between 25 and 500 μJ , and therefore the smaller species should generally get caught, while the larger species (*Eristalis* spp., for example) should be able to ignore webs altogether. After becoming entangled in a web, insects differ considerably in their behaviour, and these differences determine whether they escape. Insects such as syrphids that react to web entanglement by continuous vigorous activity are able to escape in the few seconds available before the spider attacks, and syrphids weighing as little as 9 mg escape rather easily: most syrphids are larger and more powerful than this. Orb-web spiders *Araneus diadematus* studied by Myers (1935) seized non-mimetic Diptera such as *Calliphora* immediately with no precautions, and never wrapped them in silk. When wasps were the victims, the spiders would carefully rotate the prey, showing great skill and alacrity in avoiding both the mouthparts and the apex of the abdomen, and swathe it in silk until completely helpless before biting near the centre of the dorsal surface – the safest position. Honeybees and *Eristalis* were, if tackled at all, treated with great caution and were nearly always swathed in silk. Thus spiders treated their victims differently, not according to size and vigour, but according to the perceived risk; *Eristalis* was treated like a bee rather than a fly of the same size.

Flower spiders (Thomisidae), especially *Misumena*, have evolved to catch flower-visiting insects, and most of their prey are syrphids, honeybees and bumblebees (see Morse 1986). Only a single study has addressed whether colour patterns might be protective. About half the individuals studied by Tyshchenko (1961) would avoid both wasp models and their mimics, and the other half would eat them; the reluctance of the former group to attack mimics was in proportion to their visual similarity to the model. Thus visually based predation by spiders needs systematic study, since it too seems perfectly capable of generating selection for mimicry.

Which birds might be candidates for agents of selection for mimetic colour patterns? Reviewing Palaearctic bird diets (using Cramp, 1977–1994) does not get us very far since really we need information about whether birds undergo the process of learning to avoid models, and whether they confuse models with mimics, rather than data about the endpoint of the learning process where the birds never take either (i.e. the adult and nestling diets that are normally reported). Bee-eaters (*Merops apiaster*) feed on both models and mimics, but they hawk in the open savanna on hot days; this is quite different from the habitat of most hoverfly mimics, which are overwhelmingly forest dwellers (Speight *et al.*, 1975; Maier, 1978; Speight, 1983) and avoid the hot midday (Gilbert, 1985). No protective effect occurs with this bird, since it specializes on wasps and bees, preferring them to all other prey. Hirundines such as the swallow (*Hirundo rustica*) also take syrphids and honeybees, but with their high-speed aerial scooping feeding method it is unlikely that they perceive the colour patterns before or after capture. Spotted flycatchers also take both wasps and hoverflies, but they are not deceived by the resemblance (Davies, 1977), and have an effective method of dealing with the venom of wasps. Thus for these birds, wasps and bees may not be noxious but instead may form part of their normal diet; it is possible that syrphids have longer handling times and are therefore unprofitable.

More likely candidates are birds such as *Phylloscopus*, *Sylvia* and *Hippolais* warblers, and others such as stonechats (*Saxicola torquata*). All these feed on syrphids, but we know virtually nothing about their selectivity among syrphid species. What we would be looking for would be evidence that (a) birds had contact with noxious models; (b) they also took syrphids; and (c) the spectrum of syrphids upon which they fed was biased towards non-mimetic species. This sort of evidence is amazingly sparse in the literature. For example, Greig-Smith and Quicke (1983) noted that stonechats fed many warningly coloured ichneumonids and large numbers of syrphids to their nestlings, but we do not know what kinds of syrphids these were, and hence whether they might have been mimics. Similarly, we know that wheatears (*Oenanthe oenanthe*) feed bees and 'large Diptera' to their older nestlings (Cramp, vol 5: 779), but were these large Diptera bee mimics? Then there are other birds such as *Ficedula* flycatchers, *Acrocephalus* warblers, and small passerines such as wagtails (Motacillidae), redstarts, robins and titmice (Paridae). The diet evidence suggests that these birds are minor or insignificant as hoverfly predators, but this is based only on samples of prey caught by experienced adults. Their reluctance to feed on syrphids may be entirely learned behaviour, taught to them by disastrous experiences they had when fledglings.

It is thus certainly possible that spiders and wasps are the main agents of selection for the smaller wasp mimics, whilst birds are the selective agents for bumblebee mimics. Superficially this is an attractive explanation because the much cruder visual abilities of the invertebrates would mean that imperfection of the colour pattern would not matter. However, until we know more about visual aspects of their predation, current knowledge really rules them out. Thus at the moment we can only conclude that inexperienced fledgling birds must be the selective agents responsible for the evolution and maintenance of mimicry

in syrphids across the mimicry spectrum, but very little is known about their foraging behaviour. Birds that swoop down on flower-visiting insects from perches are probably the major candidates (see below). Since very high mortalities occur between fledging and recruitment into the adult population, the numbers of such young birds are probably very high relative to those of breeding pairs of adults (the usual density estimates), and hence their selective impact on syrphids might be very large.

6.3 The nature of the mimicry: are poor mimics Müllerian rather than Batesian mimics?

For a long time various people have wondered whether poor mimics are actually Müllerian mimics: for example, Jacobi (1913) labelled wasp mimicry a specially striking form of mimicry ('sphecoidy'), but could not decide whether it was Batesian or Müllerian. Is the gradient from good to poor mimics therefore a Batesian–Müllerian spectrum? Since Müllerian mimics are not thought to evolve to resemble one another particularly closely, but Batesian mimics are, this is an attractive explanation. The basis of the 'noxiousness' of a model need not be unpalatability or stings, despite the fact that most discussions about mimicry have focused upon these elements. As Holling (1965) noted, a considerable number of other features generally related to defence can affect the acceptability of prey: stings, noxious sprays, sticky exudates, colonial defence, tough and spiny integuments, and effective escape behaviours. Thus some syrphids may be benefiting from their unprofitability, rather than hiding under the cloak of noxious models. What sort of unprofitability might be involved? There are a number of related, but subtly different possibilities of the ways in which this kind of mechanism might account for the poor-to-good spectrum of mimetic quality.

- *Is there a trade-off between flight agility and mimetic resemblance? Are poor mimics particularly agile, and therefore do they not have to be accurate visually? Aside from their conspicuous coloration, syrphids are very agile fliers and may therefore be particularly difficult for birds to catch. It would be no surprise if these two notable features were connected in some way. One obvious hypothesis is that these are alternative strategies (Grewcock, 1992). Species with relatively slow unaccomplished flight may be placed under strong selection for high-quality mimicry if their mimetic strategy is to be successful. More agile species may achieve a similar degree of protection with a less close resemblance because their agility reduces the predator's opportunity for assessing the pattern. However, cause and effect are difficult to disentangle since where selection acts to perfect resemblance, this may include mimicry of the typically slow meandering and weaving hymenopteran flight pattern, in sharp contrast to the direct, darting flight of most syrphids. Slow flight might be an integral part of high-quality mimicry, rather than a factor that promotes its evolution: high-quality mimics such as Callicera and Temnostoma are well known for this kind of behaviour (Glumac, 1962; Haeseler, 1976; Morgan and Heinrich, 1987; Speight and Lucas, 1992; Nickol, 1994; Gilbert, 2001).*

- *Is flight agility an alternative to mimetic resemblance? Is accurate mimicry only required in particular circumstances?* Flight agility and mimicry might be substitutes rather than alternatives, working at different times or places. For example, it could be argued (Grewcock, 1992) that the agility of hoverflies is such that they can rely entirely on escape as a means of protection (see below), and that the colour patterns, if they represent a protective strategy at all, confer protection under more particular circumstances, such as during the pre- and post-active flight periods of the day, or at a time when flight is hampered (e.g. when pairs fly around *in copula*). Thus Hartley and Quicke (1994) were amazed to find half of the nestling diet of corn buntings (*Miliaria calandra*) consisting of syrphids (*Helophilus* and *Rhingia*), and assumed that they must have been caught in the early morning before they had had a chance to get warm enough to fly. Although syrphids have their own endothermic warming mechanisms, remarkable for such small flies, which shorten this vulnerable time window relative to other similar-sized flies, it is certain that endothermic predators will be able to remain active for a considerable period of the day during which hoverflies will be unable to use flight as an escape response. If this were a vital component of the evolution of mimicry in syrphids, then we might predict differences in the thermoregulatory abilities between mimics and non-mimics. The only study of this question (Morgan and Heinrich, 1987) found no such differences. Alternatively, perhaps mating is the vulnerable period. Allen (1964) caught a mating pair of the rare *Pocota personata* in the early afternoon and tried in vain to persuade the couple to separate by gently pulling them apart. Most mated pairs of syrphids break apart immediately upon capture, but this pair remained *in copula* in the jar until the following morning, more than 20 h later, the male in a 'cataleptic state'. Allen thought that the mated state must therefore be a very vulnerable one, 'protected solely by the remarkable bumblebee mimicry' of this species. There are other possibilities for especially critical places and times: Speight (2000) suggested that the vulnerable period when mimicry becomes effective is when females are immobilized while ovipositing, or on hot days when models and mimics co-occur on the ground drinking at streams.
- *Escape mimicry: do syrphids constitute a Müllerian complex advertising their unprofitability?* The syrphid colour patterns may have arisen to advertise the unprofitability of great flight agility to predators (Grewcock, 1992; Dittrich *et al.*, 1993; Edmunds, 2000), and hence these syrphids would then constitute a Müllerian complex. This complex could then be mimicked by other non-agile insects, and hence such syrphids could be models rather than mimics. This would imply that predators try to catch syrphids in flight rather than on flowers, and as we shall see below, the latter seems more likely to be a significant selective force. If they were advertising their agility, then it would imply that the evolution of conspicuous coloration represents a low-cost strategy, at least in syrphids. If hoverflies are so difficult to catch, what is the point of advertising this fact? The widely accepted explanation is that, providing that the cost of advertisement is low, it can reduce an already low

risk of attack to near-zero at very little cost (Grewcock, 1992). The ability to escape from bird predators is a well-established alternative to unpalatability in butterflies (Marden and Chai, 1991; Srygley, 1994), and therefore it would be reasonable to expect it in syrphids. Thus the prediction is that syrphids with wasp-like colour patterns (the 'poor' mimics) are particularly agile, and advertise this fact to potential predators; these 'poor' Müllerian mimics should then be more agile than either the true Batesian mimics (which should mimic the unconcerned flight of their models) or non-mimics. Using phylogenetically independent contrasts, Azmeh (1999) performed a preliminary test of this hypothesis by measuring the centre-of-body-mass of 14 species (correlated with flight agility: Srygley and Dudley, 1993; Srygley, 1994, 1999) and relating it to similarity to the model: there was no relationship, but the power of the test was low because of the small sample size. Davies (1977) is the only person I know actually to have some idea of the relative difficulty of capture of different Diptera for any bird, derived from his studies of spotted flycatchers. Interestingly, he thought that syrphids were not noticeably more difficult to catch than other large Diptera, and actually seemed to be easier than muscids, whose tricky erratic flight is harder for the birds to follow.

- *Poor syrphid mimics normally have aphid-feeding larvae. Are aphidophagous hoverflies unpalatable?* Malcolm (1976, 1981) put forward the idea that there is a fundamental difference in the nature of the mimicry between the good (Batesian) and the poor (Müllerian) mimics. The good mimics usually have non-predatory larvae, and he suggested that these were true Batesian mimics. The poor wasp mimics almost always have aphidophagous larvae, and he thought some or all the individuals of a population of hoverflies might be sequestering plant poisons via their aphid prey to make themselves noxious to predators. Thus the poor mimics of the aphidophagous Syrphinae would form a Müllerian complex based on unpalatability. Statements in the literature that syrphids might be unpalatable are usually derived from very doubtful interpretations of data by Pocock (1911), Carrick (1936), Parmenter (1953) and Lane (1957): we need some strong quantitative evidence of toxin sequestering and subsequent rejections by birds. Malcolm studied the South African species *Ischiodon aegyptius*, whose bright green larvae often feed on the bright yellow *Aphis nerii* on Asclepiadaceae. Plants of the Asclepiadaceae often contain large quantities of cardenolides as a defence against herbivores. *Aphis nerii* is restricted to these plants and at least some populations on some plants sequester the host-plant cardenolides. Using thin-layer chromatography, many glycosides were detected in the plants, and some were also detected in both aphids and syrphids. Extracts of *Ischiodon* reared on *A. nerii*, however, produced four completely different spots which could not be reliably identified in any of the plant extracts. Furthermore, extracts from *Ischiodon* reared on two other aphid-plant combinations produced the same spots. Thus the experiment failed to show any evidence of transfer of cardiac glycosides from the host-plant through the aphid to the predator. There did seem to be cardiac glycosides in *Ischiodon* adults, but these were apparently not sequestered

from the prey. All extracts from *Ischiodon* fed on *A. nerii* produced a huge impact on exposed toad and chameleon hearts, which was particularly severe in chameleon hearts, where there was a dramatic and sudden drop in heart rate, followed by a slow recovery. A similar but weaker response to *Ischiodon* reared on non-aposematic aphids was seen in the frog heart. Thus cardiac glycoside activity seemed to be present in *Ischiodon* irrespective of the plant–aphid association on which it was reared. The gut lining of vertebrates is relatively impermeable to highly polar glycosides, and hence *Ischiodon* is likely to produce an emetic response rather than cardiac arrest; low polarity glycosides are readily absorbed and could result in serious cardiac toxicity and death. These hoverflies should therefore be noxious to potential predators, and their yellow-and-black colour pattern could be aposematic rather than mimetic. Malcolm (1981) tried to repeat this work in greater detail in Oxford, but rearing problems kept sample sizes very low, and *Ischiodon* showed no sign of any cardenolides after feeding on *A. nerii*. This is perhaps the reason why this remarkable work remains unpublished.

In contrast to the paucity of evidence for unpalatability, many papers show that hoverflies are extremely palatable (e.g. Mostler, 1935; Steiniger, 1937a; Evans and Waldbauer, 1982; Dlusskii, 1984; Heal, 1979, 1982). These data are very compelling, and the conclusion must be that most individual syrphids are probably palatable most of the time to most if not all predators. However, the relationships among plant, aphid and syrphid defences is both fascinating and almost unexplored, and deserve further study, taking into account the predicted variability in toxin levels among different individual aphid–host–plant rearings (cf. Vanhaelen *et al.*, 2001, 2002). Thus, in principle it is not impossible for some individual syrphids to be unpalatable and others to be wholly palatable, but it would be more convincing were there many more systematic observations of captive predators displaying behaviours indicating that apparently innocuous aphidophagous hoverflies were unpalatable.

6.4 The nature of the model: wasp models of poor mimics are exceptionally noxious, so mimics do not need to be perfect

This hypothesis certainly appears to explain at least some of the mimicry spectrum in syrphids, since wasps are particularly noxious (and hence their mimics need not be very accurate), whereas bumblebees are apparently only mildly noxious (and hence require accurate copying). Whether this is also the explanation for the differences in relative abundance is not clear, but it is certainly possible, since a very noxious model should in theory be able to support a greater relative abundance of mimics. Thus although this hypothesis seems certain to be part of the explanation, it still leaves unexplained the force counteracting the constant selection for improved mimicry, even though this force is almost certainly very weak when mimics evolve a reasonably close similarity to the model (see below).

6.5 The type of mimicry involved: poor mimics use behaviour or other factors to compensate for their visual discriminability

Dlusskii (1984) suggested that, for poor mimics, mimicry is only one of a range of strategies designed by natural selection to reduce the impact of predators; for good mimics, in contrast, mimicry is *the* mechanism, and low abundance is not the consequence but the reason for their high mimetic fidelity. Mimicry may be strongly promoted by flower-visiting behaviour, since insects are usually fairly conspicuous on flowers whatever their pattern, negating the main disadvantage of aposematic coloration, i.e. the increased attack rate caused by greater visibility (Guilford, 1990). Quantitative comparisons between the flight behaviour of models and hoverfly mimics have only just begun to be carried out, on honeybees and their *Eristalis* mimics (Golding and Edmunds, 2000; Golding *et al.*, 2001), and demonstrate some behavioural convergence in flight characteristics and visitation rates. Nickol (1994) made the interesting further suggestion that mimicry may be associated specifically with interspecific competition on flowers. Direct interactions on flowers occur very frequently, and usually the winner is the larger of the two insects (see Kikuchi, 1963). If the winner remains on the flower despite interruption by smaller insects, then the former should either be extremely good at discriminating the approaching shapes of predators from those of other insects, or be able to deter the attacks of predators via mimicry. This might explain the association between large body size and mimetic quality in syrphids.

The exact details of prey capture by birds can be very important, but we have hardly any accounts of the behaviour of wild birds when hunting for and catching bumblebees, wasps or hoverflies, especially those identified above as probable candidates as selective agents for mimicry. It would be particularly useful to have data on the foraging behaviour of juvenile birds, and any differences from adults. However, predation consists of a set of relatively rare behavioural events, often occurring in widely separated parts of the environment, and is therefore extremely difficult to study systematically, especially in juveniles learning to forage for the first time. This lack gives Dlusskii's (1984) work special significance. He and his students watched four bird species taking both models and mimics from flowers during the nesting period in the forests of Russia. The birds were two specialist flycatchers (pied and spotted) and two generalists (redstart and pied wagtail, *Motacilla alba*). When hunting for flies, redstarts and spotted flycatchers, in particular, concentrated their searching at flowers, where models and mimics were also found. Redstarts, and especially wagtails, foraged on the ground amongst low vegetation, but all four bird species used the same strategy to take insects from flowers, catching them either before or just after they tried to escape. From a perch often more than 10 m away, an individual bird noticed its prey and swooped down at speeds of between 3.5 (redstart) to 6.6 m/s (pied flycatcher). Experienced birds dived down with folded wings and steered only with the tail, taking the prey without any noticeable reduction in speed. Davies (1977) described a very similar hunting technique in spotted flycatchers in an Oxford garden, and in the USA similar behaviour has been noted in the painted redstart (*Myioborus pictus*).

Called 'flush pursuit', the birds may be exploiting escape responses built into the neural circuits of the flies: particular body movements, patterns of contrast on the wings and tail, and the looming image trigger these primitive escape responses and increase the success of the hunt (Jablonski and Strausfeld, 2000). While learning, young birds used a similar strategy, but usually after approaching the flower they braked, slowing down and practically coming to a standstill, and only then lunged for the insect. Probably the long-range fast dive requires some experience to bring off successfully.

By filming *Eristalis arbustorum* and *Lucilia* (Calliphoridae) startled by a lifelike model of a bird moved with a piece of string, Dlusskii discovered that the flies could perceive the bird and start to fly up only at a maximum distance of about 30 cm (and usually at smaller distances). This gave the fly only about 0.02 s (maximum 0.07 s) to respond before the bird was in a position to take it. Dlusskii measured the speed of *Eristalis* in level flight at about 1.1 (maximum 1.6) m/s (also possibly 10 m/s over short distances: see Golding *et al.*, 2001), but from a standing start this speed could only be reached after about 0.1–0.15 s. Thus the fly only had time to move about 0.5 to a maximum of 3 cm before being attacked. Since the bird could manoeuvre as well, the insect had almost no chance of escape. This was just as well, since despite flying four times faster than the insect, if the bird got there too late, or missed, it was practically impossible to take the fly in free flight. However, these calculations are only correct if the bird dived directly and did not reduce its speed, i.e. like experienced adults but not like naive juvenile birds. They also effectively mean that birds must select their target before making a move, making long-range cues crucial. In butterfly predation by jacamars (Galbulidae), Chai (1990) inferred a particular behavioural sequence of responses to signals from the prey, exploited by butterflies in their defence: a similar sequence for hoverfly predation is likely. Vivaldi, by far the most frequent responses by jacamars to butterflies were the categories of 'sight-rejected' and 'eaten'; thus long-range visual cues that encourage rejection on sight can make a huge difference to survival of insect prey. Only a small minority of butterflies were rejected after having been tasted, presumably because the jacamars were experienced adult birds. The most important factor leading to butterflies being rejected on sight was their colour pattern, with locally common mimetic or conspicuous patterns being rejected much more frequently than cryptic or intermediate ones. Other components contributing to being rejected on sight were a regular slow flight pattern and a long slender body.

In Dlusskii's study, flies never flew directly forwards in front of the bird, but instead always went perpendicular to the bird's path, either sideways or downwards. Thus to take the prey, the bird needed to turn quickly, and this reduced its speed, providing the fly with the possibility of escape. Of course, often or even usually there are many insects on a flower head, a complex mixture of models, mimics and non-mimetic flies. A crucial finding of Dlusskii's experiments was that upon attack by a bird, most of the flies took off in their escape response (although 40% did not, or only started up after the bird had passed – assuming they had not been snatched). However, the social hymenopterans (wasps, honeybees and bumblebees) practically never reacted

to the fake bird, or even to a light touching of the flower. This has very important consequences for the ratio of models to mimics as perceived by the attacker. Not only could a young bird not discriminate between model and mimic from a distance, but it also slowed down at the crucial moment, allowing the flies to escape and leaving only the models for the bird to experience. Thus observed model–mimic ratios by a human observer may not constitute good estimates of the ratio encountered by young birds, which can have a greatly elevated encounter frequency with models. It is therefore very likely indeed that a young bird will take a bee or a wasp during its first few foraging bouts, even if their numbers are many times lower than those of the mimics. Since the first experiences are remembered longest and recalled best (Speed, 2000), they are important in developing the long-term protective effects of mimicry. At first the stricken bird will probably generalize to all insects that even vaguely resemble the model, and imperfect mimicry will be protective. Later on, with more experience, the bird may learn how to distinguish between models and their mimics by selecting particular components of their appearance; it may even come to discriminate very good mimics from models, and then even near-perfect mimicry will not be protective. Dlusskii considered this scenario as a powerful explanation for why poor mimics appeared in such numbers only in the second half of summer, when the number of insectivorous predators was augmented several times over by the recruitment of naive young birds.

Insectivorous birds use a variety of feeding techniques to gather prey, the main ones being aerial pursuit, swooping down from a perch, gleaning from vegetation, and picking from the ground. It seems clear from the comments above that gleaning and picking are not important methods of obtaining adult hoverflies, except perhaps early in the morning when the flies are immobilized by cold (cf. Hövemeyer, 1995). Surprisingly, aerial pursuit also does not seem to be an important foraging technique for syrphids: even the most agile of birds cannot easily catch them on the wing. Future studies of bird predation in nature should probably concentrate on those species that swoop down from a perch onto flower-visiting flies, just as Dlusskii (1984) described. On current information, this seems to be a critical forum where the hunting behaviour of birds could generate selection for mimicry.

There are many components of the signal produced by an insect aimed at predators, transmitted in various different modalities (visual, sound, vibration, odour). Experimentally each modality on its own can evoke the same or similar responses in a predator because prey categorization by the predator is almost certainly multimodal, i.e. it uses information from all modalities, and these can interact in surprising ways (see Rowe, 1999). For example, in Brower and Brower's (1965) experiments with toads feeding on honeybees and their *Palpada* mimics, producing a buzz with the wings caused a 38% drop in predation, whereas the use of the sting caused only a 21% decrease in the mortality of the mimic. Thus sound seems to be a very important component of the signal that toads associate with noxiousness. The gradient of mimic quality evident in pigeon responses to whole images (Dittrich *et al.*, 1993) could also be evoked by images just of the abdomen, or just the head+thorax. In addition, the birds could also make the same categorizations (creating the

same gradient of mimetic quality) using pictures of the insects taken under natural conditions, with various different orientations and relative sizes: a quite extraordinary feat. They obviously have sophisticated polymorphous concepts of these prey categories. Each of the signal modalities may trade-off against one another, or act synergistically, in evoking predator responses, and thus one could easily imagine some mimics emphasizing one modality rather than another. The visual impact of the colour pattern is merely one component of the overall signal, more or less important to different species: these differences may result in the 'poor' mimicry of some syrphids.

6.6 The effect on the predator: poor mimics confuse rather than deceive

It is possible that the effects of good and poor mimics on a predator are different. For example, little is known about the impact of different nasty experiences on birds, but there are indications that emetic experiences are learned in a fundamentally different way from ones that merely make birds feel ill (Testa and Ternes, 1970), and have longer lasting effects that are relatively resistant to subsequent modification (Cowan and Reynolds, 2000).

Rothschild (1984) introduced the idea of '*aide-mémoire* mimicry' as a way of explaining the often poor resemblance between models and mimics. In this, predators are induced to remember an unpleasant experience at the hands of a model by features of a mimic that reproduce some but not all the characteristics of the model. Howse and Allen (1993) invented the idea of satyric mimicry to account for poor mimics among the Syrphidae; in this hypothesis, imperfection is regarded as a true ambiguity in the signal, where the black and yellow sign of noxiousness is placed in the 'wrong' context, onto a fly shape. Predators are thereby presented with two conflicting signals, and are confused, allowing more time for the insect to escape. There is no evidence that either of these explanations represent significant factors, as far as I am aware.

6.7 The speed of evolution: poor mimics are still evolving their mimetic resemblance

Poor mimics could still be in the process of evolving to be perfect (Edmunds, 2000). For example, Glumac (1962) reasoned that the low abundance of mimics relative to models was a precondition (caused by greater pre-imaginal mortality) that speeded up selection for mimetic colour patterns. The basic components of the mimetic pattern he regarded as having evolved for other non-mimicry-related reasons (parallel evolution with models); thus species that are common relative to potential models have much slower evolution of mimicry, and hence are still poor mimics. I have already discussed (see Section 6.5) the view that mimicry might form a less important part of the lifestyle of some species, and hence selection pressures for perfection of mimetic resemblance might be lower. With lower selection pressure and slower evolutionary rates, such mimics might be less likely to catch up in the coevolutionary chase, and hence be imperfect.

I have already discussed (see Section 1.2) why I think this non-equilibrial view of mimicry evolution is an unlikely scenario. Although it might sound reasonable, no mathematical theory or computer simulation predicts it, and there is no evidence at all of mimetic patterns changing through time, despite there being lots of spatial discrete variation in colour pattern morphs. On the contrary, as noted above, even simulations of the coevolutionary chase predict stasis (Franks and Noble, 2004). In my view it is better to assume that poor mimetic patterns have evolved to an equilibrium state, rather than being in the process of being perfected by constant directional selection.

6.8. Disturbance by man: poor mimics have recently become abundant, causing mimetic degradation

A related idea also involving a non-equilibrial situation concerns changes in the habitats where syrphids live. Rather than the continual process of the coevolutionary chase, this supposes that habitat change is only a very recent phenomenon that has impacted on relative abundances only.

Drawing a distinction between good mimics ('specialized Batesian mimics') and what he called 'non-mimetic syrphids' (i.e. including the poor mimics), Maier (1978) suggested that the former only occur in forested areas. The overwhelming number of such good mimics are non-predators as larvae, requiring decaying wood habitats for their development. Maier thought they had evolved their excellent mimicry because they spent a higher proportion of their time than non-mimetic syrphids in forests where potential avian predators are abundant; they have conspicuous foraging and mating behaviour at flowers that increases the chance that they will be noticed by birds; and they share foraging behaviour on flowers with the models. This habitat specificity is difficult to maintain because virtually all syrphids are native to forests and glades within forests (Speight *et al.*, 1975; Speight, 1983), including aphidophagous species (and hence many poor mimics).

The relationship between the original habitat of syrphids and modern disturbed habitats is an interesting one, which has undoubtedly affected syrphid communities and the relative abundances of mimetic species (the 'disturbed ecology' hypothesis: Grewcock, 1992). While classical mimicry theory predicts that there will be a limit to the abundance of Batesian mimics relative to their models, this is only true of undisturbed habitats. In the very disturbed habitats created by man, relative abundances of models and mimics may have greatly changed. As Maier noted, many high-fidelity mimics are restricted to relatively undisturbed forests which provide suitable larval habitats, and deforestation and human agriculture may have caused a severe reduction in the availability of such larval sites. However, this activity has also created huge areas of new habitats, allowing the expansion of many plants and insects with appropriate life-history traits. Aphids in particular are extremely common in open or ecotone habitats with a well-developed herbaceous layer (Dixon, 1998), and increases in aphid availability may boost the abundance of aphidophagous syrphids: this may account for the

fact that poor syrphid mimics greatly outnumber their models. Since most research involves habitats that are relatively disturbed as compared to truly pristine areas, we may have an unrealistic view of these relative abundances. Furthermore, it is possible that these syrphids were originally good mimics, but their vastly increased abundance over the last 1000 years or so may have caused a breakdown in mimetic fidelity (cf. Turner, 1984: 336; Carpenter and Ford, 1993: 112–114). Whether or not the mimetic pattern has degraded, it is certainly the case that syrphid communities are sensitive to human disturbance (Bankowska, 1980), and the proportion of good mimics increases in the more pristine habitats (Azmeah *et al.*, 1998).

6.9 Resistance to evolving mimetic perfection

Imperfect mimicry would be more understandable if we could identify selective forces that oppose the putative constant directional selection (in favour of more and more perfect resemblance), allowing an equilibrium state of the pattern. Virtually all considerations of mimicry, theoretical or empirical, show that there should always be an advantage, however small, in becoming more like the model. Hence without any opposing forces all mimics should either be perfect, or in the process of becoming perfect. What could the opposing forces be? There are several possibilities, as described below.

6.9.1 There are costs of producing a perfectly mimetic pattern

Various types of costs of the patterns are imaginable. The most frequently invoked is thermoregulation: syrphids are extremely good thermoregulators for their size (Morgan and Heinrich, 1987; Heinrich, 1993), and the colour pattern may play some role in this function. The development of perfect mimicry might compromise thermoregulatory abilities, placing constraints on the evolution of colour patterns: Heal (1981, 1989) put this forward as an explanation of *Eristalis* colour patterns, subsequently followed by others. In both sexes, individual and particularly seasonal variation in the pattern generated by the way the pattern responds to rearing temperature has usually also been interpreted as adaptations to thermal balance (e.g. in Holloway, 1993; Ottenheim *et al.*, 1998), since darker insects are active in cooler weather.

The cost is unlikely to involve conspicuousness. Although there may be a relationship between similarity to the model and the probability of detection, it is probably non-linear. Models may represent an optimum signal for detection and as the appearance of the prey converges on that of the model, prey are likely to suffer similar probabilities of detection under any given circumstances. However, almost any arrangement of bright pattern features will be much more conspicuous than their lack, and hence even very poor mimics are likely to be almost as detectable as their models. Thus there will probably be an asymptotic curved relationship between similarity and detectability (Grewcock, 1992), with rapid increases as the initially poor mimicry originates, followed by small or non-existent changes as mimicry is perfected.

Other types of costs are certainly possible. Heal (1995) had the novel idea that it might be much more costly to produce high-fidelity mimicry, particularly in terms of pupal duration, when the adult body is formed and the colour pattern laid down. Poor syrphid mimics are generally fast-developing aphid predators with a very short pupal duration of about a week, but it might take a long time for good mimetic patterns to develop during the pupal stage: good mimics tend to be ones with a univoltine life cycle and long pupal phases. Thus one could imagine there being two alternative strategies involved here. It may be difficult in resource terms to make the appropriate pigments for creating mimetic patterns. The black colours of syrphids are presumably created from eumelanin, a nitrogen-containing compound present as granules in the exocuticle (Chapman, 1998: 660). The yellows are probably xanthopterins (heavily nitrogenized compounds made from the nucleotide guanosine) synthesized in the epidermis, as in the wasp models. For there to be a cost of producing a mimetic pattern, it must be more costly to produce xanthopterins than melanins (since an all-black hoverfly is not mimetic); while a single molecule of xanthopterin has similar numbers of carbon, hydrogen and oxygen atoms to a single molecule of the quinone monomer of melanin, it has five times the number of nitrogen atoms. Thus it is possible that the yellow colours of hoverfly mimics are costly to the nitrogen budget; according to White (1993) nitrogen is the limiting factor for most animals. However, it is not the case that good-quality mimics have more yellow than poor-quality ones – it is the distribution of the yellow that matters.

There is only one piece of information in the literature that might indicate some possible costs; Lyon (1973) mentioned almost in passing that varieties of *Merodon equestris* differ in their ovarian development, and possibly the mechanism involves different balances between larval nutrient carryover and adult feeding. The varieties *narcissi*, *equestris* and *flavicans* showed normal development of the ovaries, whereas *nobilis* and *transversalis* had much more poorly developed gonads, more pupal fat and required less food in the adult stage. According to Conn (1972), the *transversalis* morph does not seem to be a worse or better mimic of UK bumblebees than the other morphs (the *nobilis* and *flavicans* morphs do not occur in the UK). It is therefore possible that different mimetic morphs have different costs and benefits associated with them, and hence have evolved different life histories.

6.9.2 Kin selection opposes individual selection for perfect mimicry

Johnstone (2002) used an analytical theory of predator perception and signal detection to suggest that kin selection can stabilize imperfect mimicry. Signal detection theory addresses the question of where a predator should set its visual attack threshold in order to optimize the benefit (of attacking a mimic) to cost (of attacking a model) ratio, for model and mimic populations with differing dissimilarities (see Fig. 9.3). Just as Oaten *et al.* (1975) showed some time ago, it predicts that inaccurate mimics (and their models) will suffer a lower overall attack rate than perfect mimics when the mimics are relatively common. This arises because perfect mimics and their models are all attacked, since there is no threshold that gives a higher benefit-to-cost ratio than simply

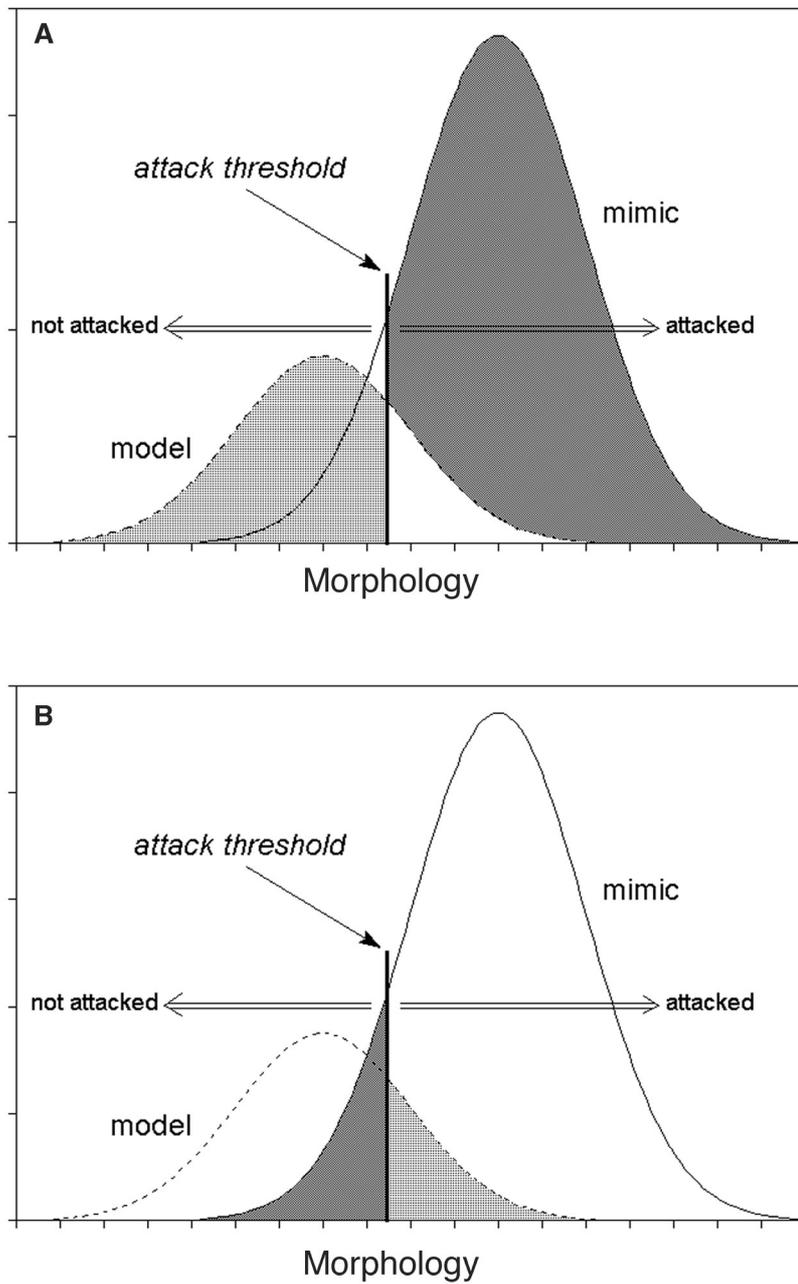


Fig. 9.3. Basis of the signal detection models of Johnstone (2002) and Sherratt (2002). **A** model and its Batesian imperfect mimic overlap in the distributions of their appearance (indexed by the *x*-axis, 'morphology'). A predator sets a threshold appearance above which it attacks, and below which it does not attack. The optimal attack threshold maximizes the ratio between **A** the benefits (i.e. mimics attacked and models not attacked); and **B** the costs (mimics not attacked and models attacked in error).

attacking everything: models are uncommon (low costs) and mimics are very common (high benefits). When mimicry is inaccurate it will always be worthwhile for the predator to set some threshold of acceptance, and hence a proportion of mimics (the more accurate ones) will escape predation. However, even here mortality is biased against the less perfect mimics in the population, creating selection for more perfect mimicry. This is where kin selection comes in. It is assumed that directional selection for perfect mimicry will not occur under the above conditions if localized groups of mimics have high relatedness: inaccurate mimetic kin effectively pay the costs for the survival of their more accurate relatives. The main prediction is that when models are common and/or strongly aversive, and hence the incentive to attack is low, mimics should evolve ever more accurate resemblance; when models are rare and/or weakly aversive, and the incentive to attack is high, kin selection can oppose individual selection sufficiently strongly for imperfect mimics to evolve. Higher levels of local relatedness and greater incentives to attack therefore both favour greater dissimilarity to the model. Thus his theory suggests that (a) kin selection will be more important in imperfect mimics; (b) more noxious models will result in more perfect mimics; and (c) high mimic abundance will favour imperfect mimicry.

On the basis of model noxiousness, this model predicts that social-wasp mimics should be the most and bumblebee mimics the least accurate of hoverfly mimics. On relative abundance grounds, however, the opposite predictions are made. Relative abundances in pristine habitats where mimicry evolved are probably less different among the mimicry complexes than they are currently in the degraded habitats of Europe. This suggests that noxiousness was the prime cause of the evolved patterns, and hence the first prediction is more appropriate; however, the predicted pattern is exactly opposite to observed situation. Furthermore, the requirement for localized relatedness is vanishingly unlikely among the very common imperfect wasp-mimicking hoverflies, since virtually all of these species migrate southwards in enormous numbers in autumn (Gatter and Schmid, 1990). In addition the high mobility of syrphids is notorious in mark-release-recapture studies (e.g. Holloway and McCaffery, 1990). Kin selection thus forms a very poor basis upon which to develop a theory of imperfect mimicry for hoverflies.

6.9.3 The existence of multiple models means the optimum is a 'jack-of-all-trades' mimetic pattern

To explain imperfect mimicry in hoverflies, Edmunds (2000) suggested that a perfect hoverfly mimic only achieves protection when it lives within the joint ranges of its model and appropriate predators, whereas a poorer mimic with some degree of resemblance to several models obtains a lower degree of protection but can be distributed over the combined ranges of all models and predators, and thus can occupy a much greater distributional range. Edmunds' argument was limited to non-overlapping model distributions, but even if models were sympatric, it is possible that a mimic evolves to resemble the average of all the models rather than any one model; Barnard (1984) put

forward the same idea in a different, behavioural context, a 'jack-of-all-trades' mimic. Just such a verbal model has been proposed as an explanation for the colour pattern of a European burnet moth (Sbordoni *et al.*, 1979). Thus the observed mimetic pattern of a widely distributed mimic is suggested to be an optimal compromise among a set of models, each with a slightly different colour pattern and (possibly) with different ranges. Glumac (1962) noted that a 'considerable number' of mimics are more widespread in their distributions than their models, but a quantitative analysis remains to be done.

This idea was modelled by Sherratt (2002) using a signal-detection approach (like Johnstone: see Fig. 9.3) and receiver operating characteristic (ROC) curves (see Shettleworth, 1998) to set an optimal attack threshold that maximizes the benefit (of avoiding models and attacking mimics) to cost (of attacking models and avoiding mimics) ratio, for model and mimic populations with differing dissimilarities. The relative frequency of mimics to models that can be supported turns out to be directly proportional to the cost-benefit ratio with no upper limit (unlike in traditional ideas of mimicry). In addition, the greater the relative frequency of mimics, and the lower the cost-benefit ratio, the closer the resemblance of the mimic needs to be to gain complete protection. As Dittrich *et al.* (1993) found experimentally with pigeon pecking rates, the relationship between attack rates and resemblance is highly non-linear, with very low selection for improvement near the model phenotype: as one might predict, the width of this region of weak selection is determined by relative frequencies and the cost-benefit ratio (Fig. 9.4A). Thus an imperfect resemblance is often sufficient, with further improvements being very close to being selectively neutral with respect to predation. The increased variability of hoverfly colour patterns with increasing similarity to their wasp model (Holloway *et al.*, 2002) is consistent with this prediction of relaxed selection.

When there are several visually different, sympatric aposematic models encountered by predators at the same time, mimics either evolve to resemble one of them, or if the models are similar, to some intermediate 'imperfect' phenotype. When the models differ in space or time, there should be selection on a mimic that spans both areas or times to develop an intermediate phenotype. The optimal intermediate phenotype should resemble more closely the model with which the mimic spends most time, or (if this is equal) the less noxious and less numerous model.

This theory is very attractive as an explanation for the patterns of mimicry in hoverflies, because it is the only one consistent with all the evidence, capable of explaining the nature of all three of the major mimicry complexes. It predicts that imperfect mimicry will arise whenever overlapping regions of protection exist in the morphological space among models. Since the sizes of these regions of protection depend on model densities and the costs of attack for a predator, the prediction is that models that are at low density and/or are not very noxious (such as bumblebees) would be least likely to overlap in their regions of protection, and therefore would be the most likely to produce discrete Müllerian mimicry rings, least likely to generate imperfect mimics, and the most likely to result in polymorphic mimics (see Fig. 9.4B). Highly noxious models (such as wasps) are much more likely to have overlapping regions of protection, and

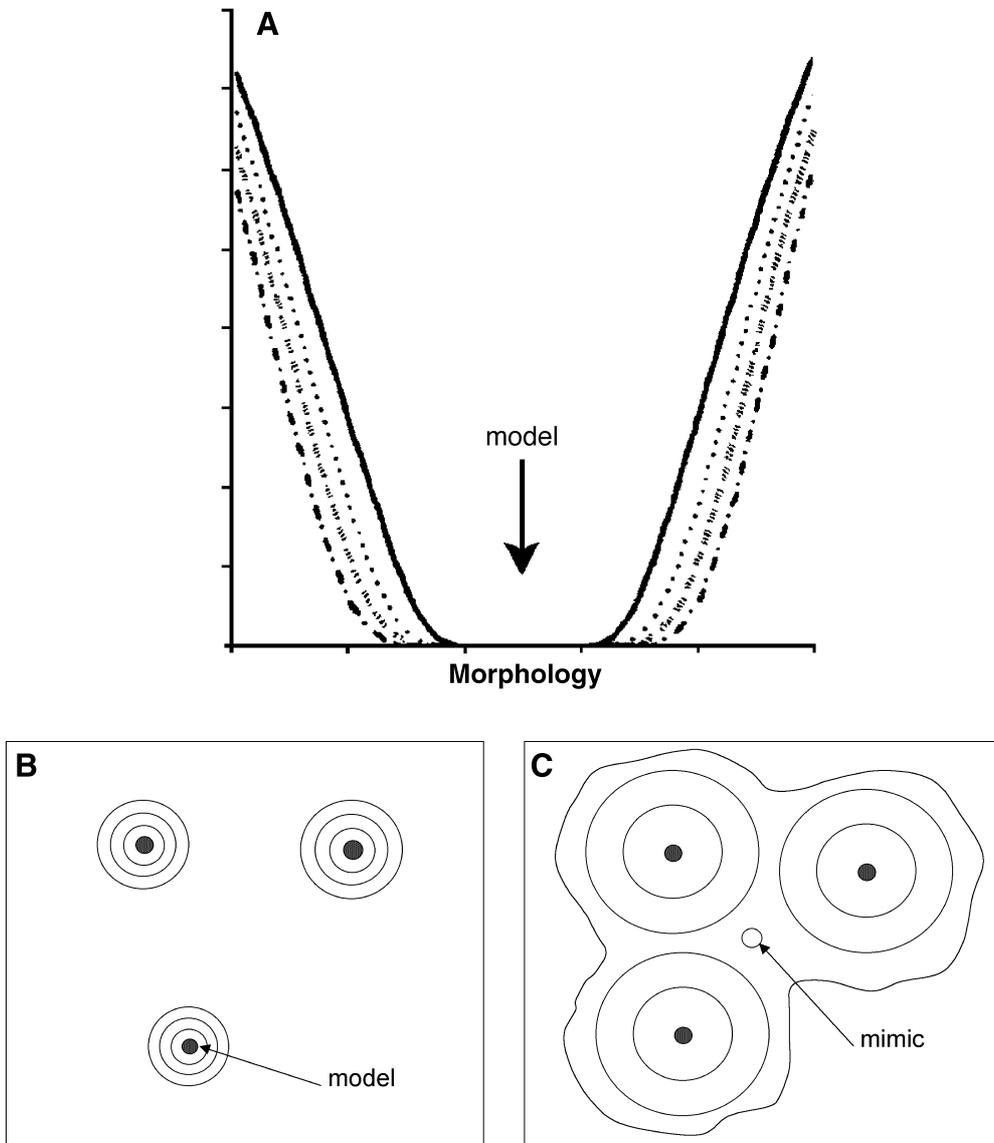


Fig. 9.4. Sherratt's (2002) multiple-model theory. **A** Mortality of a Batesian mimic in relation to its appearance ('morphology') relative to a noxious model, whose position on the morphology axis is indicated. The different lines are for gradually increasing model noxiousness. Note that there is a zone of protection where mortality is effectively zero, and hence where selection for improved resemblance is more or less neutral. **B** Three slightly noxious models in a two-dimensional morphological space, each surrounded by three isoclines of mortality (the 'zones of protection' they afford their mimics). Since the zones do not overlap, selection draws mimetic resemblance to one or other of the models, producing very accurate resemblance. **C** Three very noxious models in the same two-dimensional morphological space. Note that the 'zones of protection' now overlap because of the increased noxiousness, and mimetic resemblance is now at a selection balance of imperfect mimicry.

hence they should themselves form a large and diffuse Müllerian mimicry ring (since by definition they are already protecting one another); there should be more imperfect mimics of them, but they are not likely to promote the evolution of mimetic polymorphism (see Fig. 9.4C). It even may explain why mimicry is such a feature of the Syrphidae: since flight agility will reduce profitability, the cost–benefit ratio increases. This allows a greater density of mimics at equilibrium and a broader range of selectively neutral phenotypes, thus making the evolution of any mimetic pattern easier.

7. Conclusions

Theories of mimicry have become more sophisticated and realistic over the 20th century as they began to incorporate more of the features known to be important in the evolution of mimics. Holling (1965) identified a set of key elements of predators (rate of search, area of detection, the time exposed to prey, handling time of prey, hunger levels and their effects on attack thresholds, impact of encounters with prey on attack thresholds (i.e. ‘learning’) and forgetting) which interact with prey characteristics (relative densities, unprofitabilities, similarity to models, presence of alternative prey). To this we can now add the signal-detection process, and memory limitations which make memorizing several categories of prey much harder than keeping just one or two in mind (Bernays, 2001; cf. Schuler, 1980, in the context of mimicry).

The major conclusion to be drawn from this assessment of the ability of theory to account for the spectrum of mimicry in hoverflies is that we do have one candidate theory that potentially can explain why imperfect mimicry is so common. Sherratt’s (2002) hypothesis of the evolution of imperfect mimicry under the influence of multiple models is the only one that accounts for all the evidence. The theory and its elaborations (Sherratt, 2003) now require detailed testing. With this approach we are starting to reach a level at which real advances can be made in a more general understanding of mimicry complexes.

There are many other more restricted conclusions to be drawn from my review. Most if not all of the hoverflies labelled as mimetic actually are mimics. The apparently poor nature of their resemblance does not prevent them from obtaining at least some protection from suitably experienced birds. Mimicry is a dominant theme of this very large family of Diptera, with at least a quarter of all species in Europe being mimetic.

Hoverfly mimics fall into three major groups according to their models, involving bumblebees, honeybees and social wasps. There are striking differences in the general levels of mimetic fidelity and relative abundances of the three groups, with accurate mimicry, low abundance and polymorphism characterizing the bumblebee mimics: more than half of all the species of bumblebee mimics are polymorphic. Mimics of social wasps tend to be poor mimics, have high relative abundance, and polymorphism is completely absent. At least some apparently ‘poor’ mimetic resemblances may be much closer in birds’ perception than we imagine, and more work needs to be done on this. Thermoregulatory constraints on the evolution of colour patterns also need clarifying.

Bumblebee models fall into a small number of Müllerian mimicry rings which are very different between the Palaearctic and Nearctic regions. Social wasps and associated models form one large Müllerian complex. Together with honeybees, these complexes probably form real clusters of forms as perceived by many birds. Bumblebees are the least noxious and wasps the most noxious of the three main model groups. The basis of noxiousness seems to be different, with bumblebees being classified as non-food, whereas honeybees and wasps are nasty tasting and (rarely) sting. The distribution of mimicry is exactly what would be expected from this ordering, with polymorphic and accurate forms being a key feature of mimics of the least noxious models, while highly noxious models have poor-quality mimicry.

Mimics may not have to occur at the same season as their models, but usually do. Different model groups have different phenologies, and this may account in part for the different phenologies of their mimics. Waldbauer's phenological hypothesis that mimics can be separated in time from their models needs much more thorough testing, as does the idea that mimics avoid the early summer when fledgling birds are common.

Not enough is known about bird predation on syrphids, yet in principle this should not be too difficult to study with captive birds in large cages, or even in the field. The rates at which naive birds encounter models and mimics are likely to be very different from their relative abundances measured by human researchers, as Dlusskii's (1984) study clearly shows. We need to know more about the relationships between the noxiousness of the model, the abundances of models and mimics, and the impact of the abundance of alternative prey on the decisions that birds make about whether to attack model-mimic complexes. Similarly, we need to know much more about the psychology of birds as predators. There are at least four processes that need elucidating:

- learning about the noxiousness of models
- the erasing of that learning through contact with mimics ('extinction', or learned forgetting)
- forgetting
- deliberate risk-taking and the physiological states that promote it.

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References

- Alcock, J. (1970) Punishment levels and the response of white-throated sparrows (*Zonotrichia albicollis*) to three kinds of artificial models and mimics. *Animal Behaviour* 18, 733–739.
- Alford, D.V. (1975) *Bumblebees*. Davis-Poynter, London.
- Allen, A.A. (1964) *Pocota personata* Harr. (Diptera, Syrphidae) in SE London; with a note on the copula, etc. *Entomologists Monthly Magazine* 100, 163–164.
- Alonso-Meija, J. and Marquez, M. (1994) Dragonfly predation on butterflies in a tropical dry forest. *Biotropica* 26, 341–344.
- Archer, M.E. (1988) The aculeate wasp and bee assemblage (Hymenoptera: Aculeata) of a woodland: Bernwood Forest in the English Midlands. *Entomologist* 107, 24–33.
- Azmeh, S. (1999) Mimicry and the hoverflies. PhD thesis, Nottingham University, Nottingham, UK.
- Azmeh, S., Owen, J., Sorensen, 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.
- Bankowska, R. (1980) Fly communities of the family Syrphidae in natural and anthropogenic habitats of Poland. *Memorabilia Zoologica* 33, 3–93.
- Barnard, C.J. (1984) When cheats may prosper. In: Barnard, C.J. (ed.) *Producers and Scroungers: Strategies of Exploitation and Parasitism*. Chapman and Hall, London, pp. 6–33.
- Benton, F. (1903) Bees working on chrysanthemums. *Proceedings of the Entomological Society of Washington* 6, 102–103.
- Bernays, E.A. (2001) Neural limitations in phytophagous insects: implications for diet breadth and evolution of host affiliation. *Annual Review of Entomology* 46, 703–727.
- Birkhead, T.R. (1974) Predation by birds on social wasps. *British Birds* 67, 221–229.
- Bohart, R.M. and Menke, A.S. (1976) *Sphecid Wasps of the World: A Generic Revision*. University of California Press, Berkeley, California.
- Bombosch, S. (1963) Untersuchungen zur Vermehrung von *Aphis fabae* Scop. in Samenrübenbeständen unter besonderer Berücksichtigung der Schwebfliegen (Diptera, Syrphidae). [Studies on the increase of *Aphis fabae* Scop. in seed-beet crops with special reference to hoverflies (Diptera, Syrphidae)]. *Zeitschrift für Angewandte Entomologie* 52, 105–141.
- Bristowe, W.S. (1941) *The Comity of Spiders*, 2 vols. Ray Society, London.
- Brower, J. van Z. (1960) Experimental studies of mimicry. IV. The reactions of starlings to different proportions of models and mimics. *American Naturalist* 94, 271–282.
- Brower, J. van Z. and Brower, L.P. (1962) Experimental studies of mimicry. 6. The reaction of toads (*Bufo terrestris*) to honeybees (*Apis mellifera*) and their dronefly mimics (*Eristalis vinetorum*). *American Naturalist* 96, 297–307.
- Brower, J. van Z. and Brower, L.P. (1965) Experimental studies of mimicry. 8. Further investigations of honeybees (*Apis mellifera*) and their dronefly mimics (*Eristalis* spp.). *American Naturalist* 99, 173–187.
- Brower, L.P. (1988) Avian predation on the Monarch butterfly and its implications for mimicry theory. *American Naturalist* 131, S4–S6.
- Brower, L.P., Brower, J. van Z. and Westcott, P.W. (1960) Experimental studies of mimicry. 5. The reactions of toads (*Bufo terrestris*) to bumblebees (*Bombus americanorum*) and their robberfly mimics (*Mallophora bomboides*), with a discussion of aggressive mimicry. *American Naturalist* 94, 343–356.
- Brower, L.P. and Brower, J. van Z. (1972) Parallelism, convergence, divergence, and the new concept of advergence in the evolution of mimicry. In: Deevey, EA (ed.)

- Ecological Essays in Honour of G. Evelyn Hutchinson. Transactions of the Connecticut Academy of Science* 44, 59–67.
- Brown, E.S. (1951) Mimicry as illustrated by the British fauna. *New Biology* 10, 72–94.
- Brues, C.T. (1946) *Insect Diet: An Account of the Food Habits of Insects*. Harvard University Press, Cambridge, Massachusetts.
- Carpenter, G.D.H. and Ford, E.B. (1933) *Mimicry*. Methuen, London.
- Carrick, R. (1936) Experiments to test the efficiency of protective adaptations in insects. *Transactions of the Royal Entomological Society of London* 85, 131–140.
- Chai, P. (1990) Relationships between visual characteristics of rainforest butterflies and responses of a specialized insectivorous bird. In: Wickstein, M. (ed.) *Adaptive Coloration in Invertebrates*. Proceedings of a Symposium sponsored by the American Society of Zoologists. Texas A&M University Sea Grant College Program, Galveston, Texas, pp. 31–60.
- Chapman, R.F. (1998) *The Insects: Structure and Function*, 4th edn. Cambridge University Press, Cambridge, UK.
- Church, S.C., Bennett, A.T.D., Cuthill, I.C. and Partridge, J.C. (2004) Avian ultraviolet vision and its implications for insect protective coloration. In: van Emden, H. and Rothschild, M. (eds) *Insect and Bird Interactions*. Intercept, Andover, UK, pp. 165–184.
- Conn, D.L.T. (1972) The genetics of mimetic colour polymorphism in the large narcissus bulb fly, *Merodon equestris* Fab. (Diptera, Syrphidae). *Philosophical Transactions of the Royal Society of London B* 264, 353–402.
- Corbet, P.S. (1999) *Dragonflies: Behaviour and Ecology of Odonata*. Harley Books, Essex, UK.
- Cott, H.B. (1940) *Adaptive Coloration in Animals*. Methuen, London.
- Cowan, D.P., Reynolds, J.C. and Gill, E.L. (2000) Reducing predation through conditioned taste aversion. In: Gosling, L.M. and Sutherland, W.J. (eds) *Behaviour and Conservation*. Cambridge University Press, Cambridge, UK, pp. 281–299.
- Cramp, S. (ed.) (1977–1994) *Birds of the Western Palearctic*, 9 vols. Oxford University Press, Oxford, UK.
- Cuthill, I.C. and Bennett, A.T.D. (1993) Mimicry and the eye of the beholder. *Proceedings of the Royal Society of London B* 253, 203–204.
- Davies, N.B. (1977) Prey selection and the search strategy of the spotted flycatcher (*Muscicapa striata*): a field study on optimal foraging. *Animal Behaviour* 25, 1016–1033.
- Davies, N.B. and Green, R.E. (1976) The development and ecological significance of feeding techniques in the Reed Warbler (*Acrocephalus scirpaceus*). *Animal Behaviour* 24, 213–229.
- Dill, L. (1975) Calculated risk-taking by predators as a factor in Batesian mimicry. *Canadian Journal of Zoology* 53, 1614–1621.
- Dittrich, W., Gilbert, F., Green, P., McGregor, P. and Grewcock, D. (1993) Imperfect mimicry: a pigeon's perspective. *Proceedings of the Royal Society of London B* 251, 195–200.
- Dixon, A.F.G. (1998) *Aphid Ecology*, 2nd edn. Chapman and Hall, London.
- Duncan, C.J. and Sheppard, P.M. (1965) Sensory discrimination and its role in the evolution of Batesian mimicry. *Behaviour* 24, 269–282.
- Dlusskii, G.M. (1984) Are dipterous insects protected by their similarity to stinging hymenopterans? (in Russian). *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologicheskii* 89(5), 25–40 (translation available from <http://www.nottingham.ac.uk/~plzfg/syrphweb/Dlusski1984.doc>).
- Drees, M. (1997) Zur Hautflüglermimikry bei Schwebfliegen (Diptera, Syrphidae) [On hymenopteran mimicry by hoverflies (Diptera, Syrphidae)]. *Entomologische Zeitschrift* 107, 498–503.

- Edmunds, M. (1974) *Defence in Animals: A Survey of Anti-Predator Defences*. Longman, Harlow, Essex, UK.
- Edmunds, M. (1993) Does mimicry of ants reduce predation by wasps on salticid spiders? *Memoirs of the Queensland Museum* 11, 507–512.
- Edmunds, M. (2000) Why are there good and poor mimics? *Biological Journal of the Linnean Society* 70, 459–466.
- Evans, D.L. (1984) Reactions of some adult passerines to *Bombus pennsylvanicus* and its mimic *Mallota bautias*. *Ibis* 126, 50–58.
- Evans, D.L. and Waldbauer, G.P. (1982) Behavior of adult and naive birds when presented with a bumblebee and its mimic. *Zeitschrift für Tierpsychologie* 59, 247–259.
- Evans, H.E. (1966) *Life on a Little-Known Planet: A Journey into the Insect World*. Andre Deutsch, London.
- Evans, H.E. and Eberhard, M.J.W. (1970) *The Wasps*. University of Michigan Press, Ann Arbor, Michigan, USA.
- Fabre, J.-H. (1913) *The Life of the Fly* (translated by A. Teixeira de Mattos). Hodder and Stoughton, London.
- Fincher, F. (1951) Mimicry in *Volucella bombylans* (L.) (Diptera, Syrphidae). *Entomologists Monthly Magazine* 87, 31.
- Ford, H.A. (1971) The degree of mimetic protection gained by new partial mimics. *Heredity* 27, 227–236.
- Franks, D.W. and Noble, J. (2004) Batesian mimics influence mimicry ring evolution. *Proceedings of the Royal Society of London B* 271, 191–196.
- Gabritschewsky, E. (1924) Farbenpolymorphismus und Vererbung mimetischer Varietäten der Fliege *Volucella bombylans* und anderer “hummelähnlicher” Zweiflügler. [Colour polymorphism and genetics of mimetic varieties of the fly *Volucella bombylans* and other ‘bee-like’ Diptera]. *Zeitschrift für Induktive Abstammungs- und Vererbungslehre, Berlin* 32, 321–353.
- Gabritschewsky, E. (1926) Convergence of coloration between American pilose flies and bumblebees (*Bombus*). *Biological Bulletin* 51, 269–287.
- Gatter, W. and Schmid, U. (1990) Die Wanderungen der Schwebfliegen (Diptera: Syrphidae) am Randecker Maar. [The migration of hoverflies (Diptera: Syrphidae) at Randecker Maar]. *Spixiana* 15(S), 1–100.
- Getty, T. (1985) Discriminability and the sigmoid functional response: how optimal foragers could stabilize model–mimic complexes. *American Naturalist* 125, 239–256.
- Gilbert, F. (1985) Diurnal activity patterns in hoverflies (Diptera, Syrphidae). *Ecological Entomology* 10, 385–392.
- Gilbert, J.D.J. (2001) *Callicera aurata* in Surrey. *Entomologists Monthly Magazine* 137, 153.
- Glumac, S. (1962) The problem of mimicry in Syrphoidea. *Archiv Bioloskih Nauka, Beogradu* 14, 61–67.
- Golding, Y.C. and Edmunds, M. (2000) Behavioural mimicry of honeybees (*Apis mellifera*) by droneflies (*Eristalis* spp., Diptera, Syrphidae). *Proceedings of the Royal Society of London B* 267, 903–909.
- Golding, Y.C., Ennos, A.R. and Edmunds, M. (2001) Similarity in flight behaviour between the honeybee *Apis mellifera* (Hymenoptera: Apidae) and its presumed mimic, the dronefly *Eristalis tenax* (Diptera: Syrphidae). *Journal of Experimental Biology* 204, 139–145.
- Goodale, M.A. and Sneddon, I. (1977) The effect of distastefulness of the model on the predation of artificial Batesian mimics. *Animal Behaviour* 25, 660–665.

- Goulson, D. (2003) *Bumblebees: Their Behaviour and Ecology*. Cambridge University Press, Cambridge, UK.
- Green, P.R., Gentle, L., Peake, T.M., Scudamore, R.E., McGregor, P.K., Gilbert, F. and Dittrich, W. (1999) Conditioning pigeons to discriminate naturally lit insect specimens. *Behavioural Processes* 46, 97–102.
- Greenwood, J.J.D. (1986) Crypsis, mimicry, and switching by optimal foragers. *American Naturalist* 128, 294–300.
- Greig-Smith, P.W. and Quicke, D.L.J. (1983) The diet of nestling Stonechats. *Bird Study* 30, 47–50.
- Grewcock, D. (1992) *The Hoverflies: A Case of 'Poor' Mimicry?* PhD thesis, Nottingham University, Nottingham, UK.
- Guilford, T. (1990) The evolution of aposematism. In: Evans, D.L. and Schmidt, J.O. (eds) *Insect Defenses: Adaptive Mechanisms and Strategies of Prey and Predators*. State University of New York Press, Albany, New York, pp. 23–61.
- Haeseler, V. (1976) *Ceriana conopsoides* (L.) near Oldenburg (Diptera, Syrphidae). *Drosera*, 1976, 19–21.
- Hartley, I.R. and Quicke, D.L.J. (1994) The diet of nestling corn buntings of North Uist: insects not grain. *Scottish Birds* 17(3), 169–170.
- Heal, J.R. (1979) Colour patterns of Syrphidae. II. *Eristalis intricarius*. *Heredity* 43, 229–238.
- Heal, J.R. (1981) Colour patterns of Syrphidae. III. Sexual dimorphism in *Eristalis arbustorum*. *Ecological Entomology* 6, 119–127.
- Heal, J.R. (1982) Colour patterns of Syrphidae. 4. Mimicry and variation in natural populations of *Eristalis tenax*. *Heredity* 49, 95–110.
- Heal, J.R. (1989) Variation and seasonal changes in hoverfly species: interactions between temperature, age and genotype. *Biological Journal of the Linnean Society* 36, 251–269.
- Heal, J.R. (1995) Of what use are the bright colours of hoverflies? *Dipterists Digest* 2(1), 1–4.
- Heikertinger, F. (1918) Die Bienenmimikry von *Eristalis*: eine kritische Untersuchung. [The bee mimicry of *Eristalis*: a critical study]. *Zeitschrift für Wissenschaftliche Insektenbiologie* 14, 1–5, 73–79.
- Heikertinger, F. (1936) Noch ein Wort über Wespenmimikry. [A further note on wasp mimicry]. *Zeitschrift für Morphologie und Ökologie der Tiere* 29, 140.
- Heikertinger, F. (1954) Das Rätsel der Mimikry und seine Lösung: eine kritische Darstellung des Werdens, des Wesens und der Widerlegung der Tiertrachthypothesen. [The enigma of mimicry and its solution: a critical description of the development, nature and refutation of the hypothesis of animal colour patterns]. Gustav Fischer Verlag, Jena, Germany.
- Heinrich, B. (1993) *The Hot-Blooded Insects: Strategies and Mechanisms of Thermoregulation*. Harvard University Press, Cambridge, Massachusetts, USA.
- Hespenheide, H.A. (1973) A novel mimicry complex: beetles and flies. *Journal of Entomology* (A) 48, 49–56.
- Hetz, M. and Slobodchikoff, C.N. (1988) Predation pressure on an imperfect Batesian mimicry complex in the presence of alternative prey. *Oecologia* 76, 570–573.
- Hövmeyer, K. (1995) Seasonal and diurnal activity patterns in the hoverfly species *Cheilosia fasciata* (Diptera: Syrphidae). *Entomologia Generalis* 20, 87–102.
- Holling, C.S. (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 45, 1–60.
- Holloway, B.A. (1976) Pollen feeding in hoverflies (Diptera, Syrphidae). *New Zealand Journal of Zoology* 3, 339–350.

- Holloway, G.J. (1993) Phenotypic variation in colour pattern and seasonal plasticity in *Eristalis* hoverflies (Diptera: Syrphidae). *Ecological Entomology* 18(3), 209–217.
- Holloway, G.J. and McCaffery, A.R. (1990) Habitat utilization and dispersion in *Eristalis pertinax* (Diptera, Syrphidae). *Entomologist* 109, 116–124.
- Holloway, G.J., Gilbert, F. and Brandt, A. (2002) The relationship between mimetic imperfection and phenotypic variation in insect colour patterns. *Proceedings of the Royal Society of London B* 269, 411–416.
- Howarth, B. (1998) An ecological study of Batesian mimicry in the British Syrphidae (Diptera). PhD thesis, University of Central Lancashire, Preston, UK.
- Howarth, B. and Edmunds, M. (2000) The phenology of Syrphidae (Diptera): are they Batesian mimics of Hymenoptera? *Biological Journal of the Linnean Society* 71, 437–457.
- Howarth, B., Clee, C. and Edmunds, M. (2000) The mimicry between British Syrphidae (Diptera) and Aculeate Hymenoptera. *British Journal of Entomology and Natural History* 13, 1–40.
- Howarth, B., Edmunds, M. and Gilbert, F. (2004) Does the abundance of hoverfly mimics (Diptera: Syrphidae) depend on the numbers of their hymenopteran models? *Evolution* 58(2), 367–375.
- Howse, P.E. and Allen, J.A. (1994) Satyric mimicry: the evolution of apparent imperfection. *Proceedings of the Royal Society of London B* 257, 111–114.
- Iwata, K. (1976) *Evolution of Instinct: Comparative Ethology of Hymenoptera*. Amerind Publishing, New York.
- Jacobi, A. (1913) *Mimikry und verwandte Erscheinungen. [Mimicry and related phenomena]*. Vieweg, Braunschweig, Germany.
- Jablonski, P.G. and Strausfeld, N.J. (2000) Exploitation of an ancient escape circuit by an avian predator: prey sensitivity to model predator display in the field. *Brain Behavior and Evolution* 56(2), 94–106.
- Johnstone, R.A. (2002) The evolution of inaccurate mimics. *Nature* 418, 524–526.
- Joron, M. and Mallet, J.L.B. (1998) Diversity in mimicry: paradox or paradigm? *Trends in Ecology and Evolution* 13, 461–466.
- Kassarov, L. (2003) Are birds the primary selective force leading to evolution of mimicry and aposematism in butterflies? An opposing point of view. *Behaviour* 140, 433–451.
- Kauppinen, J. and Mappes, J. (2003) Why are wasps so intimidating: field experiments on hunting dragonflies (Odonata: *Aeschna grandis*). *Animal Behaviour* 66, 505–511.
- Kearns, C.A. and Thomson, J.D. (2001) *The Natural History of Bumblebees: A Sourcebook for Investigations*. University Press of Colorado, Boulder, Colorado, USA.
- Kikuchi, T. (1963) Studies on the coaction among insects visiting flowers. III. Dominance relationships among flower-visiting flies, bees and butterflies. *Science Reports of the Tohoku (Imperial) University, 4th Series, Biology* 29, 1–8.
- Komarek, S. (1998) *Mimicry, Aposematism and Related Phenomena in Animals and Plants: A Bibliography 1800–1990*. Vesmir, Prague.
- Kratochwil, A. (1983) Zur Phänologie von Pflanzen und blütenbesuchenden Insekten eines versäumten Halbtrockenrasens im Kaiserstuhl: ein Beitrag zur Erhaltung brachliegender Wiesen als Lizenz-Biotope gefährdeter Tierarten. [Phenological phenomena of plants and flower-visiting insects in a fallow limestone grassland in the Kaiserstuhl: remarks about the conservation of fallow grassland as 'licence biotopes' for endangered invertebrate animals]. *Beihefte der Veröffentlichung Naturschutz Landschaftspflege Bad-Würtensbergs* 34, 57–108.

- Lane, C. (1957) Preliminary note on insects eaten and rejected by a tame Shama (*Kittacincla malabarica* Gm.), with the suggestion that in certain species of butterflies and moths females are less palatable than males. *Entomologists Monthly Magazine* 93, 172–179.
- Lea, S.E.G. and Harrison, S.N. (1978) Discrimination of polymorphous stimulus sets by pigeons. *Quarterly Journal of Experimental Psychology* 30, 521–537.
- Liepelt, W. (1963) Zur Schutzwirkung des Stachelgiftes von Bienen und Wespen gegenüber Trauerfliegenschnäpper und Gartenrotschwanz. [On the defensive action of the poison stings of bees and wasps against flycatchers and robins]. *Zoologisches Jahrbuch, Abteilung Zoologie und Physiologie* 70, 167–176.
- Lindström, L., Alatalo, R. and Mappes, J. (1997) Imperfect Batesian mimicry: the effects of the frequency and the distastefulness of the model. *Proceedings of the Royal Society of London B* 264, 149–153.
- Lyon, J.-P. (1973) La mouche des Narcisses (*Merodon equestris* F., Diptère, Syrphidae). I. Identification de l'insecte et de ses dégâts et biologie dans le Sud-Est de la France. [The Narcissus fly (*Merodon equestris* F., Diptera, Syrphidae). I. Identification of the insect, and its damage and biology in the south-east of France]. *Revue de Zoologie Agricole et de Pathologie Végétale* 72(3), 65–92.
- Maier, C.T. (1978) Evolution of Batesian mimicry in the Syrphidae (Diptera). *Journal of the New York Entomological Society* 86, 307.
- Malcolm, S.B. (1976) An investigation of plant-derived cardiac glycosides as a possible basis for aposematism in the aphidophagous hoverfly *Ischiodon aegyptius* (Wiedemann) (Diptera, Syrphidae). MSc thesis, Rhodes University, Grahamstown, South Africa.
- Malcolm, S.B. (1981) Defensive use of plant-derived cardenolides by *Aphis nerii* Boyer de Fonscolombe against predation. DPhil thesis, Oxford University, Oxford, UK.
- Malcolm, S.B. (1990) Mimicry: status of a classical evolutionary paradigm. *Trends in Ecology and Evolution* 5, 57–62.
- Mallet, J. (1999) Causes and consequences of a lack of coevolution in Müllerian mimicry. *Evolutionary Ecology* 13, 777–806.
- Mallet, J. and Gilbert, L.E. (1995) Why are there so many mimicry rings? Correlations between habitat, behaviour and mimicry in *Heliconius* butterflies. *Biological Journal of the Linnean Society* 55, 159–180.
- Mallet, J. and Joron, M. (1999) Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Annual Review of Ecology and Systematics* 30, 201–233.
- Mappes, J. and Alatalo, R.V. (1997) Batesian mimicry and signal accuracy. *Evolution* 51(6): 2050–2053.
- Marden, J.H. and Chai, P. (1991) Aerial predation and butterfly design: how palatability, mimicry, and the need for evasive flight constrain mass allocation. *American Naturalist* 138, 15–36.
- McAtee, W.L. (1932) Effectiveness in nature of the so-called protective adaptations in the animal kingdom, as illustrated by the food habits of Nearctic birds. *Smithsonian Miscellaneous Collections* 87(7), 1–201.
- Morgan, K.R. and Heinrich, B. (1987) Temperature regulation in bee- and wasp-mimicking syrphid flies. *Journal of Experimental Biology* 133, 59–71.
- Morse, D.H. (1986) Predatory risk to insects foraging at flowers. *Oikos* 46, 223–228.
- Mostler, G. (1935) Beobachtungen zur Frage der Wespenmimikry. [Studies on the question of wasp mimicry]. *Zeitschrift für Morphologie und Ökologie der Tiere* 29, 381–454.
- Myers, J.G. (1935) Experiments with spiders and the bee-like *Eristalis tenax* Linn. *Proceedings of the Royal Entomological Society of London A* 9, 93–95.

- Nentwig, W. (1982) Why do only certain insects escape from a spider's web? *Oecologia* 53, 412–417.
- Nicholson, A.J. (1927) A new theory of mimicry in insects. *Australian Zoologist* 5, 10–104.
- Nickol, M. (1994) *Volucella zonaria* (Diptera: Syrphidae) in Rheinland-Pfalz: Nachweise nebst Bemerkungen über Blütenbesuch, Verhalten, Färbung und Ökologie sowie andere Gattungsvertreterinnen. [*Volucella zonaria* (Diptera: Syrphidae) in Rheinland-Pfalz: records and remarks on flower visits, behaviour, colour and ecology, as well as for other members of the genus]. *Mitteilungen der Pollichia der Pfälzischen Vereins für Naturkunde und Naturschutz* 81, 383–405.
- Nur, U. (1970) Evolutionary rates of models and mimics in Batesian mimicry. *American Naturalist* 104, 477–486.
- Oaten, A., Pearce, C.E.M. and Smyth B. (1975) Batesian mimicry and signal-detection theory. *Bulletin of Mathematical Biology* 37, 367–387.
- O'Donnell, S. (1996) Dragonflies (*Gynacantha nervosa* Rambur) avoid wasps (*Polybia aequatorialis* Zavattari and *Mischocyttarus* sp) as prey. *Journal of Insect Behavior* 9, 159–162.
- Osten-Sacken, C.R. (1894) *On the Oxen-Borne Bees of the Ancients (Bugonia), and their Relation to Eristalis Tenax, a Two-winged Insect*. Heidelberg, Germany.
- Ottenheim, M.M., Henseler, A. and Brakefield, P.M. (1998) Geographic variation in plasticity in *Eristalis arbustorum*. *Biological Journal of the Linnean Society* 65, 215–229.
- Owen, J. (1991) *Ecology of a Garden*. Cambridge University Press, Cambridge, UK.
- Parmenter, L. (1953) The hoverflies (Syrphidae). *Entomologists Record and Journal of Variation* 65, 122–238.
- Pickard, R.S. (1975) Relative abundance of syrphid [sic] species in a nest of the wasp *Ectemnius cavifrons* compared with that of the surrounding habitat. *Entomophaga* 20, 143–151.
- Pilecki, C. and O'Donald, P. (1971) The effects of predation on artificial mimetic polymorphisms with perfect and imperfect mimics at varying frequencies. *Evolution* 25, 365–370.
- Plowright, R.C. and Owen, R.E. (1980) The evolutionary significance of bumble bee color patterns: a mimetic interpretation. *Evolution* 34, 622–637.
- Pocock, R.I. (1911) On the palatability of some British insects. *Proceedings of the Zoological Society of London* 1911, 809–868.
- Poulton, E.B. (1890) *The Colours of Animals*. Trübner, London.
- Prys-Jones, O.E. and Corbet, S.A. (1991) *Bumblebees*. *Naturalists Handbook* 6. Richmond Publishing, Slough, UK.
- Rettenmeyer, C.W. (1970) Insect mimicry. *Annual Review of Entomology* 15, 43–74.
- Ritland, D.B. and Brower, L.P. (1991) The viceroy butterfly is not a Batesian mimic. *Nature* 350, 497–498.
- Röder, G. (1990) *Biologie der Schwebfliegen Deutschlands (Diptera: Syrphidae)*. [Biology of the hoverflies of Germany (Diptera: Syrphidae)]. Erna Bauer Verlag, Keltern-Weiler, Germany.
- Rotheray, G.E. (1993) Colour guide to hoverfly larvae. *Dipterists Digest* 9, 1–155.
- Rotheray, G.E. and Gilbert, F. (1999) Phylogeny of Palaearctic Syrphidae (Diptera): evidence from larval stages. *Zoological Journal of the Linnean Society* 127, 1–112.
- Rothschild, M. (1984) Aide-mémoire mimicry. *Ecological Entomology* 9, 311–319.
- Rowe, C. (1999) Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour* 58, 921–931.

- Rowe, C., Lindström, L. and Lyttinen, A. (2004) The importance of pattern similarity between Müllerian mimics in predator avoidance learning. *Proceedings of the Royal Society of London B* 271, 407–413.
- Rupp, L. (1989) Die mitteleuropäischen Arten der Gattung *Volucella* (Diptera, Syrphidae) als Kommensalen und Parasitoide in den Nestern von Hummeln und sozialen Wespen: Untersuchungen zur Wirtsfindung, Larvalbiologie und Mimikry. [The central European species of the genus *Volucella* (Diptera, Syrphidae) as commensals and parasitoids in the nests of bees and social wasps: studies on host finding, larval biology and mimicry]. PhD thesis, Albert-Ludwigs-Universität, Freiburg-im-Breisgau, Germany.
- Sbordoni, V., Bullini, L., Scarpelli, G., Forestiero, S. and Rampini, M. (1979) Mimicry in the burnet moth *Zygaena ephialtes*: population studies and evidence of a Batesian–Müllerian situation. *Ecological Entomology* 4, 83–93.
- Schmidt, R.S. (1960) Predator behaviour and the perfection of incipient mimetic resemblances. *Behaviour* 16, 149–158.
- Schuler, W. (1980) Zum Meidenlernen ungeneisbarer Beute bei Vögeln: der Einfluss der Faktoren Umlernen, neue Alternativbeute und Ähnlichkeit der Alternativbeute. [Factors influencing learning to avoid unpalatable prey in birds: relearning, new alternative prey, and similarity of appearance of alternative prey]. *Zeitschrift für Tierpsychologie* 54, 105–143.
- Seeley, T.D. (1985) *Honeybee Ecology: A Study of Adaptation in Social Life*. Princeton University Press, Princeton, New Jersey, USA.
- Shelly, T.D. and Pearson, D.L. (1978) Size and colour discrimination of the robberfly *Efferia tricella* (Diptera: Asilidae) as a predator on tiger beetles (Coleoptera: Cincidelidae). *Environmental Entomology* 7, 790–793.
- Sheppard, P.M. (1959) The evolution of mimicry: a problem in ecology and genetics. *Cold Spring Harbor Symposia in Quantitative Biology* 24, 131–140.
- Sherratt, T.N. (2002) The evolution of imperfect mimicry. *Behavioral Ecology* 13(6), 821–826.
- Sherratt, T.N. (2003) State-dependent risk-taking by predators in systems with defended prey. *Oikos* 103, 93–100.
- Shettleworth, S.J. (1998) *Cognition, Evolution and Behaviour*. Oxford University Press, Oxford, UK.
- Southwood, T.R.E. and Henderson, P.A. (2000) *Ecological Methods*, 3rd edn. Blackwell Scientific, Oxford, UK.
- Speed, M.P. (1993) Müllerian mimicry and the psychology of predation. *Animal Behaviour* 45, 571–580.
- Speed, M.P. (2000) Warning signals, receiver psychology and predator memory. *Animal Behaviour* 60, 269–278.
- Speed, M.P. (2001) Batesian, quasi-Batesian or Müllerian mimicry? Theory and data in mimicry research. *Evolutionary Ecology* 13, 755–776.
- Speed, M.P. and Turner J.R.G. (1999) Learning and memory in mimicry. II. Do we understand the mimicry spectrum? *Biological Journal of the Linnean Society* 67, 281–312.
- Speight, M.C.D. (1983) Flies: Diptera. In: Feehan, J. (ed.) *Laos: An Environmental History*. Ballykilcavan Press, Eire, pp. 172–178, 502–507.
- Speight, M.C.D. (2000) Hoverflies (Dip.: Syrphidae) with a drinking habit. *Entomologists Record and Journal of Variation* 112, 107–113.
- Speight, M.C.D. and Lucas, J.A.W. (1992) Liechtenstein Syrphidae (Diptera). *Bericht der Botanische-Zoologische Gesellschaft für Liechtenstein-Sargans-Werdenberg* 19, 327–463.

- Speight, M.C.D., Chandler, P.J. and Nash, R. (1975) Irish Syrphidae (Diptera): notes on the species and an account of their known distribution. *Proceedings of the Royal Irish Academy B* 75, 1–80.
- Spradberry, J.P. (1973) *Wasps*. Sidgwick and Jackson, London.
- Srygley, R.B. (1994) Locomotor mimicry in butterflies? The associations of positions of centres of mass among groups of mimetic, unprofitable prey. *Philosophical Transactions of the Royal Society of London B* 343, 145–155.
- Srygley, R.B. (1999) Locomotor mimicry in *Heliconius* butterflies: contrast analysis of flight morphology and kinematics. *Philosophical Transactions of the Royal Society of London B* 354, 203–214.
- Srygley, R.B. (2004) The aerodynamic costs of warning signals in palatable mimetic butterflies and their distasteful models. *Proceedings of the Royal Society of London B* 271, 589–594.
- Srygley, R.B. and Dudley, R. (1993) Correlations of the position of the centre of body mass with butterfly escape tactics. *Journal of Experimental Biology* 174, 155–166.
- Steiniger, F. (1937a) “Ekelgeschmack” und visuelle Anpassung einiger Insekten (Fütterungsversuche an Vögeln. [“Disgusting taste” and visual recognition of some insects (feeding experiments with birds)]. *Zeitschrift für Wissenschaftliche Zoologie* 149, 221–229.
- Steiniger, F. (1937b) Beobachtungen und Bemerkungen zur Mimikryfrage. [Observations and remarks on the mimicry question]. *Biologisches Zentralblatt* 57, 47–58.
- Stiles, E.W. (1979) Evolution of color pattern and pubescence characteristics in male bumblebees: automimicry vs. thermoregulation. *Evolution* 33(3), 941–957.
- Stubbs, A.E. and Falk, S. (1983) *British Hoverflies: An Illustrated Identification Guide*. British Entomological and Natural History Society, London.
- Testa, T.J. and Ternes, J.W. (1970) Specificity of conditioning mechanisms in the modification of food preferences. In: Barker, L.M., Best, M.R. and Domjan, M. (eds) *Learning Mechanisms in Food Selection*. Baylor University Press, Texas, pp. 229–253.
- Tibbetts, E.A. (2002) Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proceedings of the Royal Society of London B* 269, 1423–1428.
- Tsuneki, K. (1956) Ethological studies on *Bembix niponica* Smith, with emphasis on the psychobiological analysis of behaviour inside the nest (Hymenoptera: Sphecidae). 1. Biological part. *Memoirs of the Faculty of Liberal Arts, Fukui University, Series II: Natural Sciences* 6, 77–172.
- Turner, J.R.G. (1984) Darwin’s coffin and Doctor Pangloss: do adaptationist models explain mimicry? In: Shorrocks, B. (ed.) *Evolutionary Ecology*. Blackwell Scientific, Oxford, UK, pp 313–361.
- Turner, J.R.G. (1987) The evolutionary dynamics of Batesian and Müllerian mimicry: similarities and differences. *Ecological Entomology* 12, 81–95.
- Tyshchenko, V.P. (1961) On the relationship between flower spiders of the family Thomisidae and mimetic Diptera and their models (in Russian). *Vestnik Leningradskogo Gosudarstvennogo Universiteta. Ser. Biologiya*, 1961(3), 133–139.
- van Someren, V.G.L. and Jackson, T.H.E. (1959) Some comments on the protective resemblance amongst African Lepidoptera (Rhopalocera). *Journal of the Lepidopterists Society* 13(3), 121–150.
- Vane-Wright, R.I. (1978) Mimicry. In: Stubbs, A. and Chandler, P. (eds) *A Dipterists Handbook*. *Amateur Entomologist* 15, 239–241.
- Vanhaelen, N., Haubruge, E., Lognay, G. and Francis, F. (2001) Hoverfly glutathione S-transferases and effect of Brassicaceae secondary metabolites. *Pesticide Biochemistry and Physiology* 71(3), 170–177.

- Vanhaelen, N., Gaspar, C. and Francis, F. (2002) Influence of prey host plant on a generalist aphidophagous predator, *Episyrphus balteatus* (Diptera: Syrphidae). *European Journal of Entomology* 99(4), 561–564.
- Verrall, G.H. (1901) *British Flies, Vol. VIII*. Taylor and Francis, London.
- von Hagen, E. and Aichhorn, A. (2003) *Hummeln. [Bumblebees]*. Fauna Verlag, Nottuln, Germany.
- Waldbauer, G.P. (1970) Mimicry of hymenopteran antennae by Syrphidae. *Psyche* 77, 45–49.
- Waldbauer, G.P. (1988) Asynchrony between Batesian mimics and their models. *American Naturalist* 131, S103–S121.
- Waldbauer, G.P. and LaBerge, W.E. (1985) Phenological relationships of wasps, bumblebees, their mimics and insectivorous birds in northern Michigan. *Ecological Entomology* 10, 99–110.
- Waldbauer, G.P. and Sheldon, J.K. (1971) Phenological relationships of some aculeate Hymenoptera, their dipteran mimics, and insectivorous birds. *Evolution* 25, 371–382.
- Waldbauer, G.P., Sternberg, J.G. and Maier, C.T. (1977) Phenological relationships of wasps, bumblebees, their mimics, and insectivorous birds in an Illinois sand area. *Ecology* 58, 583–591.
- Watts, J.O. (1983) A comparative study of the Syrphidae (Diptera) from different habitats within Bernwood Forest. PhD thesis, Oxford Polytechnic, Oxford, UK.
- White, T.C.R. (1993) *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Springer Verlag, Berlin, Germany.
- Williams, P.H. (1991) The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum of Natural History (Entomology)* 60, 1–204.
- Williams, P.H. (1998) An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). *Bulletin of the Natural History Museum, London (Entomology)* 67, 79–152.