The Hoverflies: A Case of 'Poor' Mimicry ?

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Abstract.

The hoverflies (Diptera:Syrphidae) represent an apparently paradoxical visual Batesian mimicry complex, with what appear to be "poor" Mimics outnumbering their more accomplished counterparts. The purpose of this thesis is to determine how far conventional mimicry theory is capable of explaining the apparent paradoxes of mimicry in the hoverflies.

It becomes obvious that determining the mimetic status of the supposedly poor Mimics is not a trivial task. Conventional experimental tests of mimicry, using captive predators, seem incapable of predicting the degree of protection enjoyed by a Mimic in the field. The research therefore concentrates on developing some novel empirical approaches to the study of mimicry. This includes developing a method of image analysis which yields an objective, single-value measure of the similarity between Model and Mimic patterns.

This index of similarity is used to produce unique descriptions of the structure of mimetic communities in terms of Mimic frequency and similarity to the supposed Model. These profiles indicate that there is an objective basis to the perceived paradox, and suggest that there is not a simple relationship between the actual and perceived similarity of two patterns. The perceived similarity of Model and Mimic will be a key determinant of mimetic success.

The index of similarity is also used as a basis for direct comparison of the supposedly mimetic hoverflies with a more established example of mimicry in the butterflies. This exercise demonstrates that an index of pattern similarity enables a unique comparative analysis of mimicry.

It is proposed that an index of similarity also provides a unique opportunity to test our theoretical understanding of mimicry, if it is used in conjunction with a mathematical model that possesses some specific attributes. A suitable prototype model is developed and demonstrated.

The thesis concludes with an indication that the novel empirical approaches developed here, have been adopted elsewhere. This latter work indicates that those hoverfly species which are apparently "poor" Mimics, may be exploiting some constraint in predator perceptual and cognitive systems to achieve mimetic protection, despite a relatively low degree of actual similarity to the Model species.

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For Mum and Dad,
and with Claire.

Chapter One.

Introduction.

1.1 The Paradox of Apparent Mimicry in the Hoverflies.

Stubbs and Falk (1983) identify some 256 species of hoverfly (Diptera:Syrphidae) in the British Isles, with a further nine forms that are of uncertain status. The plates in that text depict around 190 species, approximately 140 of which have a coloration of the cuticle or pilosity which lends them a similarity either to the social wasps, or the social and solitary bees. While these plates are clearly not necessarily an unbiased representation of the hoverfly fauna, it is the case that the majority of British syrphids, and certainly the most common species, have features which make them similar to British stinging hymenoptera; Plate 1 (photographs c to i) in Appendix Five shows five hoverfly species with some resemblance to common wasps. It is widely assumed that such syrphids are mimetic, gaining protection from predators as a result of their resemblance to a harmful "Model" species.

If the hoverflies do constitute a mimetic complex, then it certainly appears to be a paradoxical one. As will be discussed later, some Syrphids are so similar to social wasps, both in their appearance and behaviour, that it is sometimes impossible to discriminate the two in flight without significant doubt and delay (see for example Appendix Five,

Plate 1, species c, *Temnostoma vespiforme*). Such species are rarities, however, both in terms of the number of individuals and the number of species they represent in the supposed complex. In marked contrast, it takes very little time for a human observer to learn to discriminate between the majority of the apparent Mimics, species such as *Syrphus ribesii* (Appendix Five, Plate 1 species e and f), and their supposed Models (Stubbs and Falk 1983; Waldbauer 1988). It is usually assumed that natural potential predators of these species will be yet more adept at making such discriminations, given that, for them, it represents a task pertinent to their survival and well-being.

This, then, is the central paradox of apparent mimicry in the hoverflies: how can a mimetic complex persist when what appear to be such poor Mimics greatly outnumber their more accomplished counterparts ? If the selective pressures imposed by predators and the benefits of being a Mimic are such as to cause the evolution of some very high-fidelity mimicry, how can they permit the co-existence of many more, lower quality Mimics in the same fauna ? It is the purpose of this thesis to begin the resolution of this paradox.

1.2 Alternative Hypotheses.

It is possible to formulate a number of alternative, or at least supplementary, hypotheses which seek to explain the occurrence of apparently poor Mimics through extensions to simple mimicry theory or by proposing alternative reasons for the evolution of conspicuous patterns. In the following section, a number of these alternative explanations are addressed.

1.2.1 Are Hoverflies Distasteful ?

It is a common assumption that hoverflies, being often large, common and apparently innocuous, represent a valuable and palatable prey item for most predators. There are some indications in the literature that this is not so, and that they may themselves be distasteful to some predators. Pocock (1911) records that *Volucella bombylans* was rejected by a spectacled thrush which subsequently displayed bill-wiping behaviour, taken to be an indication of distastefulness. Similarly, Lane (1957) suggested that on presentation to a tame Shama (*Kittacincla malabrica*), *Eristalis* spp., appeared as unpalatable as their supposed Models, *Apis* . Other hoverflies, such as *Syrphus* and some *Volucella* species were also suggested as being unpalatable. Such reactions do not necessarily indicate that syrhids are unpalatable; they may simply be a response to unfamiliar prey. Coppinger (1970) reports a number of "active" rejections of harmless but novel butterflies by a series of captive birds and it is possible that less marked responses such as bill-wiping may also simply be a reaction to novelty.

Malcolm (1976) reports a more distinct indication that some hoverflies may be distasteful or emetic to predators. *Ischiodon aegyptius* , a small black-and-yellow banded syrphid common in Malcolm's South African field sites, were reared on *Aphis nerii* , which in turn fed on *Asclepias* species, a rich source of cardiac glycosides. These chemicals, most familiar as the basis of aposematism in the Monarch butterfly *Danaus plexippus* , are well known for their cardiac activity and their emetic properties (Brower 1958; Brower and McEvoy 1972). Colonies of *A. nerii* infesting *Asclepias* proved a fatal food source for the larvae of another hoverfly genus, *Metasyrphus* , but successfully sustained *I. aegyptius* larvae. Four cardiac glycoside types were detected in adult *I. aegyptius* and the extract of adults had a significant effect on the myogenic activity of heart muscle from two vertebrates (*Xenopus laevis* and *Chamaeleo pumilus*). Malcolm noted that *I. aegyptius* exuded gut contents and linings at pupation, and that, therefore, the cardiac glycosides present in the adult flies must be the result of an active, non-random sequestration process. These results were clearly consistent with the hypothesis that *I. aegyptius* has adopted an aposematic strategy, at least in some parts of its range, based on cardiac glycosides sequestered via their larvae, from the host plant of the larval prey. This scenario closely parallels the Milkweed-Monarch relationship except that an intermediate species, *A. nerii* represents an additional step in the sequestration path. Further results suggested a less obvious hypothesis.

Ten cardiac glycosides were detected in extracts from the *Asclepias* species, and while one such compound was extracted from *A. nerii* , it failed to correspond with any of those found in the host plant. Furthermore, the four cardiac glycoside-like substances in *I. aegyptius* adults raised on the *Asclepias/A.nerii* pairing were also present in individuals raised on non-*Asclepias* plant/aphid pairings. Malcolm's conclusion was that *I. aegyptius, A.nerii* or the symbionts of either of these species synthesized the cardiac glycoside substances.

Whatever the particular explanation in this instance, it serves as a reminder that the sequestration or synthesis of emetic, toxic or distasteful substances could form the basis of an aposematic defence in a whole variety of insects, including, it seems, some syrphids.

There would appear to be little basis for predicting amongst which, if any, of the British hoverflies, the *synthesis* of defensive compounds is most likely to occur. By contrast, a knowledge of the larval and adult feeding habits of hoverflies, and the chemistry of native plant groups could provide indications of likely candidates for sequestration-based aposematism. What is clear, is that if British species are achieving such aposematism, the origin of the distasteful compounds cannot be the familiar *Asclepias* / cardiac glycoside relationship: the native British flora does not include an Asclepiad species (McClintock and Fitter 1982).

Were it the case that "poor mimics" are actually aposematic species, their distribution could indicate the possible source of the distasteful plant products. Many of the accomplished Mimics, particularly the bee Mimics, have larval habitats associated with ancient woodlands, *Criorhina berberina* breeds in rotting roots of dead trees, while *Pocota personata* is thought to breed in rot holes high in established trees. In contrast, many of the common, apparently poor mimics are associated as adults with plants of open or disturbed ground, gardens, urban wastelands and woodland and field margins. Although there can be a high degree of adult mobility (Daine and McGlashan 1987), it seems likely that such associations occur at the larval stage too. These "poor mimics" are often from the sub-family *Syrphinae* , such as the *Syrphus* , *Metasyrphus* , *Epistrophe* and *Scaeva* species, well known for their predatory, usually aphidophagous, larvae. The *Umbelliferae* are also noted colonists of open and disturbed land; species such as *Heracleum sphondylium* and *Pastinaca sativa* ; these commonly suffer aphid infestations and provide a season-long attraction to adult hoverflies (Stubbs and Falk 1983). If some British hoverflies are sequestering secondary plant products, then the Umbellifers must certainly qualify as a candidate for the source of such substances.

Hemlock (*Conium* spp.), with its high concentrations of alkaloids, is an Umbellifer famous for its poisonous properties. Although the alkaloid content of Hemlock is thought to be unusually high (Frohne and Pfander 1983), lower concentrations are found in other species, including *Pastinaca* and *Heracleum* (Raffouf 1970). Another group of chemicals may, however, be more significant and interesting because their distribution within the Umbellifers fits with the observed distribution of apparent mimicry quality. The furanocoumarins have long been known to cause a photo-toxic skin reaction in humans; in the presence of some ultraviolet frequencies, these chemicals bind to epidermal DNA, causing weals on the skin (Musajo *et al* 1967) and the same reaction proves lethal to bacteria (Fowlks *et al* 1958). Berenbaum (1981a) reveals an interesting pattern of distribution of these furanocoumarins within the Umbelliferae. Plants of open ground, road sides and waste ground possess relatively high levels of furanocoumarins compared with woodland plants, the majority of this variation being explained by variation in light intensity. (Similar variations occur, incidentally, in the cardiac glycoside content of *Asclepias* , with plants on habitat margins containing higher concentrations than those of either completely open, or well-wooded sites (Malcolm *et al* 1989)). This distribution of furanocoumarins is reflected in the structure of the insect herbivore community. Berenbaum's analysis excluded the aphids, but across other insect groups, more specialized insect communities occurred on those plant species with the most complex furanocoumarin chemistries. Specialist species can escape this toxicity: Berenbaum and Feeny (1981) demonstrate, for example, that the butterfly *Papilio polyxenes* can be successfully raised on *Pastinaca sativa* , implying some biochemical adaptation to these poisons.

This circumstantial evidence immediately suggests an alternative explanation for the abundance of "poor mimics". Outside established woodland sites, species with specialized aphidophagous larvae may be sequestering furanocoumarins from common umbellifers, making them distasteful to predators, and making their abdominal patterns examples of warning coloration rather than an instance of poor mimicry. In woodlands, where these furanocoumarins are less widely available, the less equivocal examples of mimicry may have evolved.

Unfortunately, other evidence makes this elegant explanation less likely. While the furanocoumarins are clearly photo-toxic, the discussion so far has assumed that they are also distasteful or emetic, clearly a necessity if the warning coloration hypothesis is to hold. In addition, photo-toxicity is a feature of only one of the two families of these of chemicals, the linear furanocoumarins; it is this family that some specialist insect herbivores are able to tolerate. The angular furanocoumarins, although less photo-toxic, inhibit the growth of insects able to withstand high concentrations of linear furanocoumarins (Berenbaum and Feeny 1981; Berenbaum 1978) and they are common in the umbellifers of disturbed waste ground. This is not fatal to the hypothesis. It is possible that the larvae and adults of some hoverflies are able to accumulate the toxic angular furanocoumarins without detriment, but the suggestion must be that such species are highly specialized, and therefore perhaps less widespread.

A more serious difficulty is with the distribution of furanocoumarins within the aphid host plant. Berenbaum (1981b) reports that furanocoumarin concentrations are highest in those parts of the plant related to growth and reproduction: flowers, buds and seeds. In some respects this appears hopeful, since aphid infestations often begin among such tissue. The difficulty is that there is no evidence that furanocoumarins are transported in the vascular system in at least one umbellifer species, *Heracleum lanatum* (Camm *et al* 1976). This latter study found that furanocoumarins are not translocated in the phloem of the plant and there were no indications that these substances were taken up in wild aphid populations. In laboratory conditions, furanocoumarins were found in a bound form in aphid tissue, but there is clearly a serious doubt over whether hoverflies could obtain these substances from their aphid prey.

Again, this single finding is not alone sufficient to dismiss the possibility that some hoverflies are distasteful; it may be that for other hoverfly, aphid and host umbellifer combinations, the transfer of furanocoumarins is possible. Many of the umbellifers used in analyses such as those above will have come from stock cultures, Berenbaum *et al* (1984) indicate that the concentration of furanocoumarins can be as much as three times higher in the seed of wild *Pastinaca sativa* compared to cultivated plants, clearly a factor which may determine whether these substances reach the tissues of feeding aphids in appreciable quantities. The furanocoumarins are also, of course, just an example of a candidate for sequestration, it is entirely possible that a similar sequestration path exists for other distasteful plant products.

The possibility that some hoverflies are distasteful, and that their pattern therefore represents a warning signal rather than mimicry, is certainly one that warrants further attention. What is clear, and what caused this hypothesis to be passed over for the present, is that identifying, isolating and measuring the distribution of such plant products represents a very significant research undertaking in its own right. The techniques which must be employed to explore this possibility are those of analytical chemistry, not behavioural ecology. What the zoologists' perspective does suggest is that before any such detailed analyses are undertaken there must be many more systematic observations of captive predators displaying behaviours which indicate that apparently innoucous hoverflies are unpalatable.

1.2.2 The Anthropocentric View.

The "paradoxes" of apparent mimicry in the hoverflies are, of course, "human" paradoxes, failures to reconcile our perceptions of a natural system with the predictions of a simple model of that system. The anthropocentric view has no biological relevance, since mimetic systems are shaped by the perceptions of predators, not human beings, and there are at least two respects in which these perceptions might diverge. The first is simply that the perceptual and cognitive systems of a typical predator and a human being might operate differently; this is a theme dealt with elsewhere in this thesis. A more obvious divergence is in the respective perceptual and cognitive *experience* enjoyed by predators and human observers. It is true that, with a little practice, many of the common apparently mimetic hoverflies can be promptly and reliably discriminated from their supposed Models by human observers. Nevertheless, human judgements about the lack of similarity between supposed Models and Mimics are often based on experiences for which natural predators are unlikely to have any parallel. Human observers are often afforded the privilege of studying tubed or pinned samples, which are well-lit and pose no threat in the event of a misjudgement about their appearance. This is in sharp contrast to the natural circumstance of predators, which are required to deal with, and largely only have experience of, fast moving, evasive prey, some of which may represent a significant threat to well-being. Given this, it is improbable that human and predator judgements about the appearance of hoverflies are co-incident, and this must distort our perception of the biological reality. In principle, this distortion is simple to remove, providing that models of mimicry rely on realistic, predator-based assessments of the degree of Model-Mimic confusion; in practice such assessments are extremely difficult to obtain.

This is not to suggest that the paradox of mimicry in the hoverflies is necessarily more apparent than real. Denied the "privileged" experience discussed above, it is certainly still the case that human observers could learn to discriminate between the apparently poor Mimics and their supposed Models. Since predators are likely to be capable of at least the same degree of discrimination, the central paradox still stands and our model of this particular natural system still requires revision. However, the conclusion that human perceptions and experiences of Mimics differ from those of predators, must imply that the quality of a species' mimicry cannot be reliably assessed from human judgements about the similarity of hoverflies and their apparent Models.

1.2.3 Incipient Mimicry.

Could the apparently poor Mimic species simply be in a transitory phase, destined for high-fidelity mimicry? It would be naive to assume that species are at some stable endpoint in their evolution at the time we happen to be studying them, but the hypothesis of incipient mimicry is unlikely to explain the paradox.

The fact that a species is in a transitory phase does not excuse it from the pressures which govern mimetic systems. An incipient Mimic is still a poor Mimic and current mimicry theory would seem to predict that it should occur at a lower frequency than high-fidelity Mimics. The incipient mimicry hypothesis is further countered by the aforementioned observation that the pattern of distribution of apparent mimcry quality is repeated in the British and American faunas, even though the constituent species differ. To continue to entertain the hypothesis of incipient mimicry, it would be necessary to speculate that similar selection pressures have been applied to these separate faunas at a similar point in time and that those faunas have responded in much the same way.

1.2.4 Disturbed Ecology Hypothesis.

Despite their physical separation, the British and North American faunas do have in common massive disturbances to their natural habitats through the agricultural activities of man. Many of the high-fidelity Mimics are restricted to tracts of ancient woodland which provide suitable larval habitats. As a consequence of expanding human populations and the adoption of intensive farming techniques, deforestation may have caused a severe reduction in the availability of larval sites. Conversely, large areas of disturbed ground have been created at the margins of this activity and plant species which favour such situations have probably flourished. Along with them, perhaps, have those hoverfly species, often apparently poor mimics, which have a sufficiently general larval habit to expand into this new, widespread habitat. Originally such species may have been genuinely poor Mimics, capable of occurring only at low frequencies. One could speculate, for instance, that such a species was ancestrally restricted to low absolute population sizes given their predominantly ancient woodland environment. Mimicry may have been a beneficial strategy, but their low rate of encounter may have meant that the quality of mimicry need not have been that high. The appearance of large areas of suitable habitat may have fuelled an expansion so great that the action of predators during recent ecological time has had little impact either on population size or the reproductive fitness of individuals.

1.2.5 Flight Related Hypotheses.

Aside from their conspicuous coloration, hoverflies are noted for their agility in the air; it would be no surprise if these two notable features of the group proved to be connected in some way.

1.2.5.1 Flight Agility Offsets Poor Mimicry.

The most immediately obvious hypothesis proposes that despite the apparent variation in mimicry quality within the group, its functional success is relatively invariant. Species with a 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. Were this to prove the case, it would be in contrast to a fascinating series of studies on the flight characteristics and mimetic status of some neo-tropical butterflies (Chai 1986; Chai and Srygley

1990; Marden and Chai 1991). These studies reveal that mimetic species of butterfly typically have slow or regular flight patterns and have proportionately less flight muscle than palatable species, which tend to fly quickly or erratically and with high rates of acceleration. The implication is that here, mimicry reduces the pressure to fly quickly, but there is no logical reason why a different scenario may not be true in the hoverflies. In casual field observation, there is no obvious correlation between flight agility (though this is difficult to assess) and apparent mimicry quality, but rigorous comparative data would not seem particularly difficult to gather. While this hypothesis could not alone explain the variation in hoverfly patterns, it remains credible as a contributory factor. In its simplest form, an immediate objection to it is that cause and effect are not easily separable. Where selection acts to produce a close mimetic resemblance, that resemblance might include mimicry of the hymenopteran flight patterns, typically slow, meandering and weaving when compared to the direct, darting flight of most syrphids. Slow flight may be an integral part of high quality mimicry, rather than a factor which promotes its evolution.

1.2.5.2. Agile Flight and Aposematism.

A mimetic species is most often described as one which gains protection from predators through a resemblance to an aposematic species that such predators would normally avoid. "Aposematism" describes the strategy some species adopt in conspicuously advertising that they possess a noxious or unpalatable property. This definition most obviously covers those instances where a brightly coloured species possesses a sting, is venomous, or which contains or can release a chemical which is distasteful or emetic to a predator. These are clear cases where the predator has information which indicates that an attack would be unsafe or at least unprofitable. This latter point is significant; there seems no logical reason why aposematism cannot be based simply on low profitability rather than the possession of a noxious property.

Their visual sensitivity to movement and the agility of many hoverflies make it likely that only some predators could successfully conclude an attack against them during their active flight period. Could it be, then, that hoverfly coloration is an advertisement that they represent prey of very low profitability, unlikely to give a return on the effort required to try to catch them ? Are hoverflies thus aposematic ?

If this were the case it would, incidentally, imply that the evolution of bright coloration represents a low-cost strategy. If hoverflies are so difficult to catch, what point is there in advertising this fact? The widely accepted explanation in such situations is that providing the cost of advertisement is low, it can reduce an already low risk of attack to near-zero at very little cost. This is interesting in a later context of trying to model the evolution of mimicry, where one of the main difficulties is in assessing the costs of the mimetic strategy.

If the notion that some hoverflies display an agile-flight-based aposematic strategy is accepted, then so too must the possibility that other species are Mimics of them; that is that species which are not particularly agile falsely advertise that they are. Gibson (1974) provides some laboratory data which supports this hypothesis. These experiments involved dropping away the feeding platform when an experimental group of captive finches (*Lagonosticta*) attempted to feed on particular colours of dyed millet seed, simulating an efficient escape response for these artificial prey. After an initial learning phase, the platform was permitted to remain in place and the coloured seeds were then considered to be perfect Mimics of the formerly "escaping" prey. In this period of the experiment, the experimental group of birds showed a significant discrimination against the so-called Mimics, when compared to a control group which had always fed on the coloured seeds from a fixed platform. This experimental situation is certainly analagous to a hypothetical scenario where some hoverfly species advertise that they have an efficient escape response, while other, "mimetic" species falsely display a similar advertisement.

These flight related hypotheses assume that the protection, be it aposematic or mimetic, is conferred during the active flight period. It could be argued that the agility of most hoverflies is such that they can rely entirely on escape as a means of protection, and that the coloration, if it represents a protective strategy at all, confers protection during the pre- and post-active flight periods of the day. Though hoverflies have endothermic warming mechanisms which shorten this vulnerable period relative to other similar-sized flies, it is certainly likely that endothermic foragers are active for a considerable period of the day during which, hoverflies are unable to use flight as an escape response.

1.2.6 Thermoregulation.

Heal (1979, 1982) discusses the genetic basis of abdominal pattern variation in *Eristalis tenax* , a species widely considered to be a honey-bee mimic. Heal proposes that the abdominal pattern of the hoverflies may be related to their thermoregulatory requirements. The pattern of *E. tenax* , and many other species, includes a break in the pattern of yellow or orange tergite spots or stripes around the dorsal midline, creating a black band which overlies the dorsal blood vessel. Heal briefly speculated that the quality of a mimic might be compromised by the need to retain this region to maximize absorption of sunlight needed to heat the blood. There are, however, an appreciable number of species where the abdominal banding is continuous and it is improbable that the need to heat the dorsal blood vessel can account for the subtlety of some patterns. Morgan and Heinrich (1987) note that all syrphids have some mechanism for endothermic pre-flight warming and their data indicates that mimetic and non-mimetic syrphids do not differ greatly in their thermoregulation. They do, however, suggest that the acquisition and maintenance of a high thoracic temperature may be a prerequisite for the evolution of a mimetic strategy; a high thoracic temperature permits fast and immediate flight which may be part of the mimicry of a Model's flight pattern.

While thermoregulatory considerations could play a contributory role, it is unlikely that they constitute a prime force in the evolution of hoverfly patterns.

1.2.7. Summary.

It is quite evident from the hypotheses raised above that the paradoxes of apparent mimicry in the hoverflies could have a complex, multifactorial explanation, for few of them are in any way mutually exclusive and all have some credibility. Some, like the issue of sequestration of secondary plant products, constitute significant, detailed research in their own right and, given this, it already seems unlikely that this thesis can yield anything approaching a definitive resolution of the paradox. In these circumstances there is a very urgent need to redefine the specific aims of this project to focus attention on just one or a few aspects of the problem. The following section explains why mimicry, rather than any of the alternative hypotheses above, was retained as the primary vehicle for the research described in this thesis.

1.3 The True Role of Mimicry.

Whatever the complete explanation of the paradoxes of hoverfly coloration, it is almost inconceivable that mimicry theory will not have at least some role, for there are syrphids which are, beyond doubt, mimics of hymenoptera. Waldbauer (1988) contains a plate showing Syrphids which were defined as "high-fidelity" mimics of wasps and bees and the extent of the similarity is, in these cases, astonishing (see Appendix Five, Plate 1, species c, *Temnostoma vespiforme*). Many of these species have particular morphological features which increase their similarity to hymenoptera and which are difficult to account for if they are not mimetic adaptations. Most, for instance, have a band of dark pigment in the wing which closely resembles the darkened multiple wing thickness created when a resting wasp folds its wings longitudinally. Waldbauer's unpublished data indicates that this pigmented band occurs only in species which have a wasp-like colour pattern on the abdomen. Additionally, some species have adaptations which resemble the distinctive long, dark antenna that most wasp species have. In some species (e.g. *Temnostoma*) this adaptation involves waving the black front legs in front of the head, giving the appearance of long black antennae. In others (e.g. *Chrysotoxum*) the usually short syrphid antennae have become greatly extended and darkened. Again these antennal adaptations occur only in those species that have a wasp-like pattern.

Syrphid species displaying such features really must be accepted as mimicking hymenoptera; such specialized adaptations could not credibly be explained except by invoking mimicry theory. If they were to be rejected as Mimics then so too must many other instances of mimicry, including such widely accepted examples as the mimicry complex surrounding the Monarch butterfly *Danaus plexippus* , for the similarity seems at least as great. The high-fidelity Mimics discussed above come from the apparent mimicry complexes in Waldbauer's North American study sites, but this does not undermine the argument that some British syrphids must also be true mimics. Much the same paradox exists at these American sites, with apparently relatively poor mimics such as *Syrphus* outnumbering the high fidelity mimics and some of the adaptations described do occur in Britain: *Chrysotoxum* with its complex wasp-like pattern and well developed, darkened antennae occurs in many British sites. In the British complexes, the high-fidelity Mimics appear to be more common among the bee Mimics: *Pocota personata* bears an astonishingly close resemblance to some bumblebees, while other species such as *Volucella bombylans* are relatively common and appear only slightly less accomplished as Mimics.

Some syrphid species have certainly adopted mimicry as a defensive strategy, and their appearance and abundance could probably be described by a sufficiently sophisticated and complete, but conventional, model of mimicry. What of those more abundant, low-fidelity mimics? Is some extension of conventional mimicry theory capable of explaining the abundance and appearance of these species ? If not, at what point does mimicry theory cease to be a sufficiently adequate explanation, and when is it necessary to exploit some alternative or supplementary hypothesis, perhaps such as those above, in order to provide a convincing explanation of the apparent paradoxes ?

The intention here is to focus the attention of the study in order to bring its remit into manageable proportions; it is the purpose of the remainder of this thesis to try to determine *how far* mimicry theory is able to explain the paradoxes of apparent mimicry in the hoverflies.

Chapter Two.

What Determines the Success of a Mimic ?

2.1 Introduction.

Given the range of hypotheses forwarded in the previous chapter, it is obvious that some very substantial and diverse sections of the biological literature could be pertinent to the specific problems of apparent mimicry in the hoverflies. The possible sequestration of plant products immediately makes the literature on insect-plant chemistry significant, while the possibility of large scale ecological disturbance similarly makes the literature on community structure and stability relevant. As detailed questions about the properties and performance of predator perceptual and cognitive systems arise, parts of the psychological literature on human perception provide an insight into the constraints under which predators may operate. The reaction to this volume and diversity of information is evidenced in the previous chapter by an effort to concentrate on the extent to which mimicry theory alone provides an explanation for hoverfly coloration; this selectivity extends into the current chapter.

The intrinsic appeal and fundamental simplicity of mimicry has ensured a steady addition to the literature, periodically punctuated by enthusiastic exchanges on specific issues; the recent calls by Ritland *et al* (1991) for the re-assessment of the classic example of Batesian mimicry, the Monarch-Viceroy-Queen system, are typical of the latter. Despite this almost constant attention, the current literature on mimicry is testament to only the most modest progress towards a detailed understanding of natural mimetic systems. New examples of the phenomenon are documented routinely (eg Oliveira 1988), revised definitions and classifications are produced, new models are presented and there are the inevitable experiments with artificial mimicry complexes and wild or captive predators. Yet, there is still a lack of convincing evidence that natural purported mimics do enjoy a reduced risk of predation in the wild (Malcolm 1990), and there is certainly no comprehensive theoretical description of mimicry capable of predicting the observable characteristics of a natural mimetic system. That the theoretical speculation about the principles and dynamics of mimetic systems has so outpaced the empirical evidence should not be a surprise. It is impossible to witness a significant number of natural encounters between predators and mimics (Boyden 1976), and, as the following chapter will explore, there are limits to the validity of reproducing such encounters in controlled conditions. Even if such encounters were routinely observable, it is an extremely difficult exercise to determine how a predator arrives at a given decision about the identity of an ambiguous prey item.

2.2 Definitions and Remit.

One intention in writing this thesis is to contribute to the erosion of this fundamental intractability. Such efforts will certainly raise issues which require incorporation into our theoretical understanding of mimicry, but it is unlikely that anything presented here will prompt a significant revision of our definition or classification of mimetic phenomena. The following literature review will therefore not consider some substantial components of the literature on mimicry.

Specifically, this review, and the rest of the thesis, will assume only the simplest definitions of mimicry and will refer only to the visual modality, though it is acknowledged that Batesian mimicry in other modalities can occur (see Czaplicki *et al* 1975 for an example of possible olfactory mimicry, and Rettenmeyer 1970 for examples of audio-mimicry). "Batesian mimicry" will define a situation where a palatable species, the Mimic, enjoys a lower risk of predation as a consequence of its resemblance to a noxious, unpalatable or unprofitable species, the Model. In contrast, "Mullerian mimicry" will describe a situation where a number of species, with varying degrees of unpalatability, each sustain a lower risk of predation through a shared similarity in appearance. These simple definitions avoid participation in the ample and involved discussions about the definition and classification of mimicry; such debates are of arguable value in the aforementioned absence of a strong empirical literature (Berry 1981), but Malcolm (1990) provides a concise starting point for those interested in the semantics of mimicry. There are two prominent issues. One is concerned with whether there is any real distinction between Batesian mimicry and crypsis, there clearly being a sense in which crypsis is the mimicry of a natural background or inanimate object. Cloudsley-Thompson (1981), Rothschild (1981), Robinson (1981), Edmunds (1981), Vane-Wright (1976, 1980, 1981) and Endler (1981), all provide an insight into the subtle and complex debate which surrounds this apparently simple idea.

The other major component of the theoretical literature addresses the differences and similarities between the two dominant forms of mimicry, Batesian and Mullerian (see Sheppard and Turner 1977, Benson 1977, Huheey 1980, Owen and Owen 1984, Turner 1984). Again, the debate surrounding this issue is more complex than is first apparent, and while it is of little direct interest here, it is briefly discussed in a subsequent chapter on the Monarch-Viceroy mimicry complex, and in the separate review of mathematical models of mimicry presented in Chapter Seven.

A truly comprehensive understanding of mimicry must include an appreciation of the literature on the separate, but obviously related, issue of the evolution and maintenance of warning coloration. Again, this topic will not be addressed here, except to acknowledge that the theoretical and empirical literature on the subject gives an impression of greater cohesion than the equivalent literature on mimicry (see Guilford 1988, Guilford 1981, Malcolm 1986 and Evans 1987, for example).

What the following review will address is the observational, experimental and anecdotal literature on the factors which affect the success of a strategy of visual Batesian mimicry. As already mentioned, some of the intrinsic appeal of mimicry must stem from the ease with which apparently significant factors can be identified, even from the simplest of definitions. As a result, there is a relatively stable concensus on what determines mimetic success (see Table 1, Huheey 1988), and new work seems only to lengthen and elaborate, rather than revise, the accumulated list. Consequently, the following review exhibits substantial overlap with similar, still useful, but now slightly dated, reviews by Rettenmeyer (1970) and Wickler (1968); to minimize repetition, the review will, where possible, concentrate on work published in the last two decades.

2.3 The Determinants of Batesian Mimetic Success.

2.3.1. Perfection of Resemblance.

The degree of perfection in the resemblance between Model and Mimic would appear to be an obvious determinant of mimetic success, but only rarely has this issue received explicit consideration. Mathematical models almost exclusively assume perfect mimicry (see Chapter Seven), and the expected differences in the degree of Model-Mimic resemblance in Batesian and Mullerian systems (see Chapter Six) is the only context in which mimetic resemblance and success attracts repeated theoretical attention. The empirical treatment of mimetic resemblance appears to illustrate only two points.

O'Donald and Pilecki (1970) investigated frequency dependent effects on mimetic success using an artificial pastry bait complex exposed to wild sparrow predators. The "Models" in this complex were made distasteful by treatment with a 1% or 3% quinine solution and could take one of two colour forms, blue and green, by including food dye into the pastry mix. In one set of experiments, the two colour forms appeared at equal frequencies, comprising 50% of the total complex population, and were equally distasteful (1% quinine). The perfect blue and green palatable "Mimics" appeared in different frequencies, respectively making up 5% and 25% of the population, with the remaining 20% of the population made up of palatable yellow dyed alternative prey. The predation rates on the two Mimic types indicated a differential advantage in favour of the rarer mimics, with the blue mimic being taken relatively less often than their green counterparts. In a second experiment with 3% quinine treated Models, this advantage in favour of rare mimics disappeared. The issues of frequency dependent predator responses and Model noxiousness are dealt with later, but O'Donald and Pilecki explored the evolutionary implications of this result and suggested one particular effect of imperfection in mimicry. They speculated that the loss of advantage to rare mimics when Models became increasingly distasteful, prevented the appearance of mimetic polymorphism in the Batesian Mimics of particularly noxious Models. It was proposed that imperfect mimicry (by implication imperfect resemblance) may allow predators to discriminate between Model and Mimic on some occasions and perhaps thus establish frequency dependent effects which could sustain mimetic polymorphism even in the presence of a noxious Model. The same authors (Pilecki and O'Donald 1971) specifically explored the interaction of imperfect mimicry and frequency dependent selection using a similar artificial complex. "Imperfect" Mimics were created by less intense dyeing of palatable Mimic baits, so that a "pale green" bait was regarded as a poor Mimic of a green Model, while a perfect Mimic was dyed identically to the Model.

Predation on the artificial complex by wild blue jays *Cyanocitta cristata* did reveal an interaction of mimetic quality and Mimic frequency. At low frequencies, "poor" Mimics suffered no higher risk of predation than their perfect counterparts; only as Mimic frequency increased did poor Mimics suffer proportionately higher predation than perfect Mimics. The most obvious implication is that poor Mimics are subject to a threshold on their frequency, above which, encounters with predators are sufficiently frequent that the latter begin to discriminate between them and the Model. This conclusion appears entirely plausible and is in obvious contrast to the apparent situation in the hoverflies, where it is the accomplished Mimics which appear to be subject to some form of limitation. However, the meaning of "poor mimicry" is evidently different in the context of the hoverfly system and Pilecki and O'Donald's artificial system. The predators of the artificial system are assessing prey quality on the basis of a one dimensional attribute, "colour brightness", whereas predators of a natural complex are almost certainly making more sophisticated judgements about pattern structure and prey behaviour, as well as colour.

Hetz and Slobodchikoff (1988) report predation rates on a real Batesian mimicry complex exposed to semi-natural encounters with a range of wild predators. *Eleodes obscura* , its Mimic *Stenomorpha marginata* (Coleoptera) and a palatable alternative (House crickets) were placed singly into a series of plastic pots arranged in a grid at a field site where these species occur naturally. These pots were accessible to a range of natural predators (bats, skunks and ringtails) during each night. The palatable crickets were eaten more often, and the Models less often, than would be expected if prey were taken in proportion to their frequency in the grid. As expected, predators did exhibit some avoidance of the noxious Model, but predation rates on Mimics indicated that they were taken neither more nor less often than expected. This implies that *on average* , the assemblage of predators was capable of discriminating Mimic and Model, which limits the sense in which *Stenomorpha marginata* can be regarded as a successful Batesian Mimic. That Mimics were neither over- nor under-sampled was regarded, however, as evidence that in the presence of palatable alternatives, some individual predators or predator species, failed to identify and actively exploit the Mimic population. There are alternative explanations for this pattern of predation and while far from clear, these observations do illustrate one obvious generality about imperfection in mimicry. The cost-benefit relationships may be such that mimicry may evolve and be maintained in a species even if predators mis-identify Mimics as Models in only a proportion of encounters: "imperfect" Mimics, in the sense of imperfect resemblance, should not necessarily be regarded as unsuccessful Mimics.

2.3.2 Mimic Frequency.

The experiments by O'Donald and Pilecki reported above indicate that predator responses to Mimics are in part determined by absolute frequency in the environment. The issue of frequency dependent prey selection has significance not only for mimicry theory (Greenwood 1984, Greenwood *et al* 1984); there is evidence from a wide variety of systems that predators are sensitive to the frequency of prey types (Greenwood

1986) and evidence that frequency dependent selection is the product of an optimal foraging strategy (Hubbard *et al* 1982). If predators do exhibit frequency dependent responses, Greenwood (1986) proposes one specific implication for mimetic success. The predictions of a model of frequency dependent responses to prey (Staddon and Gendron 1983) implies that in some circumstances, the optimal predator should "switch" between available prey types, that is, to accept all examples of one prey type and disregard all of those of another. Greenwood's extension of Staddon and Gendron's model predicts some circumstances in which predators should switch to the more common of two Batesian Mimics and wholly disregard the rarer form, while in others, no switching occurs. As in the experiments by Pilecki and O'Donald, the tendency to switch prey types is influenced by the discriminability of Model and Mimic (ie the perfection of mimicry), but the pattern of switching is more generally determined by the relative costs and benefits of Models and Mimics. Greenwood has clearly demonstrated the potential significance of frequency dependence in determining mimetic success, but the incorporation of such effects into accounts of mimicry has not yet occurred.

2.3.3 Model:Mimic Ratio.

In addition to the relative costs and benefits of Model and Mimic, a key determinant of predator behaviour in Greenwood's model was the Model:Mimic ratio. Traditionally, mimicry was seen as being sustainable only if Models outnumbered Mimics, the argument being that if predators encountered Mimics more often than Models, they would never learn to exclude Model-like prey from the diet, thus precluding any mimetic protection. Brower (1960) provided the first demonstration that Mimics could outnumber Models and still enjoy a significant degree of protection. In these experiments, captive starlings (*Sturnus vulgaris*) were exposed to an artificial Batesian complex consisting of painted, and in the case of "Models", quinine treated, mealworms (*Tenebrio* larvae). Distasteful Model and palatable Mimic mealworms were presented in different proportions to simulate different Model:Mimic ratios. Contrary to popular expectation, the number of Mimics had relatively little effect on the establishment of learned avoidance of the Model pattern; predators associated the appearance and unpalatability of the Model equally well regardless of whether the ratio was biased marginally in favour of Mimics or heavily in favour of Models. Furthermore, significant levels of protection were subsequently enjoyed by Mimics, even if they outnumbered Models; a prey population of 10% Models, for instance, protected 17% of the remaining Mimics. Brower and Brower (1962) report that in a natural butterfly mimicry complex, the Model *Battus philenor* is heavily outnumbered by its Mimics in some part of its range; it was clearly no longer appropriate, however, to assume that the more numerous Mimics did not enjoy at least some degree of protection.

2.3.4 Model Noxiousness.

The most significant determinant of the maximum sustainable Mimic to Model ratio is likely to be the noxiousness of the Model. Traditionally, the Model is seen as a species which possesses a sting or contains or secretes a toxic, unpalatable or emetic substance, but relatively mild deterrents may be sufficient to support a mimetic complex. Gibson (1974) provides an experimental demonstration that an artificial prey item with a simulated efficient escape response effectively acts as a Model to similar prey which lack the same ability. Unprofitability, rather than unpalatability, may be a sufficient deterrent to predators, and mimetic effects may therefore be a more widespread feature of nature than is generally appreciated. Goodale and Sneddon (1977) confirm that in an artificial mimicry complex supported by a "conventionally" distasteful Model, increasing unpalatability enhanced the predator's tendency to generalize from their unpleasant experience and effectively supported a higher Mimic:Model ratio. Similarly, Alcock (1970 a,b) demonstrates that in another artificial complex, a higher degree of protection was afforded to Mimics when the Model was emetic than when it was merely distasteful (see also Duncan and Sheppard 1965). Particularly noxious Models represent a high risk to predators and thus discourage them from attacking what may be even vaguely similar Mimics. In this context, Leipelt's (1963) observation that a wasp sting rendered a captive shrike inactive for several hours, indicates that encounters with Models may have serious consequences for the well-being of predators, to the extent that predators may be discouraged entirely from sampling further Model-like prey. The indiscriminate exclusion of Models and Mimics from the diet is predicted as the optimum predator strategy in some mathematical models (see Chapter Seven), and where this is the case, the implication must be that very large Mimic populations will be sustained by relatively few Models.

2.3.5 Palatable Alternatives.

The majority of authors on mimicry acknowledge Holling's (1965) demonstration that mimetic success is heavily dependent upon the abundance and profitability of species which represent an alternative food source for foraging predators. Tests of mimetic effects using captive predators now routinely (Slobodchikoff 1987), but not exclusively (Bowers 1983), incorporate the presentation of alternative palatable prey. Although there is no specific, rigorous demonstration of the effects of palatable alternatives, such studies (eg Nonacs 1985) do incidentally confirm the expectations about the role of palatable alternatives. Generally for instance, decreasing the profitability or density of palatable alternatives increases the obligation on predators to attempt to incorporate the Model-Mimic complex into its diet. The extent of this predatory pressure therefore determines the viability and utility of a mimetic strategy (see Getty 1985; Luedeman *et al* 1981), and in the long-term may influence the development of the prey characteristics which are required to achieve it.

2.3.6 Spatial Distribution.

Variation in the spatial distribution of Models, Mimics and palatable alternatives will determine the immediate effective ratios of these prey types which are encountered by a foraging predator. Nonacs (1985) examined the effect of spatial distribution in an artificial mimicry complex preyed upon by captive chipmunks, *Eutamias quadrimaculatus* . With a random prey distribution, a population of 30% Models was sufficient to deter significant sampling of the Mimic population. When prey were arranged into a clumped distribution, the predators' appeared sensitive to the patchiness in the distribution of their food source and were able to increase their exploitation of Mimics; higher Model frequencies were required to re-inhibit the sampling of the complex. This observation is in agreement with the predictions of several mathematical models reported in Chapter Seven which are capable of accounting for distributional effects. Clumping is usually regarded as advantageous for Models because it efficiently discourages predators from repeated sampling. In this respect, Nonacs' results only partially fulfiled expectations; Models were actually sampled more in clumped distributions than when randomly dispersed, though the disadvantage of clumping was certainly greater for Mimics than for Models. Nonacs suggested that this slight contradiction with theory may be an artifact of the experimental method, wherein Model patches are less obvious and less widely spaced than is likely to be the case in nature. Despite this possible qualification, Nonacs provides a convincing demonstration that prey spatial distribution does have the potential to affect mimetic success.

2.3.7 Large Scale Spatial Relationships.

Larger scale spatial relationships are also likely to be significant for mimetic success. The simplest interpretation of mimicry theory implies that Mimics must be geographically co-incident with their Model to be afforded any protection. Reports that Mimics occur outside the range of their supposed Models are not, however, uncommon. Clarke *et al* (1989) record that the mimetic morphs of *Hypolimnas misippus* persist in locations where the Model, *Danaus chrysippus* is absent. Brower and Brower (1962) similarly report that *Papilio troilus* continues to survive in mimetic form beyond the range of its Model, *Battus philenor* . Some of these apparent exceptions to the mimetic rules are doubtless explicable in terms of secondary defensive mechanisms that ameliorate the predation load expected when the Model is absent; *H. misippus* may, for example, be synthesizing or sequestering compounds distasteful to predators (Clarke *et al* 1989). A more general explanation for such cases is that mimetic protection is sustained because migratory or highly mobile predators learn to avoid the Model pattern elsewhere in their feeding range.

2.3.8 Temporal Synchrony.

By implication, mimetic success will further be determined by temporal as well as spatial relationships between Model, Mimic and predator. Bobisud (1978) presented a simple mathematical model which predicted that Mimics would be selected to appear after their Model, by which time naive predators will already have established their avoidance of Model-like patterns. Huheey (1980) stressed that Model phenologies are likely to be subject to similar selection for temporal separation from Mimics, since the presence of the latter effectively disrupts predator learning and therefore increases sampling predation on Models. Precisely this pattern of temporal separation is evident in salamander populations (Brodie

1981). The noxious *Plethodon cinereus* is most common in the leaf litter during March and April of each season, which co-incides with the arrival of migratory ground foraging birds at the studied site. The mimetic *Desmognathus ochrophaeus* is more common than the Model later in the season, by which time predators have presumably learned to avoid Model-like patterns.

The most comprehensive investigation of temporal synchrony concerns part of the mimetic complex which is the subject of this thesis, the Syrphid Mimics of Hymenoptera, and is reviewed by Waldbauer (1988). Waldbauer and Sheldon (1971) systematically surveyed the abundance of the most accomplished wasp- and bee-mimicking hoverflies (eg the wasp mimics *Temnostoma* spp. and *Spilomyia* spp., see plate in Waldbauer and Sheldon 1971) and confirmed that they were largely absent during mid-summer when there was a high risk of sampling predation by naive fledglings. The Mimics of one sub-complex exhibited a temporal relationship to Model abundance and maximum predator activity similar to that reported for salamanders, reaching peak abundance at a point where the Model population was in decline and when 90% of bird broods had fledged. However, the syrphid Mimics of a different Model, which tended to occur throughout the season, emerged *prior* to the fledgling period. Similar patterns of emergence were recorded in different sites, with different assemblages of species (Waldbauer *et al* 1977, Waldbauer and LaBerge 1985). Waldbauer *et al* have suggested that emergence prior to the fledging period is consistent with the prediction that Mimics should be selected to appear at a point in the season which maximizes their protection, if one assumes that predators are capable of retaining the noxious associations of the Model pattern over the winter period. There are documented cases of individual birds avoiding noxious insects several months after naive exposure, and if such capacites are widespread, the most favourable period for Mimic emergence may indeed be prior to the appearance of naive predators.

2.3.9 Predator Learning, Memory and Innate Abilities.

The sensitivity of Mimic phenologies to the appearance of predators which have no prior experience of Model or Mimic, emphasizes that predators' ability to learn and retain the noxious associations of the Model are a key determinant of mimetic success. All of the early experimental demonstrations of mimetic protection (Brower 1958, 1960, Brower and Brower 1962,1965, Brower, Brower and Westacott 1960) do illustrate that predators do require sometimes repeated exposure to the Model in order to establish a pattern of learned avoidance. There is often considerable inter-individual variation in the number of trials required to establish an aversion to the Model, and in the individual behavioural reactions to Model presentations. Nevertheless there are indications that such learning does occur in the wild; Evans and Waldbauer (1982) reported that naive captive bred birds were more likely to attack the syrphid Mimic of a bumblebee, than were adult wild-caught birds. There is anecdotal evidence that such avoidance can persist in some predators for several months without reinforcement. Mostler (1935) reported flycatchers (*Muscicapa* spp) rejecting common wasps more than 14 months after their last encounter. Rothschild (1964, cited by Waldbauer and Sheldon 1971) records that an individual crow (*Corvus corvus*) rejected aposematic prey encountered a year previously. The ease with which predators acquire and retain an aversion to the Model will determine the rate at which the Model-Mimic complex is re-sampled, and, therefore, the degree of protection obtained by the Mimic, but the latter will also depend on the extent to which predators generalize from their experience of the Model. Morrell and Turner (1970) provided the first indication that predators do generalize from noxious experiences, and Mason and Reidinger (1983) present evidence that the pattern of generalization is adaptively significant inasmuch as the tendency to do so is greater when the stimulus is biologically relevant than when it is abstract.

In addition to confirming that predator learning and generalization is significant, the literature also contains clear indications that some predators have an innate predisposition to avoid particular prey types. Davies and Green (1976) observed that hand-reared reed warblers (*Acrocephalus scirpaceus*) not previously exposed to common wasps rejected them on sight. Such abilities might be expected in species which routinely encounter Models and Mimics, species which can to some extent be regarded as specialist predators. However, innate predispositions to avoid prey of a particular appearance may be more widespread than expected. Smith (1975, 1977) established that two species of birds, motmots and great kiskadees, avoided artificial models of highly venomous coral snakes without experience of any noxious associations. Similarly, Schuler and Hesse (1985) exposed warningly coloured artificial prey to naive domestic chicks, descended from a ground foraging species (*Gallus gallus*) which have had a reasonable risk of encounter with aposematic and mimetic prey, but which could not be regarded as a specialist insectivore. The chicks directed first pecks at both warningly coloured and non-warningly coloured prey items with equal probability, but ate the former significantly less often. Schuler and Hesse suggested that the first peck at apparently aposematic prey activated a genetically fixed pre-disposition to avoid further attack, though they noted that this avoidance diminished unless reinforced by an unpleasant experience. The occurrence of these innate predator abilities will enhance the effectiveness of mimicry as Mimic populations are relieved of some of the predation load imposed by naive predators learning to avoid Models. Innate avoidance of aposematic species is clearly not universal, and we may legitimately expect it to be more commonplace among specialist predators which have an atypically high probability of encountering Models and Mimics. Although numerically in a minority, such species may represent a very significant component of the predatory pressure which determines the nett benefit of a mimetic strategy. Future models of mimicry may have to take into account that a significant proportion of Mimic encounters with predators, may involve specialists which impose lower than expected sampling predation.

2.3.10 Specialist Prey Handling.

Frequent, repeated exposure to Models may prompt a quite different adaptive response among some elements of the predator community. There is ample evidence that some specialist predators are able to circumvent the defensive mechanisms of species which are likely to act as Models to a mimetic complex, and thereby routinely include them in the normal diet (Birkhead 1974). Gwinner (1986) reports wild White-eyed slaty flycatchers (*Melaenornis chocolatina*) repeatedly catching and de-stinging bees (*Apis*), while Fry (1969) reports similar behaviour in bee-eaters (*Merops* spp), between 60% and 90% of the diet of which may be hymenoptera. Similarly Plate IX in Davies (1977) clearly shows that common wasps (*Vespula vulgaris*) caught by Spotted-flycatchers (*Muscicapa striata*) had had their stings removed, while, incidentally, three species of apparently poorly mimetic hoverflies were not subjected to the same treatment.

Clearly, where predators do possess such capabilities, Mimics cannot be regarded as successful, even if those predators fail to discriminate Model and Mimics and, for instance, falsely treat Mimics as Models (Evans 1984).

2.3.11 Between Species Variation.

The presence of a minority of predators with the ability to handle Models obviously does not render mimetic strategies ineffective. In most cases, Mimics will encounter a variety of predators and it is the nett outcome of all these predatory responses that will determine the viability and effectiveness of mimicry. Slobodchikoff (1987) exposed members of a natural mimetic complex, the noxious beetle *Eleodes longicollis* and its mimic *Moneilema aggressum* , in semi-natural conditions, to a variety of biologically pertinent predators, including coyotes, mice and kangaroo rats. In this particular instance, it proved impossible to witness the precise behaviour of each predator species, or determine the proportion of total predation for which each was responsible (Hetz and Slobodchikoff 1988 are able to be more specific), but Slobodchikoff asserted that the measured decline in predation on Models was the outcome of aversive conditioning among the complement of predator species. Alcock (1970 a,b) reports a series of specific observations of the behaviour of two species of captive birds, Black capped chickadees and White crowned sparrows, which lends support to the argument that predatory behaviour will not be uniform across all species significant to the success of a mimic. Alcock proposed that the particular differences in observed behaviour were related to the degree of predatory specificity of each species; this is entirely plausible and is certainly consistent with the evolution of prey handling techniques described above. All mathematical models currently assume "the predator" to represent a uniform entity, but as such models increase in realism, they will certainly require modification to explore the effect of predator diversity on mimetic success.

2.3.12 Individual Variation.

Whatever adaptations and abilities are reported in a given predator species, there are clear indications that substantial inter-individual variation in responses to Models and Mimics is to be expected. Such variation is a striking feature of early and contemporary experimental demonstrations of mimetic protection (see Brower and Brower 1962, Brower, Brower and Westacott 1960). Often this variation appears to be regarded as an unfortunate confounding factor, though it is likely that such variation occurs in the wild and should therefore be treated as a further factor which determines mimetic success. Codella and Lederhouse (1989) report very significant variation in the reactions of Blue jays (*Cyanocitta cristata*), a species frequently used in experiments on mimicry, to the presentation of *Battus philenor* (Model) and *Papilio polyxenes* (Mimic). Some experimental birds rejected almost all presented Mimics, but one individual consistently rejected Models and continued to take Mimics. Codella and Lederhouse specifically acknowledge that such variation is significant; as such it should be incorporated into future theoretical descriptions of mimicry.

2.3.13 Neophobia.

Inter-individual variation has made it difficult to summarize the typical response of a given predator species to a mimicry complex, a problem only exacerbated by the practical difficulty of obtaining large numbers of captive predators. The problem is further compounded by so-called "neophobic" predator reactions to the presentation of novel prey. Coppinger (1970) recorded intense fear reactions among a group of naive captive birds; astonishingly, 16 of the 30 subjects required training to accept entirely palatable but novel mealworms (*Tenebrio* larvae). Seventeen birds completely refused to eat novel palatable butterflies and displayed reactions interpreted as indicating extreme fear. Similar, but less intense, reactions were evident in the remaining 13 birds. When these birds were divided into two groups, one of which was presented with predominantly brown and white butterflies and the other black and red butterflies, the former group gradually habituated to the presentation of butterflies, while fear reactions persisted in the latter. The continued alarm reactions in this second group is reminiscent of the apparently adaptive innate pre-dispostions to avoid particular prey types, but it would be wrong to assume that more general neophobic reactions are not of some adaptive significance. There may be some benefit to survival in young predators avoiding some types of novel prey and if such reactions occur naturally in some predators, any tendancy to avoid Models and Mimics will certainly be enhanced.

2.3.14. Constraints on Predators.

It would be wrong, however, to assume that every aspect of predatory behaviour is perfectly adapted; there are likely to be imperfections in a predator's perceptual system, and inadequacies in the quality of information that it can gather about the environment (Orians 1981). To offset any imperfections and constraints, predators may undergo learning processes more complex than simply acquiring an aversion to Models or developing the discrimination of Model and Mimic. The formation of search images for cryptic prey (Pietrewicz and Kamil 1981, 1979) is one example from a different context of such processes, but analogous processes in foragers encountering mimetic systems may provide a mechanism for the acquisition of, for example, information about spatial distribution and Model:Mimic ratios which are demonstrably important to the success of mimics.

2.3.15 Predators as Psychological Systems.

For the most part, predators are currently regarded as having very simple perceptual and cognitive systems, capable of learning and retaining the association between a Model's appearance and its unpalatability, and exhibiting a tendency to generalize subsequent reactions to prey with a similar appearance. Such attributes are certainly prerequisites for the evolution of mimicry, but such a simple description of predators fails to acknowledge the probable complexity and sophistication of their information processing systems. Shepard (1984) and Shepard and Hurwitz (1984) argue that higher-order organization of incoming sensory information is likely to be relatively invariant between species, at least among "higher" animals. It is entirely possible that the perceptual and cognitive systems of the predators which drive the evolution of mimetic systems, will share some of the attributes of human perception and cognition. The psychological literature may therefore provide some insights into the constraints under which predators may operate and this, in turn, may indicate how the phenotypes of Mimics might be adapted to maximize their mimetic success. As an example, assume that predators effectively fix a mental representation of the Model pattern when learning its noxious associations, and that upon new encounters with Model-like patterns, they are required to mentally rotate the pattern represented by the incoming information in order to determine its correspondence with the internal representation of the Model pattern.

Shepard and Metzler (1971) reported that the reaction times of human subjects required to perform mental rotation and pattern matching exercises, indicated that there was a maximum rate of rotation of 60 degrees / sec. Cooper and Podgorny (1976) report upper limits on the rate of mental rotation (350-850 degrees/sec) and, surprisingly, conclude that pattern complexity had no effect on the rate or success of rotation. If the natural predators of mimetic complexes operate under similar constraints , any attempt by the predator to discriminate between Model and Mimic will be affected by the particular circumstances of the encounter and the degree of mental rotation that is required. Mimics may then, for example, develop efficient escape responses which exploit this limitation in the predator's cognitive system and perhaps gain significant protection with a substantially imperfect resemblance to the Model.

The possible utility of the psychological literature which this hypothetical example demonstrates is only rarely acknowledged. Ikin and Turner (1972) attempted to interpret the performance of a captive avian predator encountering a series of pastry bait Models and Mimics in terms of Gestalt psychology. This assumes that pattern discrimination, for instance, relies not on the identification and comparison of a particular subset of pattern features, but on a global assessment of the similarity in overall form between the patterns. Ikin and Turner predicted that if predators did operate a Gestalt approach, Mimics would be more successful if they reproduced the overall form of the Model rather than a set of its specific features. They presented predators with distasteful Models, identical, palatable perfect Mimics, and "imperfect" Mimics with a colour reversed copy of the Model pattern. In the presence of a Gestalt predator, they argued, the perfect and imperfect Mimics should fare equally well. In fact, the imperfect Mimics did suffer higher rates of predation, suggesting that the predator was exploiting a specific diagnostic cue to prey identity rather than overall appearance. There must be some question as to the basis of Ikin and Turner's prediction: it is not obvious that a colour reversed Mimic pattern does have the same form as the Model in the sense which is usually implied by Gestalt psychology. Nevertheless, Terhune (1977) demonstrated that while some predators do indeed exploit specific Mimic attributes, others may be operating a broader assessment of similarity. In Terhune's experiments, captive predators were presented with artificial Models and a set of Mimics which differed from the Model with respect to size, pattern and colour. Three of the six experimental subjects relied solely on colour to discriminate Model and Mimic, while one assessed size, pattern and colour simultaneously, and in a sense did therefore fulfil the definition of a Gestalt predator. This single result does indicate that in some cases, mimetic success will be contingent on the particular properties of the predator's cognitive and perceptual systems, and demonstrates that future formulations of mimicry theory may need to regard predators as sophisticated signal receivers.

2.3.16 Field Tests of Mimicry.

It should be more than apparent that the vast majority of empirical evidence about the factors which determine mimetic success are derived from experiments which rely either on artificial mimicry complexes, captive predators, or both. Similarly, the conventional test of a species' mimetic status is to present a small number of individuals to a captive model predator (eg Platt *et al* 1971). How well are these experimental observations corroborated by evidence from the field? Field tests of mimicry theory are rare, but represent the most ingenious component of the mimicry literature. Such tests do not always confirm that mimetic protection is effective; Waldbauer and Sternburg (1986) report that the re-capture rates of diurnal moths (*Collosamia promethea*) painted to resemble the Monarch butterfly, *Danaus plexippus* indicated no advantage to this artificial mimicry. In this particular instance, the explanation of this paradox may actually be consistent with mimicry theory, if the authors prove correct in their prediction that the larval food plant (*Asclepias* spp.) of the Monarch at the tested field site, is not sufficiently toxic to make the adult butterfly unpalatable to predators. The same authors did confirm a mimetic advantage elsewhere (Sternburg, Waldbauer and Jeffords 1977, see also Jeffords, Waldbauer and Sternburg 1980) using the same experimental methods, and others have demonstrated mimetic protection in other butterfly systems using similar techniques (Gordon 1987). Despite the ingenuity of this approach, such tests have as yet confirmed only the most basic tenet of mimicry theory: that individuals which resemble a noxious or unpalatable species can enjoy a measurable degree of protection from predators as a result. It seems unlikely, however, that such appoaches will ever be able to explore subtle interactions of the factors which laboratory experiments reveal to be significant in determining mimetic success.

2.4 Summary.

The structure and content of the preceding review is in many ways typical of conventional approaches to mimicry. It is not difficult to identify and illustrate, with cited experimental results, a wide range of factors that are likely determinants of mimetic success. As yet there is no comprehensive synthesis of the interaction and relative importance of these factors. As a form of summary, the review does, however, at least make it possible to specify the components of a model which would provide a reasonably comprehensive, general description of mimetic systems.

Such a model must be capable of separately simulating the phenotypic attributes of Models and Mimics so that we can assess the significance of the variation within each, and the degree of similarity between them, in determining the success of mimicry. Simulated Models and Mimics must be capable of occuring in varying absolute and relative abundance so that the effect of Model:Mimic ratio and possible frequency dependent effects can be explored. The costs and benefits of Models, Mimics and a range of palatable alternatives must be open to manipulation, and predator foraging behaviour must be modelled in such a way that simulated predators are capable of selecting a diet which maximizes their gain from the foraging effort. Both Models and Mimics must further be capable of varying their distribution in time and space so as to maximize the benefit of their respective defensive strategies under the prevailing predatory pressures. Predatory pressure must result from the individual activities of an assemblage of predator species, each of which may have particular attributes and tolerences, but each must be capable of exhibiting significant variation. To achieve such sophistication, the model of predator behaviour may be required to convincingly simulate the properties and limitations of the potentially sophisticated perceptual and cognitive processes of predator nervous systems.

None of the mathematical models of mimicry reviewed in Chapter Seven approach this degree of complexity, and obviously, the preceding summary represents an ideal rather than a minimum specification; mathematical models which achieve only part of this ideal are still capable of making a valuable contribution. Nevertheless, the review is still testament to that fact that after over a century of research into mimicry theory, we are still capable of only the most basic formal description of mimicry systems.

Chapter Three

Testing the Success of Apparent Mimics.

3.1 Introduction.

In the introductory chapter of this thesis, the common, conspicuously coloured hoverflies were referred to as "poor Mimics" and, though alternative explanations were acknowledged, the implication has been that these species are in some sense inadequate or compromised as visual Mimics of wasps and bees. This chapter describes the first practical work undertaken to determine whether the similarity between two of these common, apparently poor Mimics and their supposed Models, is sufficient to confuse a laboratory model predator and thus cause it to erroneously reject apparently palatable and profitable hoverflies.

There is clear evidence that hoverflies do form a regular and substantial part of the diet of some avian predators. Henry (1977) reports that syrphids constituted between 4.5% and 13.5% of the diet of young Reed Warblers (*Acrocephalus scirpaceus*). Kozena (1979) similarly determined that syrphids were present in 55% of the faecal samples of young swallows (*Hirundo rustica*), most commonly *Eristalis tenax* , widely considered to be a honey bee mimic, *Episyrphus balteatus* , apparently a very poor mimic, and various wasp-like *Syrphus* species. Such figures might imply that, for these predators at least, the common hoverflies are not successful Mimics and this is confirmed by some direct observations. Chaplin (1937) observed that a tame Bee-Eater (*Merops apiaster*) instantly swallowed "bee-like hoverflies" which were apparently easily distinguished from their bee Models. Davies and Green (1976) noted that a clutch of young Reed Warblers (*Acrocephalus scirpaceus*) accepted apparently mimetic syrphids without hesitation, while the presentation of common wasps (*Vespula vulgaris*) resulted in bill-wiping and bill-snapping conflict behaviours.

The literature does, however, yield some anecdotal evidence of successful mimicry in the hoverflies. Pocock (1911) reported Poulton's informal experiments on the palatability of British insects to a range of exotic captive predators. A pair of Brazilian Hangnests (*Icterus jamacaii*) tried and then rejected the bumblebee *Bombus hortorum* and subsequently refused to take *Volucella bombylans* , its supposed syrhpid Mimic, though another apparent Mimic, *Cheilosa illustrata* did prove acceptable. A North American catbird rejected all three of these species, while a Sulphury tyrant again took *C. illustrata* but rejected the *Bombus* and *Volucella* species; a Shama (*Kittacincla malabarica*) showed similar reactions.

These supposed Mimics have, however, been the subject of more rigorous and systematic observations. Brower and Brower (1962) tested the relative acceptability of honeybees (*Apis mellifera*) and their hoverfly Mimics *Eristalis vinetorum* to common toads (*Bufo terrestris*). The investigation compared the reaction of 22 toads in a test group with the 22 in the control group, responses being dichotomised as "eaten" or "not eaten". Most control toads ate honeybees from which the sting had been artificially removed, indicating that the species is palatable apart from the presence of the sting, and most *E. vinetorum*. Experimental animals were exposed to intact honeybees and many learned to reject them after initial encounters. The frequency of "eaten" versus "not eaten" events indicated that animals in the experimental group were statistically less likely to accept an example of the Mimic species than those in the control group; Brower and Brower concluded that *E. vinetorum* was a successful Mimic of honey bees.

Evans and Waldbauer (1982) detail reactions of captive birds to the bee *Bombus pennsylvannicus* and its syrphid mimic, *Mallota bautias*. These experiments investigated the reactions of wild caught adult and hand-reared young birds of two species, Red Winged Blackbirds (*Agelaius phoeniceus*) and Common Grackles (*Quiscalus quiscula*). All five adult Blackbirds and all but one of the six adult Grackles refused to eat *B. pennsylvanicus*. Some young birds of both species rejected *B. pennsylvanicus* even though they had no prior experience of this species. All but one adult Blackbird and one adult Grackle also refused the apparent mimic *M. bautias* , while the naive young of both species frequently accepted three consecutive presentations of this syrphid. Evans (1984) investigated the reactions of adults of five further species, Blue Jays, Brown Thrashers, American Robins, Song Sparrows and Northern Catbirds to the same Model-Mimic pair. Most subject birds refused to eat either the Model or the supposed Mimic and it was concluded that the Mimics were successful. The behaviour of some birds represented specialized prey handling techniques which, when applied to the *B. pennsylvannicus* rendered it edible by destroying the sting or diluting its venom. These techniques were often also applied to the supposed Mimic, so that, though the birds appeared unable to discriminate Model from Mimic, the Mimic gained no protection as a consequence.

The following sections describe how tests similar to those described above were undertaken to test the effectiveness of apparent Mimics from British syrphid communities.

3.2 Method.

3.2.1 Subjects.

The Pekin Robin (*Leothrix lutea lutea*) was adopted as the laboratory model predator. It is a well known cage and aviary bird from South East Asia which is easy to procure and maintain and which requires little encouragement to feed on live insect prey (Yealland, 1958). Williams (1988) demonstrated that this species does use available visual cues to discriminate between Models and Mimics in an artificial complex. It is something of a generalist predator, thriving on a mixture of fruit and varied insect prey, rather than a specialized insect predator and for this reason was thought to be a good general model for the type of predator which might be active in British sites.

Four adult *L. lutea* were obtained, and though detailed histories of these birds were not available, an assurance was given that they were captive bred in aviary conditions. It was therefore assumed that they had no previous experience of either hymenoptera or syrphids. Birds were referred to by their individual plastic ring colour. The birds fed freely on *Sluis Softbill* mix except for short periods prior to, and during, experiments. Fresh water was always available.

3.2.2 Prey Delivery

The birds were normally housed in a well ventilated, naturally lit room but were released into an adjoining artificially lit room immediately prior to each experiment. The experimental room contained a simple conveyor system consisting of a 3 metre length of 2.5 cm square metal tube, mounted horizontally 1 metre from the floor, and containing a 1cm deep polystyrene strip. Fixed onto the polystyrene belt at regular intervals were small polystyrene blocks, which, when the strip was inserted into the tube, formed a series of small sealed compartments into each of which a single prey item could be inserted. A 2.5 x 2.5 cm square hole was cut into the upper side of the tube so that, as the belt was pulled by hand through the tube, each of these compartments could be exposed in turn. The robins quickly learned to sit on the top of the tube near the hole or on a small platform mounted below it, and feed on the prey in the compartments as each became exposed. The end of the tube passed through the wall into an observational room where the observer could control the belt by hand and watch the birds at very close quarters through a piece of "one way" perspex mounted into the wall. The comparments on the belt were loaded with prey immediately prior to the experiment and a series of up to thirty live prey items could be delivered to the birds using this method. To encourage feeding from the tube, the birds were denied access to the standard food mix for up to two hours prior to each trial.

3.2.3 Prey Types.

On three separate trial days, the robins were presented with a random series of common wasps *Vespula* spp. and their apparent syrphid Mimics from the genus *Syrphus* . Neither the Model nor the Mimic were identified to species level, though it is likely that most of the syrphids were *Syrphus ribesii* ; the patterns of the three British *Syrphus* species, *S. ribesii* , *S. torvus* and *S. vitripennis* are very closely similar and are difficult to separate quickly by eye. Similarly the wasp species is likely to have been *Vespula vulgaris* , though again pattern variation is such that *Vespula* species appear very similar.

In a second series of tests over three further days, the birds were presented with a random series of honeybees (*Apis mellifera*) and their supposed Mimics *Eristalis tenax* . No distinction was made between the various races of *A. mellifera* and it is possible that some of the *Eristalis* were actually *E. pertinax* , a species very similar in appearance.

3.2.4 Observations.

The close proximity of the birds made it possible to make detailed observations of their behaviour. In addition, the 'handling time' for each presentation was recorded, being defined as the time from the prey is made available on the delivery system to the point at which the prey was either completely consumed or actively rejected. Within the span defined as 'handling time', no record was made of periods when the bird was not in physical contact with the prey; handling time is a measure of the length of the interaction, it reveals nothing of its temporal structure.

3.3 Results.

3.3.1 General Observations.

The four birds formed a well defined dominance hierarchy which affected feeding behaviour during the trials. The dominant bird achieved near exclusive access to the feeding hole until satiation, at which point the next most dominant bird began to deal with prey, until it in turn reached satiation and so on. There were, however, some instances where subordinate birds stole prey from a dominant; the handling times for these cases are excluded, and the following results refer only to single bird responses.

3.3.2 Wasps and Wasp-Mimics.

There were a total of 31 single-bird responses to *Syrphus* and 21 such responses to wasps. *Syrphus* individuals were taken from the conveyor cell immediately they were made available and swallowed head first. In marked contrast, wasps were subject to specialized prey handling. Wasps were struck in the thorax immediately they became visible and carried away to the corners of the experimental room. The tip of the abdomen was subjected to a series of sharp pecks, though no part of the abdominal contents appeared to be removed. After such treatment, the wasps were completely consumed, except for a few fragments of the abdominal cuticle. The handling times for Model and apparent Mimic did not overlap; the mean handling time for *Syrphus* was 3.16 s (s.e. +/- 0.4s, *n* =31) compared with 97.7 s for *Vespula* (s.e. +/- 8.9s, *n* =21)

These responses to *Syrphus* and *Vespula* described above were displayed by all four birds from their first encounter with the two prey types and did not alter during subsequent presentations; there was no indication of any learning.

3.3.3 Bees and Bee Mimics.

There were 21 single bird responses to the presentation of *A. mellifera* and 39 to *E. tenax*. Bees were struck in the thorax immediately they became visible in the conveyor cell, and thrown away from the exit hole, often in a single movement. If this initial strike failed to kill and remove the bees from the feeding area, the birds were slow to return to feeding from the tube, indicating that a living bee may have represented a significant threat. In all such instances, however, one of the birds eventually approached the injured bee and threw it from the feeding platform. All bees were recovered, dead or immobilized, from the feeding platform, or from the floor below it; none showed any signs of handling other than the thoracic wound from the initial strike.

The handling of the supposed Mimic was more involved. After the initial strike, the legs and wings were often removed and eaten separately. The majority of the handling involved drawing the tip of the abdomen into a curving projection, approximately 3-5mm long, by a series of rapid bill-squeezes. The carcass was then eaten whole, including the projection. Thirty-seven of the thirty-nine recorded responses involved this treatment.

Once more, all birds displayed these responses and did so from their first encounter with each prey type and again, the handling times for the Model-Mimic pair never overlapped, with a mean time for *A. mellifera* of 10.7 s (s.e. +/- 1.8s, *n* =21) against 62.3 s (s.e. +/- 4.1s, *n* =39) for *E.tenax* .

3.4 Discussion

3.4.1 The Mimetic Status of Hoverflies.

The purpose of these trials was to determine whether two common hoverflies, *Syrphus* and *Eristalis* , were successful Mimics of their respective supposed hymenopteran Models *V. vulgaris* and *A . mellifera* . The observations of prey behaviour and the handling time data clearly indicate that all four prey types elicited distinctly different responses. Within each supposed Model-Mimic pair, there were no cases of the dipteran receiving the treatment normally applied to the hymenopteran. These particular model predators did not appear to confuse the four prey types presented, and in this much, the conclusion must be that the two hoverfly species were not successful as Mimics.

The only predator response which could be construed as indicating that a Mimic was being confused with a hymenopteran is the apparent "de-stinging" of *Eristalis tenax*. There are two obvious points to make about this response. The first is simply that if *E. tenax* is being confused with a bee species, that species cannot be *Apis mellifera* , which is not subject to similar treatment and is exclusively rejected. The second point is that despite the apparent misidentification, *E. tenax* does not survive encounters with this predator and cannot be regarded as a successful Mimic.

3.4.2 Wider Implications for Mimicry Theory.

In addition to indicating that the two tested hoverflies are not successful Mimics, the experiment has incidentally reiterated the significance of some of the determinants of Batesian mimetic success outlined in the previous chapter.

The treatment of wasps provides a further example, for instance, of the way in which a sufficiently specialized predator can render an apparently noxious prey item edible through sting-removal or destruction. Secondly, the trials revealed no evidence of predator learning; the various reactions to prey, evident on the first encounter with each prey type and showed no subsequent qualitative change. Since the histories of these individual model predators cannot be established beyond doubt, it is impossible to determine whether these are innate responses, or ones which have survived, without reinforcement, during several months of captivity, from some prior learning period.

Despite their simplicity, these tests have even contributed some novel suggestions about the factors which determine mimetic success. The very obvious dominance hierarchy within the subject group significantly affected an individual bird's access to the available food source. In wild, group-feeding predators, such hierarchies may restrict subordinate birds' access to high quality food resources and perhaps place them under greater pressure to include an available mimicry complex into their diet. This may be a minor source of non-uniformity in the predatory pressure that such species impose on Mimic populations. In contrast to this variation in propensity to attack, the group exhibited a remarkable uniformity in the way prey types were handled. If these reponses are not innate, one source of such uniformity may be social learning; in group feeding species, individuals may observe and exploit the experience of congeners, and this has interesting implications for mimetic success. Finally, although it has been demonstrated that these predators do exploit available visual cues when attempting to discriminate Model and

Mimic in an artificial mimicry complex (Williams 1988), their reaction to the presentation of natural species may indicate that the optimum behaviour in some situations is to attack all available prey, including potential Models, and to assess prey identity and value subsequently. Such "attack all" strategies are the predicted optimum predator strategy in a number of mathematical models of mimicry (see Chapter Seven). Where predators do operate such a rule, Mimics cannot, of course, gain any protection through a resemblance to the Model.

3.4.3 Biological Relevance.

The curious and anomalous handling of *Eristalis tenax* , however, provides one specific example of the way in which these tests, although interesting and very fruitful, may in some ways be biologically inappropriate. If, for instance, the Pekin robins *are* confusing *E. tenax* with a bee species from their native habitat, it suggests that the birds are performing a task of prey categorization, not prey type discrimination. This constrains the extent to which the birds' behaviour can be interpreted as a response to the particular prey pairings presented during the tests, and must limit the sense in which we are able to draw any conclusion about the mimetic relationships between the supposed Model and Mimic.

3.4.4 Practical Constraints.

This qualification is in some senses rather trivial in that it could, subject to logistical constraints, be removed through more stringent selection of test predators (both individuals and species) and prey. General conclusions about the success of mimicry in the hoverflies could be extracted from a series of such tests, using different combinations of predator and syrphid species. There are however, practical constraints on the validity of such tests which apply regardless of the identity of the predator and prey species selected.

The willingness of these particular predators to attack hymenoptera may demonstrate how experimental procedure may distort the predator's natural behaviour. All birds were food stressed during these trials and the prey sequences did not include palatable alternative prey. Though wasps clearly were palatable after pre-treatment, the time required for this specialized handling may have rendered them unprofitable in the presence of palatable alternatives. Similarly, bees were often approached with apparent caution, and there may have been some premium in immobilizing, and removing them from the normal feeding area, so that feeding on the palatable *E. tenax* could continue without threat. In the field, there may be no such premium; the presence of bees will not normally hinder feeding on alternative palatable prey and may, therefore, be avoided. Clearly, these artificial test conditions may elicit predator responses which are not representative of wild behaviour. This does not necessarily preclude valid judgements about a predator's capacity to discriminate between the Model and Mimic; here, for example, it is obvious that even if Pekin Robins did exclude species like the common wasp from its natural diet on the basis of profitability, this would not afford any protection to *Syrphus* -like hoverflies. Nevertheless the above does illustrate that experimental prey presentation schedules can place predators under pressures which elicit responses not representative of natural predator behaviour or indicative of the success of Mimics.

3.4.5 Fundamental Constraints.

If laboratory tests of mimicry are to reflect the success of mimicry in the field, the experimental regime must capture the critical features of the natural situation. In principle, and with the appropriate data, it would be possible to remove the practical constraint described above by designing schedules of prey delivery which replicated the predator's natural rate of encounter with Models, Mimics and various palatable alternatives. Some elements of the field situation are more easily transposed into the laboratory environment; apart from possible effects of the quality of ambient light, there seems no reason to suppose, for instance, that the perceptual system of predators will operate fundamentally differently when they are brought into the laboratory. However, other critical features of mimetic systems would seem to defy reproduction.

Consider the particular circumstances of the experimental predator-prey encounters described above. Prey were always delivered to the same, well-lit location, with movement of the conveyor belt reliably cueing their arrival. The prey, having been enclosed in the dark and often cool conveyor cell, were often docile and were usually attacked immediately they became visible to the waiting predator. Little is known about natural encounters between hoverflies and their predators in the field, but it is improbable that wild predators enjoy the bias that the experimental procedure afforded this laboratory predator; wild predators must forage more actively and will encounter prey unpredictably.

It is entirely possible, then, that the natural and simulated encounters between predator and prey bear little resemblance. The value and validity of laboratory based conclusions about the success of mimicry in the hoverflies must remain questionable as predictors of their success in natural encounters.

3.4.6 The Predominance of Laboratory Based Tests of Mimicry.

It might be supposed that the criticisms about the disparity between real and simulated encounters are applicable only to the particular trials detailed here, given the unusual potential agility of the prey and the rather restrictive delivery system adopted. While certainly true to an extent, empirical studies of other examples of mimicry display similar limitations in simulating real encounters. Evans and Waldbauer (1982), for instance, presented a bee species *Bombus pennsylvanicus*, and its apparent hoverfly mimic *Mallota bautias* to captive birds. Their method of prey delivery involved presenting the caged predators with a dish containing a frozen and thawed example of one or other of these species, paired with an alternative palatable prey item. The presentation of prey to caged predators is the method routinely used to estimate the success of apparently mimetic butterflies (eg Codella and Lederhouse 1989; Platt *et al* 1971). Each of these tests of mimetic success has its own particular set of merits and disadvantages; what they share with each other, and with the trials detailed in this chapter, is that captive predators are presented with the test prey in some relatively fixed, potentially well-cued procedure which can place captive predators at an advantage and may restrict the natural behaviour of the supposed Mimic. The criticism that simulated encounters may be poor predictors of the outcome of real encounters is not necessarily specific to the hoverflies, it is one which may be levelled, to some extent, at the majority of empirical tests of natural Mimics. Introducing a bias in favour of captive predators would seem to be an inevitable consequence of the routine, controlled presentation of test prey.

3.4.7 The Positive Value of Live Trials.

The doubts raised about the value of captive predator tests of Mimics might be taken to suggest that the technique has few merits. That is not what is being implied, even the very simple tests described above are informative about the factors that might determine mimetic success. Why is it, however, that so many who have attempted to investigate mimicry empirically, have elected to adopt this particular technique? One reason is that there are few obvious alternatives. The encounters between predators and Models or Mimics represent the fundamental elements of the phenomenon of mimicry. Modelling and predicting the dynamics of any mimetic system will require reliable assessments of the frequency, timing and predator reaction to these events. These encounters are by their nature usually rare, brief and unpredictable; systematic observation of mimicry systems at this level is simply impossible. It is no surprise that the most obvious reaction to this intractable difficulty is to seek to reproduce those encounters under controlled conditions, a process which, it is argued above, suffers inherent limitations.

3.4.8 The Need for New Approaches.

Of course, all experimental techniques have some limitation which lays their results open to question. Usually, this is not a problem. Progress towards an understanding of any phenomenon is achieved as the conclusions derived from one technique corroborate those from others, until a mutually supportive body of results is established. In the instance of mimicry there are few indications that this process has, or is about to, occur. The objection, then, is not merely that the experimental technique of presenting captive predators with prey may be flawed, but that so much of the empirical support for the debate about mimicry is derived from it. That this reliance is understandable, stemming as it does from the impossibility of directly observing mimicry, in no way reduces the need for alternative approaches. If this chapter argues for a change in the way that mimicry is studied, then it argues not for the abandonment of captive predator tests, but for the development of new techniques to supplement the conclusions derived from them.

The remainder of this thesis endeavours to create a novel approach to studying mimicry, one which, though its primary purpose is to assist in the study of supposed mimicry in the hoverflies, is sufficiently general to be applicable to other mimetic systems.

3.4.9 What Sort of New Approach?

To return to the specific example of apparent mimicry in the hoverflies, what particular facility would assist in determining the success of supposed Mimics ?

A central determinant of the success of a Mimic must be its similarity to the model species (though, as will be demonstrated shortly, the issue of similarity becomes more complex than might first be apparent). Assessing similarity becomes peculiarly difficult in the hoverflies because of the sheer number and variety of pattern types. Judgements about the similarity of a hoverfly to its supposed Mimic prove extremely fluid, changing rapidly with experience of different pattern types, so that arranging all but the most coarsely graded rank orders of similarity becomes a difficult task, producing unreliable results. In such circumstances, extracting generalizations about the effect of similarity on predator decision making will prove equally difficult; conclusions drawn from tests of one particular pattern are likely to remain pattern specific, limiting their value.

A technique which succeeded in objectively quantifying the similarity of patterns, and thus brought order to the diversity of hoverfly patterns, has immediately obvious potential. It could provide a common basis for describing the performance of predator individuals and species in making particular pattern discriminations. It may permit the structure of different mimetic complexes to be directly compared, opening mimicry up to a new form of comparative approach.

The facility to allocate an objective, numerical value to the similarity of Model and Mimic patterns clearly makes possible a whole series of approaches, not only to the case of mimicry in the hoverflies, but to all examples of visual mimetic systems. The next chapter of this thesis describes the design and development of a software package which provides precisely this facility.

Particular thanks are extended to Louise Forsythe and Mark Williams for their assistance in the trials described in this Chapter; their contribution is gratefully acknowledged.

Chapter Four

An Index of Pattern Similarity.

4.1 Introduction.

The previous chapter argued that the study of mimicry has been severely hampered by a lack of variety in the techniques available to it. Considering the specific example of apparent mimicry in the hoverflies, it asked what facility would enable an original and productive approach to this particular problem. It suggested that the most immediate barrier to the study of apparently mimetic hoverflies was the diversity of abdominal patterns in the complex, and the fluidity of subjective judgements about the similarity of those patterns to that of the supposed Model pattern. It proposed, therefore, that a valuable technique would be one which allowed the consistent quantification of pattern similarities, with minimal reliance on subjective judgements. Such a facility has immediately obvious potential benefits, both in organising and targetting research, and as basis for approaching specific aspects of mimetic systems, such as the perceptual performance of predators.

This chapter describes the design, development and testing of a computer software package intended to achieve this aim.

4.2 Developing an Index of Similarity.

4.2.1. The Value of a Software-Based Technique.

A variety of manual methods for assessing similarity were considered before the final decision to use a computer-aided technique was taken. One proposed manual technique involved tracing pattern outlines onto transparencies and measuring the area of overlap between the compared patterns. Another proposed to exploit cladistic methods, by scoring the occurrence of particular classes of pattern features. These and other basically manual methods were eventually rejected, either on the basis that they still relied too heavily on the subjective or because there were reasons to question their sensitivity and reliability in measuring similarity.

Two properties of computer software made the possibility of a computer-aided method more attractive than manual alternatives. In order to be practical and reliable, a manual method would have to have been simple, and the simple methods mentioned above often appeared to result in indicies of similarity which had significant limitations. As will be discussed later, a simple measure of the overlap between two patterns has, for example, the disadvantage that it contains no information about how the difference between patterns is distributed. It was possible that if the final index of similarity was to be reasonably robust and universal, a relatively sophisticated method of analysis might be required. The first advantage of software was that it made it possible to sustain complex sampling and measurement routines. The second, obvious, advantage was that once defined in software, those analyses could be applied with complete consistency through time and between users. This latter consideration was of particular importance since it was always the intention to devise methods advantageous to the study of other mimetic complexes and which had a useful life beyond the term of the current project.

4.2.2 Basic Facilities.

The clear advantages promised by a software-based technique prompted an investigation of the available equipment. It proved possible to use existing hardware to capture the output from a monochrome video camera using a Watford Electronics Video digitizer. When this device was plugged into the User Port of a BBC Model "B" micro-computer, the camera's field of view could be represented on the computer's monitor by a four logical colour format with a resolution of 320x256 pixels. The four logical colours available made it possible to represent patterns in up to three colours, the fourth being used to represent the background. Using a small program written in BBC Basic it was possible to determine the logical colour of each point (pixel) on the computer screen.

These few facilities demonstrated that the initial steps of a computer-aided method of measuring pattern similarity were possible, and thereby encouraged further development of the techniques that would be required to compare images. The following sections describe the principles and development of a system designed to measure the similarities of digitized patterns.

4.2.3 A Definition of "Similarity".

There is no hope or intention here of mimicking the complex cognitive processes which must be involved when an observer assesses the similarity of two objects. Indeed, it is precisely the subtlety and apparent inconsistency of this mental process which the system is required to avoid. A more restrictive and unambiguous definition of "similarity" is required for the purpose of this thesis. The definition selected obviously has much in common with the intuitive notion of similarity, but it is one which immediately suggests a simple mechanism for comparing patterns.

The definition arises from a simple assumption about the fundamental processes which must underlie similarity judgements. The assumption is that two patterns which are very dissimilar can be reliably discriminated on the basis of poor information about those patterns. Conversely, when patterns are very similar, more pattern information is required to discriminate between them. In effect, the similarity of two patterns could be defined as the amount or quality of information required to discriminate reliably between them. This definition has an obvious link with the established capacity to determine the logical colour of any pixel in a high resolution, digitized image; the "quality" of information gathered about a pattern can be manipulated by varying the number or distribution of pixels sampled from the digitized pattern image.

4.2.4. The Proposed System.

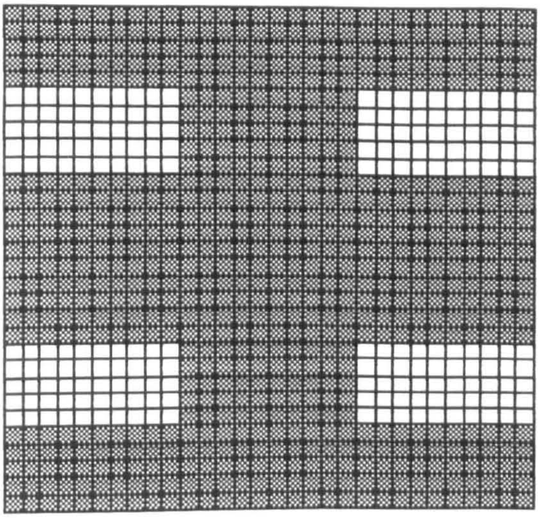
How were these basic elements, a definition, a method of measurement and the technical facility for implementing that method, to be integrated into a practical system for measuring the similarity of patterns ?

Some properties required of system are already apparent. It must hold a body of detailed information describing each pattern in the comparison and some mechanism must exist for sampling that information in varying densities. The system must then be capable of sustaining a cycle of sampling, testing and re-sampling in order to determine the quality of information required to discriminate between the patterns. If the system begins with sparse samples and cycles through progressively greater sampling densities, an index of similarity can be defined as the number of cycles required to achieve reliable pattern discrimination. Dissimilar patterns will require few cycles and will therefore have a low index of similarity, while similar patterns should require many cycles.

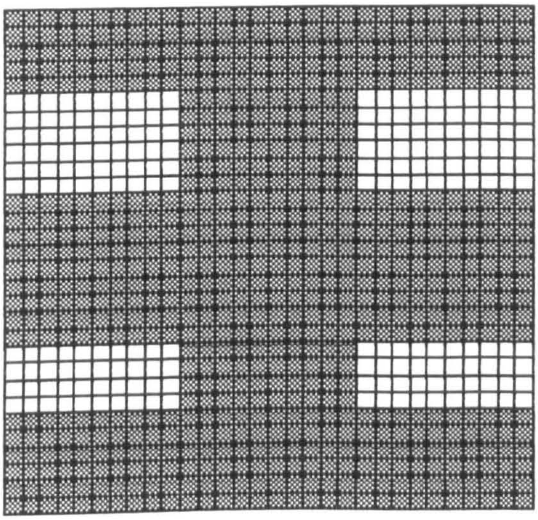
4.2.5. Image Sampling Method.

This description of the strategy for determining pattern similarity leaves unspecified two key aspects of the system, the image sampling technique and the test for discrimination between patterns. This latter aspect was of secondary concern since the type of statistical test used would depend upon the nature of the data available from the adopted image sampling technique.

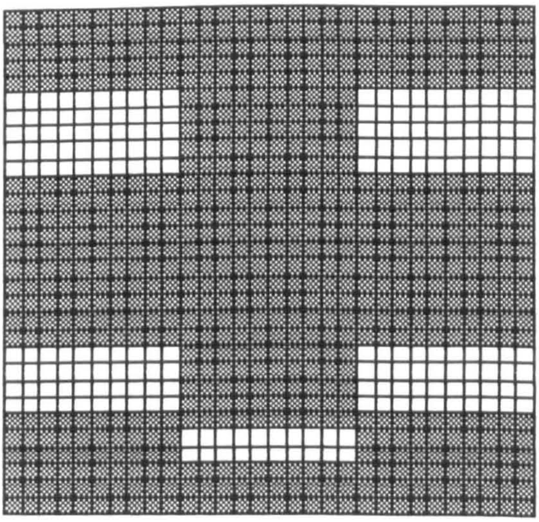
A variety of image sampling techniques were developed and tested, and some were successful in discriminating between different pattern types. One of these techniques selected individual lines of pixels from the images under comparison and determined the proportion of the logical colours in each line. This method was based on the assumption that if each pattern type was sampled in its entirety it would have a unique profile of colour proportions and that this profile would become more apparent as the number of sampled lines increased. This method was rejected, despite its success in separating the abdominal patterns of *Chrysotoxum* and *Scaeva pyrastri* , because of a lack of conviction in the assumption of the uniqueness of each pattern's colour profile. It was, nevertheless, significant in that it illustrated a property which was apparently common to simple sampling methods. Methods which yielded a simple measure of the magnitude of difference between patterns, or which recorded the proportionate colour make up of patterns, did not contain any information about how the differences between patterns are distributed. It is possible, at least for abstract patterns, to conceive of instances where an index should reflect a low similarity, not because of the number of differences between patterns, but because of the distribution of those differences. Consider Figure 4.1, which represents three simplified, hoverfly-like patterns, each mapped on a 30x30 grid. Imagine that Figure 4.1*a* represents the Model pattern and that *b* and *c* are two Mimic patterns. An image sampling technique which recorded the proportions of the two colours in each of the patterns would fail to distinguish between them because all three have the same number of shaded and clear squares. Similarly, a method which recorded the frequency of mismatches between the patterns would fail to discriminate



a. Model Pattern



b. Similar Mimic



c. Dissimilar Mimic

Figure 4.1 Abstract Model and Mimic Patterns.

between them because both Mimic patterns have forty mismatching squares compared to the Model. It would be preferable if the selected image sampling method yielded results which indicated that pattern *b* was more similar to pattern *a* than was pattern *c* , for although the number of mismatches are the same in *b* and *c* , in *c* they are distributed so as to create a pattern feature which has no counterpart in the Model. In pattern *b* the mismatches have been distributed such that they extend a pattern feature also found in the Model. Clearly, if the required index of similarity is to be at all in accord with the common sense notion of similarity, the image sampling technique from which it derives its data must be one which is sensitive to the distribution of differences between patterns, not merely their frequency.

The selected method of image sampling achieves the required sensitivity by recording the frequency of pattern differences over a range of sampling densities. It is a technique analogous to one sometimes used in television game shows where an image of a well-known personality is broken down into a number of coloured blocks which obscure facial details. The block size is then progressively reduced so that more detail emerges from the picture, until the identity of the personality has been guessed.

Recall that patterns can be digitized onto a 320x256 pixel format in four logical colours. The chosen sampling method initially divides this image into a small number of large blocks, each of which covers a large number of individual pixels. Each block is assigned the colour of the most common colour among the pixels which it covers; if, for instance, a 10x10 pixel block contains 80 yellow pixels, the block colour is assigned yellow. Obviously, when the original image is divided into a series of large blocks, the result represents very coarse information about the original image. If progressively smaller block sizes are used, the block colour data represents increasingly reliable and detailed information about the composition of the original image.

How this method of image sampling accords with the overall strategy of measuring pattern similarity should be immediately obvious. The system begins by dividing Model and Mimic patterns into a few large blocks. At this early stage it is unlikely that the block colour data will provide sufficient information to discriminate statistically between the two patterns. The image is then re-divided using smaller block dimensions and the test repeated. Eventually, if the patterns are different, differences in the block colour data will become sufficient to separate statistically the two patterns. The block size at which there is enough information to discriminate between the Model and Mimic patterns is an index of the similarity of those two patterns. This index of similarity will, furthermore, be sensitive to the distribution of pattern differences. Differences in pattern structure are likely to register at large block sizes, early in the sampling regime, whereas more subtle differences in the shape of pattern features will not become apparent until much later, when smaller block sizes are used. In the case of Figure 4.1, the difference between pattern *c* and pattern *a* are likely to be revealed by large block sizes, whilst the variation on the Model pattern represented by pattern *b* is likely to require smaller block sizes before the pattern differences become apparent.

4.2.6. Implementing the Sampling Method.

A considerable proportion of the research time was dedicated to writing the software procedures required to implement the chosen image sampling method. The result was a suite of BBC Basic and Assembler routines named, for ease of reference, *Simpack* . This package effectively performs the image analysis described in section 4.2.5, though it operates not on the images themselves, but on data files which represent them. It repeatedly re-divides image data using progressively smaller block sizes, a process referred to as "blocking", and at each stage generates a file recording block colours. The result of analysing a single pattern image is a series of data files describing the image in progressively greater detail. Pairs of patterns are then compared by analysing corresponding files in the two file series. This analysis determines the frequency with which corresponding blocks, represented in those files, match in colour. The nett result of analysing two complete file series is a summary of the frequency of colour matches across a range of sampling densities.

Detailed information on *Simpack* can be found in Appendix One, the *Simpack* User Guide and Appendix Two, the Programming Guide. However, the brief summary of the main elements of the software provides a context for the remaining discussion.

Simpack consists of a series of individual software modules linked by a simple menu system. Each module is referred to by a three-letter mnemonic and a summary of each module appears below in the probable order of use during an analysis:

Image Capture Routine (ICP). This module allows the repeated re-capture of images from the video camera and digitizer. It provides a simple cross-hair overlay to assist in image alignment and permits the stored image to be saved to disc.

Image Editor (FSE). The Watford Electronics VideoBeeb digitizer is among the most basic of its kind and was limited in the quality of its output. Lighting reflections caused image high spots which appeared white on the digitized image even if the pattern colour at that point was black. Careful lighting could minimize these effects but some imperfections were always evident in the captured image. The Image Editor provides the operator with an on-screen pen which allows stored images to be edited. This routine can be used to correct the inconsistencies suffered by the digitizer.

Primary File Generator (PFG). The basis of the analysis is a file, referred to as a Primary File, which records the logical colour of every pixel in the 320x256 image. The primary file generator scans stored, edited images and lays down this file on floppy disc.

Image Data Blocking (MLO,CML,RML). It is the data in the Primary File, rather than the original pattern image itself, which are subjected to the "blocking" process. Blocking is controlled by a software list, the Master List, which specifies the series of block sizes in terms of the number of pixels on each axis of the block. This list is assembled using a simple editor (MLO) and processed by a compiling program (CML) to calculate the disc space requirements and disc destinations for the file series. This compiled Master List is then "run" (RML) against each of the Primary files to be analysed. The result of these runs is a blocked file series for each original image.

Scoring Colour Matches (GFC, SFC). The first of the final pair of *Simpack* modules analyses corresponding files in two blocked file series. For each such file pair, the block colour of corresponding blocks is tested for equivalence. Where block colours are the same, and are not the designated background colour, a match is scored. The Primary File is effectively a part of the blocked file series where the block size is one pixel, and a further module carries out this matching analysis specifically for these files. The outcome of these analyses is a match score for each level of the file series for each pair of compared images.

4.2.7. Analysis of Results.

The previous section describes facilities which permit a series of match scores to be calculated for any two digitized pattern images. How are these data manipulated to derive an index of similarity for two or more patterns ?

It is obvious from the preceding discussion that during the inception of *Simpack* , the block size at which two patterns became statistically separable would serve as the index of pattern similarity. This is still an appropriate means of visualizing the underlying principle of the system; in particular it makes obvious how the system is sensitive to the distribution of differences between patterns. However, experience with a real pattern series indicated a number of practical limitations which precluded this method of deriving an index of similarity.

The origin of one of the limitations is that screen pixels represent the basic, indivisible units of each image. This creates a problem if one specifies block sizes which involve fractions of pixels. There are several options in such instances. Fractions of pixels could be rounded up, creating slight overlaps between adjacent blocks and causing some pixels to be referenced twice in the same image. Alternatively, fractions could be rounded down, thus creating "gaps" between blocks where pixels are not referenced at all. A third option was taken in the development of *Simpack* . Fractions of pixels were rounded to the nearest whole number and the construction of the next block proceeds on the next whole pixel. The obvious consequence is that for some block sizes, the blocking process fails to cover all of the image, while for others, the software exceeds the limits of the image when creating the last few blocks. The advantage of this approach is that it is computationally quite easy to implement; the disadvantage is that the choice of block sizes is restricted if the significance of this "cut-off" effect is to be minimized. The block dimensions used throughout this thesis are selected to reduce the cut-off so that only a small percentage of pixels at the periphery of the image fail to be sampled. In most cases, the patterns under measurement do not reach the extreme edge of the screen, so the unsampled part of the image usually represents the background logical colour, which does not contribute to the between-image match scores.

A second limitation arises from the processing speed of the available machine at the time of the image data-blocking process. Even for the nine block dimensions specified throughout this thesis, the blocking process took some four hours to produce the file series describing each Primary file. This, in addition to the time taken to capture and edit each image, conspired to make even comparisons using few samples, a protracted process.

The consequence of these two limitations, i.e. the need to minimize cut-off effects and processing time, is that only a small subset of potential block sizes can be used. In practice, using the block *size* at which two image data sets are separable could therefore only represent a coarsely grained index which offered few advantages over the broad classifications of similarity which might be achievable using manual or subjective methods of assessment. A different method of analysis was sought which exploited the available match-rate data, retaining sensitivity to the distribution of pattern differences, whilst providing a sensitive, high resolution index of similarity.

The selected method of analysis involves regressing data on the match rates of patterns, or pattern types, against the number of blocks produced by the specified block dimensions. The detail of this analysis will be demonstrated shortly in the context of a specific example. However, a brief outline will be given here for the purpose of explaining how the analysis retains sensitivity to the distribution of pattern differences.

At the beginning of a *Simpack* analysis of two or more patterns, one pattern is designated as the Model. Several examples of the Model pattern are captured and processed using the various *Simpack* modules described above. The result is a whole group of file series, each of which describes an example of the Model pattern in varying levels of detail. Each unique pairing of Model patterns is then compared, by scoring the number of matches between corresponding files in the two file series. The result is a number of estimates of Model-Model match rates for each level of the blocking process. These results are then averaged to obtain a plot of mean Model-Model match rates versus the *number* of blocks (rather than block dimension) which result from each stage of the blocking process. This process is repeated for each unique Model-Mimic pairing, this time to obtain an estimate of mean Model-Mimic match rate versus block numbers, which can be represented on the same axes as the Model-Model estimates. A hypothetical example of such a plot is shown in Figure 4.2. The Model-Model and Model-Mimic match rates can be regressed against block numbers, and an index of similarity can be derived from the differences in slopes of these regressions. In this thesis, the objective similarity between Models and Mimics is described by the ratio of these two lines, expressed as a percentage.

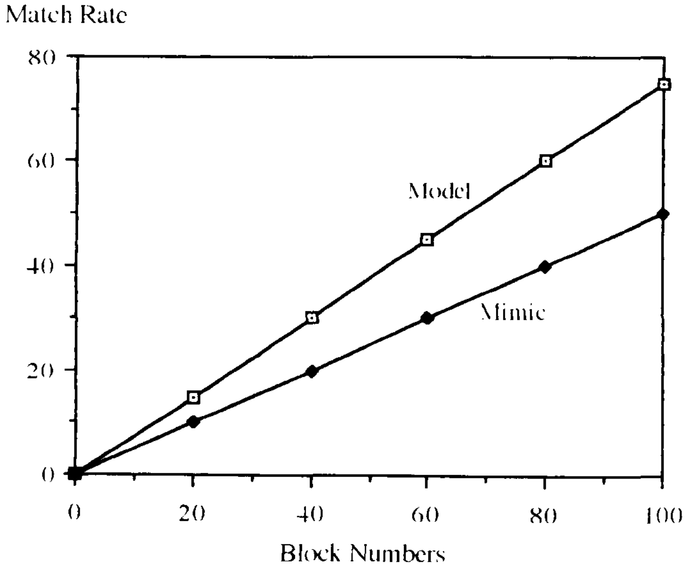


Figure 4.2 Regressions of *Simpack* Similarity data.

As already mentioned, the details of this analysis are best understood in the context of the example which is presented shortly. The purpose of this summary is to illustrate how this method of analysis, which apparently abandons part of the original basis of *Simpack*, still retains a sensitivity to the distribution of difference between patterns. Consider Figure 4.3, which illustrates a small data set from a hypothetical *Simpack* analysis.

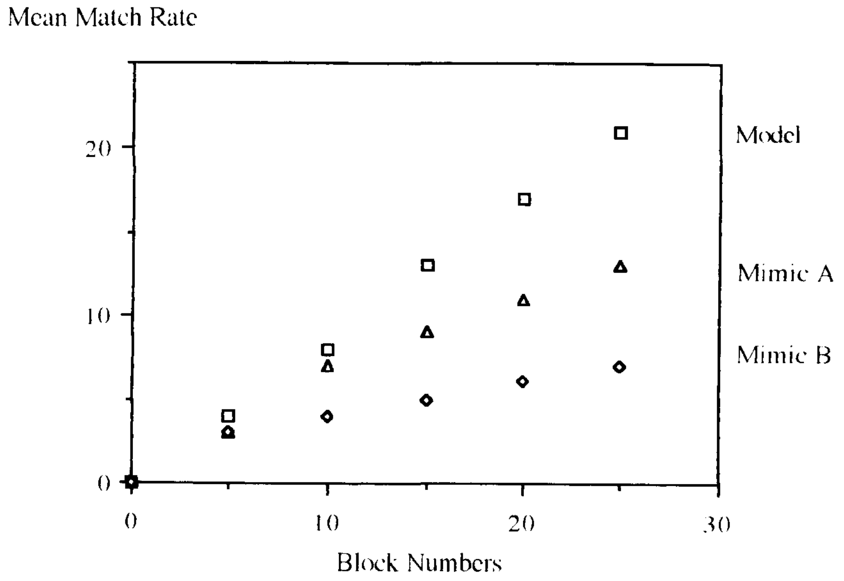


Figure 4.3 Illustrative example of the sensitivity of *Simpack* regressions to the distribution of differences between patterns.

The mean Model-Model match rate data is represented by squares, data for Model-Mimic A comparisons by triangles and data for Model-Mimic B by trapezoids. At a block size which produces five blocks in total, the data for the three types of comparison show little separation. With ten blocks, pattern differences between the Model and Mimic B cause the match rates for these two patterns to separate, while Mimic A retains a similar match rate to Model-Model comparisons. Fifteen blocks are sufficient to separate the Mimic A data from that of the Model. Clearly, when regression lines are fitted to these data, they will reflect, for each Mimic pattern, the match rate at a *range* of sampling densities, not merely the final, highest sampling resolution possible. An index of similarity derived from such regression lines will be sensitive to the distribution of differences between patterns because the data which determines the value of those regressions has that sensitivity.

4.3 Testing Simpack.

Simpack is effectively a self contained definition of, and system of measurement for, pattern similarity. How can such a system be tested ? What alternative method can be used to assess its results when the very *raison d'etre* for the system implies that the most obvious source of corroboration, our subjectively based expectations, are not sufficiently reliable ? A convincing trial of *Simpack* clearly required the selection of test patterns which satisfied two criteria.

4.3.1 Test Pattern Selection.

The reason for the creation of *Simpack* was that judgements about the similarity of hoverfly patterns appear particularly fluid, being heavily dependent on time of exposure and the observer's previous experience. The first criteria for selection was simply that the test patterns should not be hoverfly abdominal patterns, but that they should share with them a similar degree of structural complexity. The underlying method of *Simpack* is intended to be universal, independent of the pattern structure with which it is presented, and it should be possible to test for the correct operation of the software on any type of pattern. It is clearly more pragmatic, however, to test the system on patterns which are broadly similar to those which require analysis in this thesis.

The second criterion for selecting test patterns was that an argument should exist for predicting, independently of their perceived similarity, the expected distribution of the patterns' *Simpack* similarity ratings. Without becoming too involved in the precise semantics of the situation, it is here that the apparent paradox of *Simpack* is most evident. "Similarity" is a perceived property of two or more objects, and to propose an objective method for evaluating a subjective property might appear something of a contradiction. It is important to re-iterate that there is no paradox. *Simpack* is not attempting to capture and evaluate the subtlety and complexity of perceived, subjective similarity. "Similarity" here has only a very restricted definition and is intended only as a label to refer to the actual co-incidence between two patterns. The primary purpose of this initial evaluation of *Simpack* was not to test the validity of this definition or the underlying logic of the resulting system; rather, it is to determine whether the chosen system has been correctly implemented.

The test patterns were additionally required to satisfy some practical considerations, primarily that a number of examples of each pattern type should be easily available and that image capture and editing should be as straightforward as possible. It was decided that the front elevation view of cars most obviously satisfied these criteria.

This selection was partly inspired while efforts were being made to find an analogy for the difficulties which must be encountered by an avian predator which has chanced upon a brightly banded insect and must promptly decide whether it represents a valuable food resource, or a potential threat to well being. It was thought that this situation was not unlike a driver attempting to discriminate between approaching Ford Granada and the later Ford Sierra models, as seen through a rear view mirror at motorway speeds. This situation is analogous to the hoverfly paradox in that were one's experience of these models those of a non-driver and based solely upon static examples in car parks, it would be difficult to appreciate how the two could ever be confused. In practice, the discrimination, in the circumstances described above, proves extremely difficult.

The increasing similarity between makes of car over recent years has received much popular comment. Some of this similarity obviously results from the efforts of stylists to incorporate into their own designs, styling features originated by other manufacturers, which have met with favourable public reaction. As such they represent direct appeals to the subjective and therefore undermine the choice of cars as the test patterns, since they may confound attempts to predict the distribution of similarity ratings. At the same time, a proportion of this convergence is derived from factors which have nothing to do with the superficial appearance. For example, for any given size and type of car there will be a body shape which represents the aerodynamic optimum. As fuel economy has become increasingly important, so manufacturers have had no option but to converge on this optimum shape, and this will inevitably be reflected to some extent in the proportions of the front elevation of their products. Further aerodynamic considerations will also, for instance, determine the locations of radiator grilles, spoilers and bonnet shapes. Similarly, legal requirements of minimum illumination and absolute optima of reflector design might dictate the size and shape of headlamps and so on. The size and intended purpose of a vehicle therefore have a very substantial effect upon its final appearence, long before any stylist is called upon to consider its aesthetic appeal. As part of the initial trial of *Simpack* , it was assumed that the distribution of similarity ratings for car patterns could be predicted from properties, such as the vehicles' size and intended role, which did not depend upon subjective assessment. These specific predictions are dealt with in the following section.

The pattern representing the front elevations of cars are broadly similar to hoverfly patterns when digitized in the *Simpack* image capture screen, being bilaterally symmetrical with horizontally orientated bands. Since a number of examples of each car are also readily available, it appears that front elevation car patterns satisfy the practical considerations and both of the criteria detailed above, they were therefore adopted as the test patterns.

4.3.2 Predicting Similarity Rating Distribution.

If one accepts the proposition that car similarity ratings are predictable from other properties of the vehicle, one might elect to derive specific quantitative predictions from entirely objective factors such as car length, price, top speed or engine size and thus avoid some influence of the subjective. For the current purpose, carrying the argument to this degree seems unwarranted since quite adequate predictions can be made from simple assumptions which, unlike similarity, are barely disputable.

The Ford Granada will serve as the model pattern for this analysis and it can be seen as effectively an enhancement of the Ford Sierra concept, having approximately the same size, performance and intended role; it is predicted that the similarity rating of the Sierra should be very high. The Escort is recognisably a vehicle of smaller size and lower price and performance, and should have a substantially lower rating than that of the Sierra. Of the three non-model cars, the Mini is clearly the most exceptional, being a small, low performance, urban car, and its similarity rating should be the lowest. Moreover, since the disparity in size, purpose and peformance appears greater between the Mini and the Escort than it is between the Escort and the Sierra, the Mini-Escort similarity interval should be greater than the Escort-Sierra interval.

4.3.3 Method

Photographs of the front elevations of six Ford Granadas, five Ford Sierras, four Ford Escorts and four British Leyland Minis were taken using 35mm colour slide film and a single lens reflex camera fitted with a 50mm standard lens. Irrespective of the size of the car, the photographs were taken from a distance such that the highest point of the roofline and the lower edge of the number plate corresponded to the upper and lower edges, respectively, of the camera's viewfinder. The image of the car was centralised with respect to the estimated vertical midline of the viewfinder.

The developed slides were used to produce 10x8 inch, high contrast monochrome prints. Owing to the poor, under-exposed quality of some prints, the car images were cut from the background, with all features below the lower edge of the front bumper or spoiler being discarded, thus removing the wheel outlines. Minor details such as aerials and wing mirrors were also disregarded. The windscreen area was removed leaving an outline which, when mounted on white paper, produced a high contrast silhouette of the car.

These photographic outlines were then analysed with the *Simpack* software package, the use of which is described in detail in Appendix One; modules of the software referred to below by their three letter mnemonic are explained in that Appendix.

Digitized images of the silhouettes of all cars were obtained using the image capture routine (ICP). The criteria for image alignment were similar to those adopted in obtaining the original photographs; the top-most part of the image met the top edge of the image capture screen, whilst the lowest part met the lower edge. The image was centred to be symmetrical about the vertical cross hair of the image capture screen. Other than alignment, the primary consideration was to obtain a well defined image outline. Large areas of inappropriate digitized coloration were tolerated if they did not affect the image outline and could be easily corrected with the image editor. Such alterations did not represent subjective input to the image capture process since they did not affect image features. Relatively small errors in outline digitising were, however, afforded much more attention. These outline errors were most often corrected by the application of black marker pen or typist's correction fluid to the photograph in order to tone down or highlight image features, thus forcing the digitizer to recognise an otherwise poorly defined outline.

Final revisions to the images were effected using the *Simpack* image editor (FSE), mostly to ensure correct coloration. The car body area was coloured black, the background filled white, while the windscreen, headlamp, radiator and number plate areas were highlighted in yellow. A Primary file was constructed for each image using the Primary File generator (PFG).

A *Simpack* analysis requires that a series of blocked files be generated from this Primary file; the creation of this series is directed by a Master List which specifies the horizontal and vertical block size to be adopted at each stage of the blocking process. In principle, the software is capable of handling any specified block size, however, fractions of pixels cannot be dealt with and resulting approximations can mean that the final row or column of blocks fails to cover the image. In practice, a set of block sizes which minimises this cut-off is used, ensuring that at most only a few lines are missed from the extremities of the image. These block sizes (specified as the number of pixels on the vertical and horizontal axis of the block) were edited into the Master List, which is represented in Table 4.1.

Master List Level	Vertical Block Axis	Horizontal Block Axis	Number of Blocks Produced
Primary	1	1	81920
1	4	4	5120
2	5	5	3264
3	8	8	1280
4	10	10	800
5	16	16	320
6	21	21	180
7	32	32	80
8	42	42	42
9	64	64	20

Table 4.1 The Simpack Master List used in the analysis of car patterns, specifying the vertical and horizontal block dimensions in terms of the number of pixels on the block axes.

This Master List was then compiled, a process which calculates the disc space requirements and file locations for the file series generation.

Each Primary File was then processed according to the parameters specified in this compiled Master List. The product of this operation was a file series for each image, with each file in the series *equivalent* to a progressively poorer, more coarsely grained representation of the original image. The corresponding points in a pair of series are then compared, yielding a score of the number of matches at each level of the Master List.

4.3.4 Results

4.3.4.1 Mean Match Rates

The first stage of the procedure required scoring the match rate for each unique pairwise comparison of the model patterns, this establishes a baseline for the rest of the analysis. A score was obtained for the match rate of each unique pairwise comparison of Granadas at each level of the file series, and the mean and standard deviation of these scores are represented in the first column of Table 4.2 below. Similar scores were then obtained for each unique comparison between each of the Granada patterns and each example of the three non-model pattern types; the mean and standard deviations for these comparisons are also shown in Table 4.2.

Granada Mean ± sd	Sierra Mean ± sd	Escort Mean ± sd	Mini Mean ± sd
53512.20 ± 2174.50	51506.33 ± 1315.00	46074.25 ± 2645.28	39635.47 ± 878.76
3325.13 ± 140.31	3199.37 ± 83.36	2858.79 ± 169.25	2463.30 ± 61.38
2113.53 ± 88.75	2053.00 ± 55.56	1829.38 ± 108.93	1553.83 ± 35.23
840.67 ± 47.14	804.77 ± 23.87	711.75 ± 46.64	609.87 + 27.20
516.27 ± 24.96	498.13 ± 17.43	435.29 ± 27.08	378.73 ± 9.92
175.27 ± 13.38	166.80 ± 11.81	149.17 ± 11.57	125.50 ± 8.05
118.93 ± 6.79	111.00 ± 8.31	111.71 ± 8.98	97.33 ± 4.05
46.87 ± 2.33	45.10 ± 3.63	37.92 ± 4.30	33.17 ± 3.87
31.33 ± 1.45	30.13 ± 1.01	27.92 ± 2.48	22.47 ± 1.83
13.60 ± 0.83	12.77 ± 1.04	10.79 ± 0.88	11.10 ± 0.31

Table 4.2 Means and standard deviations of match scores for each pattern type compared to the Granada Model (Comparisons: Granada *n* =15, Sierra *n* =30, Escort *n* =24, Mini *n* =30).

4.3.4.2 Match Score Regressions.

The mean match rates shown in Table 4.2 are regressed on block numbers; these regressions are depicted in Figure 4.4, though data for the highest level of the Master List (81,920 blocks) are omitted from the plot for clarity.

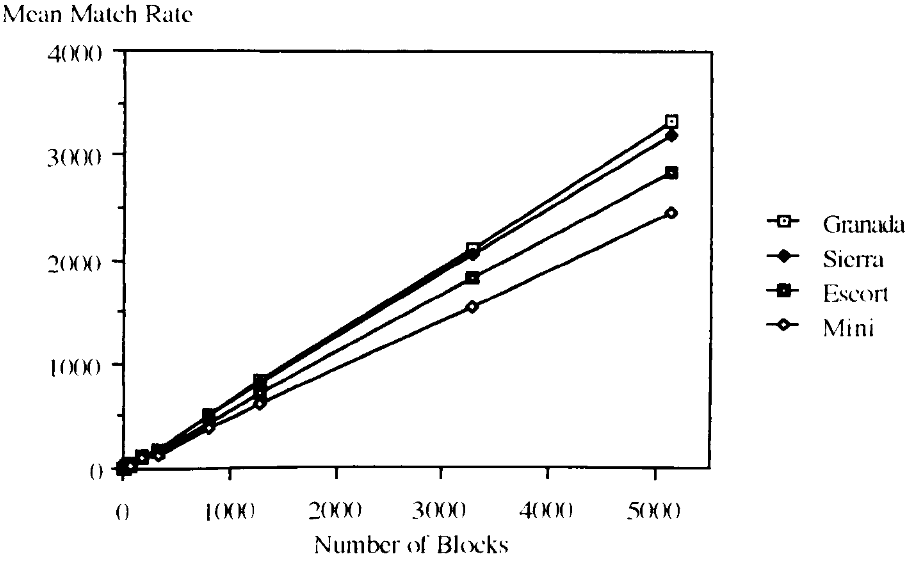


Figure 4.4 Regressions of mean match scores vs block numbers. (All "Mimic" pattern regressions were significantly different from the Model pattern using analysis of co-variance in Snedecor and Cochran 1972, $p<0.001$).

The regressions for Sierra, Escort and Mini patterns are all significantly different from the Granada (model) regression.

4.3.4.3. An Index of Similarity.

The similarity between Model and non-Model patterns can be expressed as the difference in their regression co-efficients. In the index of similarity used here, this difference is subtracted from 1 so that dissimilar patterns have lower index values. The first column of Table 4.3 shows the regression co-efficients for each pattern type, while the second shows the index of similarity to the model pattern.

	Co-efficient of Regression	Difference from Model Regression	Index of Similarity	% Similarity
Granada	0.6533	0.0000	1.0000	100%
Sierra	0.6288	0.0245	0.9755	97.55%
Escort	0.5625	0.0908	0.9092	90.92%
Mini	0.4839	0.1694	0.8306	83.06%

Table 4.3 Regression co-efficients and computed index of similarity for car patterns.

4.4 Discussion.

4.4.1 Predicted and Observed Similarity Ratings.

For the reasons outlined in section 4.3.2 of this chapter, no specific, quantitative predictions were made about the results that *Simpack* should produce, having analysed the car patterns. However, the observed distribution of similarity ratings follows the predicted rank order and may fulfil the qualitative predictions made about the intervals between ratings. As predicted, the Sierra pattern is first in the rank order with an expectedly high similarity rating of 97%. This is followed next by the Escort rating and then by the Mini rating, again as expected. However, the prediction that the difference between Escort and Mini ratings should be much greater than that between the Escort and the Sierra may be only weakly supported. The Escort-Mini interval of 7.86% certainly appears only slightly greater than the Escort-Sierra interval of 6.63%. The present lack of experience with *Simpack* results makes it difficult to assess the significance of this 1.23% difference; the only yardstick available for comparison is that a 16.94% interval proves sufficient to describe the difference between patterns so radically different as those of the Granada and Mini. With this perspective, a difference in ratings of 1.23% may be interpreted as appreciable, and the prediction that the Mini should represent an outlier may be upheld by the data. If this is so, then *Simpack* would appear to have fulfilled all of the predictions made and further patterns could be subjected to *Simpack* analysis with confidence.

Assuming, however, the worst case, that the data do not support the predictions about intervals between the Sierra, Escort and Mini ratings, the conclusion must be either that those predictions are unwarranted or that *Simpack* is not operating correctly. This latter conclusion was rejected for two reasons.

Firstly, as argued elsewhere, the rank order of *Simpack* similarity ratings and the intervals between ratings are simply different aspects of the same result. In accepting that the rank order produced by *Simpack* is correct, one is implicitly accepting that the intervals between ratings, a consequence of the same process, are also correct. An error of implementation which resulted in correct rank orders but illogical intervals would have to be extremely subtle, and it is difficult to see how such an error could arise when the underlying process of *Simpack* amounts to little more than testing for correspondences between two sets of numbers; were an error present in this process it would be unlikely to manifest itself so subtley.

The second reason was that though the predictions about *Simpack* 's results were not necessarily unwarranted, the particular prediction about the Escort-Mini rating interval was not sufficiently specific or well founded to give grounds for rejecting what is otherwise a successful analysis. In retrospect, it seems likely that the reasoning used to generate this specific prediction underestimated the extent to which the subjective continued to contribute to expectations. The mental image of a Mini inevitably includes its size and since *Simpack* corrects for differences in pattern size, at least in one dimension, the actual discrepancy between the Escort and the Mini pattern might indeed be much less marked than expected. It is likely that this departure from the expected, far from being an indication of an error, is a perfect demonstration that *Simpack* performs precisely the role for which it was intended, that of removing the uncertain influence of subjectively based assumptions.

4.4.2 Limits of the Method.

These test analyses highlight two properties of the *Simpack* system which should be kept in mind when analysing the results it produces.

In the analysis described in this chapter, the image capture criteria adopted correct for differences in pattern size in the vertical dimension. For the purpose of this thesis, size independent indicies of similarity were considered most desirable, partly because the role of size, and its relationship to distance, in pattern perception is likely to be a complex one, but also because size-independent indicies can be corrected retrospectively using a simple measure of size. If a size inclusive index of similarity is required, different framing criteria could be adopted to maintain relative pattern sizes during image capture.

Since this attempt to standardise patterns on some common basis involves only one dimension, the resulting index of similarity is considered to be independent of size, but sensitive to pattern shape.

"Shape" differences are recorded as the failures to match which occur when a non-background colour block in one pattern corresponds to a background colour block in another. It is possible that such shape differences largely account for the distribution of similarity indicies observed in this particular analysis. These shape differences are considered to form a legitimate component of the concept of similarity being pursued in this thesis, so the conclusion that the *Simpack* analysis is reflecting shape differences does not represent a difficulty in the current context. It is equally true, however, that shape differences could be adequately summarised with much less sophisticated and protracted analyses than those written into *Simpack* . Clearly, where differences in pattern shape account for much of the diversity in a range of patterns, *Simpack* may represent an overly complex method of analysis. Conversely, *Simpack* is most valuable where pattern structure is more diverse, relative to pattern shape.

4.4.3 Repeatibility.

The single most valuable property of *Simpack* is that its analyses are almost perfectly repeatable. The process of creating a restricted definition for "similarity", designing a method for measuring pattern similarity and the fixing of that method in software, has resulted in a procedure which promises complete consistency over a diversity of patterns and through time. This feature alone overcomes one of the major difficulties in studying apparent mimicry in hoverflies and a variety of other problems in mimicry.

There are really only four aspects of the procedure which permit the introduction of confounding variation within and between pattern analyses.

The first occurs in those cases where the pixel count during the blocking process reveals two colours to be equally common in the same block. In such instances, the block is randomly designated to be one of the two colours and this obviously means there is potential for very minor differences in duplicates of the same analysis. The effect of this random allocation is likely to be negligible for all practical purposes. Where the block size is large, the probability of an equal number of different colour pixels is likely to be low. At smaller block sizes, this likelihood increases but the effect on the overall pattern analysis is small because of the larger number of blocks.

The three further potential sources of variation occur where the process cannot avoid some degree of subjective input, namely sample collection, *Simpack* image capture and image editing.

4.4.4 Introduced Variation.

Table 4.2 above reveals very low degrees of variation about the mean match rates, the co-efficients of variation for the Sierra, Escort and Mini patterns are, respectively, 2.55%, 5.74% and 2.22%. If it is assumed that within each type, the sampled cars are completely uniform, this variation represents the variation introduced during sample collection and image manipulation. That is it so low, indicates that the framing criteria used during sample collection and image capture have been well defined and closely adhered to. This suggests that in those aspects of the process where some subjective input cannot be avoided, the adoption of sampling and placing criteria is successful in minimizing and standardizing its effect. However, the success with which these criteria have been applied must be largely due to the uniformity and symmetry of the patterns within each type and the commonality of form between types. The lower edge of the number plates of Minis, for instance, provides a clear reference point and always occupies the same position relative to all other parts of the image, in every example of the Mini pattern. Similarly, the symmetry of each pattern, and the fundamental similarity of form between patterns, ensures that corresponding parts of different patterns can be located on a common basis. This means, for example that the vertical midline of the image always passes through the windscreen of every type of car and that differences between patterns, registering in the windscreen area, can be considered as being due to differences in the size and shape of the windscreen rather than variation in the placing of the windscreen in *Simpack's* frame of reference.

It is unlikely that such clear cues for image placing will be evident in natural patterns or that such cues as do exist will permit such uniformity; natural variation will cause pattern features to change position with respect to each other. Clearly such variation would produce a greater standard deviation about the mean than appears here. While some of this will be "legitimate" variation, reflecting the actual pattern differences, another component will be due to the confounding effect that such variation has on applying criteria designed to locate corresponding parts of different images at the same point in the sampling frame of reference. Other pattern features, such as bilateral symmetry will, however, still be evident in many natural patterns and will assist in image placing.

As yet then, the efficacy with which any framing criteria can be applied to natural patterns remains uncertain. The most obvious strategy for offsetting any difficulty with natural patterns is to increase the sample size to achieve a good estimate of pattern variation statistically.

4.4.5 What the System is Not

Even at this early stage it is important to pre-empt any misconceptions about what *Simpack* is for, and what it might be expected to achieve.

Simpack is emphatically not an index of mimicry quality. How accomplished a Mimic is in its deception depends on its resemblance to the Model species *as perceived by a predator* . *Simpack* is not a model of predator perception, it is designed to measure actual, not perceived, similarity.

Simpack could serve as an index of mimicry quality only if measured and perceived similarity co-incide. This is improbable given that perceptual and cognitive systems are often demonstrably selective agents which might, for instance, attend to particular pattern features when making discriminations. At the same time, perceived similarity cannot be completely independent of actual similarity, so it is reasonable to expect there to be some co-incidence between an index of similarity and an index of mimicry. One potential application of *Simpack* is to provide a basis for exploring the relationship between actual and perceived pattern similarity.

4.4.6 The Properties of *Simpack* Similarity.

If *Simpack* is not an index of mimicry, what is its value in the study of mimetic phenomena ? To re-iterate, the purpose of the package is to facilitate new approaches to mimicry by providing a mechanism for objectively and consistently assessing the most obvious feature of mimetic systems, the similarity between Model and Mimic.

Despite a more formal definition of, and mechanism for measuring, "similarity", there are some inherent limitations to such a system which must restrict expectations about what it can achieve. There are important differences between "similarity" and other perceived properties of objects. Suppose, for example, one developed an objective approach to the subjective property "colour" by measuring the wavelengths of light reflected by an object. Such a procedure would probably reveal that most human individuals would respond "blue" to the same particular narrow band of wavelengths, and it would be unlikely that individuals will at some future date begin calling that same band of wavelengths "red". In these two respects, consistency between and within individuals, judgements about colour would already be different from those about pattern similarity, but there is a more fundamental difference in the *measures* of colour and *Simpack* similarity. Wavelength is an exclusive measure of colour, a particular wavelength cannot describe both red and blue. A *Simpack* similarity value is a distribution-sensitive measure of the magnitude of pattern differences; it does not describe pattern structures. Consequently, two patterns can be significantly different from each other, yet have the same degree of similarity to a third pattern.

4.5 Conclusion

Simpack has been entirely successful in its intended purpose of assessing pattern similarity. It has confirmed a reliable subjective rank order, and, in doing so, has yielded numerical estimates for relative pattern similarity. This single success is of great significance since the method upon which it is founded is fixed in software, guaranteeing a degree of repeatibility which would be impossible to mimic with any subjectively based system. The few theoretical and practical constraints which have been discussed will not be sufficient to prevent *Simpack* becoming a powerful tool in assisting research into mimetic systems.

Chapter Five

Using *Simpack* to Describe Mimic Communities - A Test of the Disturbed Ecology Hypothesis.

5.1 Introduction.

The practical tests described in the latter part of the preceding chapter were sufficient to demonstrate that *Simpack* provides a reliable index of objective pattern similarity. How can this new facility be exploited to help establish the mimetic status of the hoverflies, and how might it contribute to much wider issues in mimicry theory ? This chapter is the first of two intended to demonstrate novel applications of a similarity index and in it, *Simpack* will be used in conjunction with a simple census technique in order to produce unique "similarity profiles" of hoverfly communities. These profiles will effectively describe hoverfly community structure in terms of species' relative abundance and their similarity to a putative Model species. The ability that these profiles give, to compare and contrast different examples of the same mimicry complex, obviously has the potential to contribute to our understanding of mimicry by indicating the origin of specific variations in the structure of a complex. A later chapter, however, will propose a broader and yet more significant role for such similarity profiles in testing our theoretical understanding of mimicry against field observations.

As a vehicle for this novel application, this chapter will provide a test of the "Disturbed Ecology" hypothesis, put forward in the introductory chapter as a possible explanation of the paradoxes of apparent mimicry in the hoverflies. Briefly, this hypothesis proposes that recent large-scale changes in agricultural practice have perturbed "natural" hoverfly populations to the extent that accomplished Mimics have become relatively much rarer than in their historical state.

In order to test this hypothesis, *Simpack* will be used to compare hoverfly community structure in two typical British woodland sites with that in a continental habitat considered to be relatively free from agricultural disturbance. To establish a focus for these comparisons, the research will address four specific questions:

1. Is the absolute abundance of hoverflies greater in disturbed sites than in undisturbed sites ?

2. Do hoverflies represent a greater proportion of flying insects in disturbed sites ?

3. Are supposedly mimetic hoverflies more common in disturbed sites, relative to their putative Models ?

4. In terms of relative abundance and Model-Mimic similarity, is the hoverfly community significantly different in disturbed and undisturbed sites ?

The first three of these questions can be answered with reference to census data on the frequency of hoverflies in the compared sites; *Simpack* similarity analyses will be required to provide an answer to the fourth question.

The current literature on hoverfly abundances indicate that some general features of community structure can be anticipated. Owen and Gilbert (1989) report on the analysis of Malaise trap catches of hoverflies at a British suburban site over a period of fifteen years. They reveal some patterns of species abundance, distribution and population stability which, if the structure of European museum collections is representative of local community structure, may be repeated at other European sites and which may be of direct relevance here. For instance, species which were common in one year's trap data showed a significant tendency to be common in other years; the rank order of abundance was relatively invariant between years. Species which were in some way specialized, either in the specificity of their predatory larval stage, or in their reproductive habitat requirements, were relatively rare. These specialized species, and their generalist counterparts, exhibited a greater variation in mean annual abundance than an intermediate class of "moderately specialized" species. These local trends were related to patterns of abundance and distribution on regional and national scales. Species which were abundant at the British site were likely to be the commonest recorded species in other northern European countries, and have widespread national distributions; it would not be unreasonable, then, to expect similar species properties at newly sampled sites. There *are* consistent differences between the hoverfly communities of very different habitats. Barkenmeyer (1984) reports that in a German marshland site, the Eristalines were by far the most common species, in contrast to woodland sites. However, the patterns of abundance, distribution and stability indicated by Owen and Gilbert may be interpreted as an indication that in broadly similar habitats, woodlands for example, the hoverfly communities are essentially similar in structure and certainly not in a massive state of flux. If one wishes to continue to invoke the disturbed ecology hypothesis one must therefore assume both that the ecological disturbance has been essentially similar at many sites, and that the affected communities have reacted similarly to arrive at a new stable equilibrium. Such a scenario is not inconceivable, but it does not explain why the new equilibrium, apparently at odds with the predictions of mimicry theory, remains stable. There are no indications that any of the observed patterns of abundance and stability are related to any mimetic effects. However, the suggestion that a variety of forms of specialization somehow impose a condition of low abundance compared to more generalized species is consistent with the paradoxes of apparent mimicry, if one assumes that very close resemblance represents or entails some specialization. It is not easy, however, to conceive of a mechanism which relates mimicry quality to, for example, a limited resource, in the same sense that specialized larval requirements are related to the scarcity of suitable sites.

While the patterns of abundance, distribution and stability described above may be fundamental to many, widespread hoverfly communities, there is certainly one indication that community structure can be perturbed by the activities of man. Bankowska (1980) analysed data on hoverfly abundance in terms of groups of larval feeding type (zoophages, phytophages etc). Bankowka's conclusions were that the activity of man had in many cases decreased the overall diversity of species and increased the relative abundance of the most dominant species in the community. These conclusions offer partial support for the disturbed ecology hypothesis. If the "loss" of species through agricultural or urban activity affects those species considered to be accomplished Mimics, the disturbed ecology hypothesis might explain the paradox of mimicry in the hoverflies. However, the suggestion that the effect of disturbance is to accentuate existing patterns of abundance indicates that while the paradoxes of mimicry in the hoverflies may be more extreme in disturbed sites, they should still be evident to some extent in natural communities.

5.2 Method.

5.2.1. Field Sites.

Census data were gathered from two widely separated British woodland sites surrounded by predominantly cereal producing agricultural land and therefore regarded as potentially ecologically disturbed.

Owston Wood, Leicestershire , is a well established mixed woodland, through which pass a series of grass tracks which provide a linear census path. The border of these tracks are colonized by plants which are typical of disturbed ground, for example, a range of Umbellifers (Candlish 1976). Owston Wood was censused on 8 days in August 1987 between 10am and 1pm. Each census consisted of 18 individual 15m walks.

Bunny Wood, Nottinghamshire , is a narrow, linear, sloping Elm wood running along a steep, north facing ridge. As a result of Dutch Elm disease, there are a large number of dead trees and open glades which provide ideal habitats for colonizing plants and many species of hoverfly. A path running along the top and bottom edges of the ridge provides well defined census walk paths. Bunny Wood was censused 11 times between the 14th of May and the 9th of September 1988. Each census consisted of between 9 and 25 individual 15m walks, depending on hoverfly abundance. Censuses usually took place during the period 10am to 1pm, but one afternoon survey was carried out, extending to 4.40 pm.

For comparison, censusing was also carried out in the Massane Forest Reserve, near Perpignan in south-eastern France. This Reserve consists of a 4 km. long valley bordered by three peaks of the Oriental Pyrenees between approximately 800 and 1100 metres above sea level; the total area of the reserve is some 350 ha (Duran and Trave 1988). Censuses were carried out in two separate sites:

Massane Site 1 lay outside the boundaries of the Reserve along a sloping irregular track leading away from the entrance to the reserve. This track was unwooded, though there was a dense covering of shrub approximately 1m high. Massane Site 1 was censused on 19th, 24th, 25th and 26th of August 1988.

Massane Site 2 ran along the upper edge of the river valley on the north west facing margin of the Reserve. At the time of the visit, almost all ground level vegetation had died back, leaving only dried grasses with very few flowering plants and only occasional patches of flowering shrubs under the canopy edge. There was no established path running along this woodland edge, but landmarks could be used to approximately repeat the census route. Massane Site 2 was censused on 23rd and 27th August 1988.

5.2.2. Census Technique.

Simple visual scan surveys were used to assess the abundance of hoverflies and similarly sized flying insects. At both British sites, a single census consisted of a variable number of 15m walks. Airborne and resting flying insects within 2m either side of the census walk were recorded. Hoverfly frequencies were scored in terms of categories which described pattern type or appearance. For instance, a single category "Eristalis" would account for *Eristalis tenax* , *E. pertinax* and *E. arbustorum* , all of which have the same basic appearance and can be construed as honey-bee Mimics, but a further category would be required for another member of the same genus, *E. intricarius* , which more closely resembles bumblebees. As another example, the category "Syrphus" would include *Syrphus ribesii* , *S. torvus* and *S. vitripennis* since these species all share the same wasp-like pattern and are not rapidly discriminable in the field. Where new species or pattern types were encountered, a new category was created and an individual caught for identification.

The census method used at the British sites could not be precisely repeated at the French sites. It quickly became evident that hoverfly abundance was much lower in the Massane and that much more extensive surveys would be required to obtain a reliable estimate of relative species abundance. French censuses were therefore comprised of a series of individual walks, each timed at thirty minutes. The distance walked during each thirty minute-period varied slightly according to the amount of insect activity and the resulting workload in classifying, scoring and catching. Time and distance measurements taken on the first day of censusing at Massane Site 1 were compared with similar data from Bunny and Owston Woods. The calculated estimate of the length of the Massane Site 1 walk was 1365m, a figure which was consistent with measurements taken from maps of the area. Similar measurements at Massane Site 2 indicate that the walking speed did not differ from that at Site 1, and the nominal distance of 1365m was also adopted for this site.

5.2.3. Similarity Analyses.

The general procedure for *Simpack* image analysis is the same as that adopted in the previous demonstration chapter and outlined in Appendix One. There were some relatively minor deviations from this method, however. Specifically, images were captured directly from pinned samples rather than photographic enlargements, using a macro lens fitted to the video camera. This method was advantageous in that it eliminated the troublesome effect of photographic highspots and avoided some of the loss of definition caused by this method. However, it did result in much smaller images which meant that it was not possible to use the screen edge for consistent image alignment. Instead, two thin paper tapes were attached horizontally to the screen to define a more restricted frame of reference. Images of hoverfly abdominal patterns were aligned with respect to these paper strips such that the central horizontal axis of the restricted sampling area passed through the anterior-posterior axis of the abdomen and the cross hair of the image capture screen was located on the estimated centre of the pattern. Image size was adjusted so that the edges of the abdomen image just met the edges of the sampling strip defined by the paper tapes. Imperfections in image capture were corrected with the editor such that all background areas became filled white, with black areas of the pattern digitizing as black, and yellow or orange pattern features digitizing as yellow. The blocked file series was generated using the block dimensions adopted in the previous chapter.

5.3 Results.

5.3.1. Species-Pattern Categories.

Table 5.1 a-c describe the species-pattern categories used in the British and French surveys. Each category effectively describes a particular pattern or (where there is no distinct pattern) "appearance" type encountered during the censuses. The categories are defined either by a

Group	Category Name	Exemplar Species	UK		Fr	
			1	2	1	2
Hive Bees	Honey Bee	*Apis mellifera*	●	●	●	●
Syrphid Hive Bee Mimics	ETenax	*Eristalis tenax* *Eristalis pertinax* *Eristalis arbustorum*	●	●	●	●
Bumble Bees	Tawny	*Bombus pascuorum*	●	●	●	●
	TerrLuc	*Bombus lucorum* *Bombus terrestris*	●	●	●	●
	Other Bees	*Not known*			●	●
Syrphid Bumble Bee Mimics	Cheilosal	*Cheilosa illustrata*	●			
	VBomb	*Volucella bombylans*	●			
	Merodon	*Merodon equestris*		●		
	Criorhina	*Criorhina berberina*		●		
Small Solitary Wasps	SolWasp	*Ichneumon spp*	●			●
Syrphid Solitary Wasp Mimics	Xylota	*Xylota segnis*	●	●	●	●

Table 5.1 a Species Pattern Categories used during Visual Censuses of British and French Sites. (Uk 1 Refers to Bunny Wood, UK 2 to Owston, Fr 1 and 2 to Massane Sites 1 and 2).

Group	Category Name	Exemplar Species	UK		Fr	
			1	2	1	2
Large Social Wasps	Normal Wasp	*Vespula vulgaris* *Vespula germanica*	●		●	●
	LLWasp	*Polistes*			●	●
	Wasp7	*Ancistrocerus*			●	●
	FurryThor	*Not identified*			●	
	LongAbd	*Amblyteles*			●	
Syrphid Social Wasp Mimics	Episyrphus	*Episyrphus balteatus*	●	●	●	●
	PlatyYellow	*Platycheirus scutatus*	●	●		●
	Syrphus	*Syrphus ribesii* *Syrhus vitripennis*	●	●	●	●
	Epistrophe	*Epistrophe grossulariae*	●			
	Chrysotoxum	*Chrysotoxum bicinctum*		●	●	
	Helophilus	*Helophilus pendulus*	●	●		
	Scaeva	*Scaeva pyrastri*		●	●	
	Metasyrphus	*Metasyrphus corollae*	●		●	●
	Dasysyrphus	*Dasysyrphus venustus*	●	●	●	
	Myathropa	*Myathropa florea*			●	

Table 5.1 b Species Pattern Categories used during Visual Censuses of British and French Sites. (Uk 1 Refers to Bunny Wood, UK 2 to Owston, Fr 1 and 2 to Massane Sites 1 and 2).

Group	**Category Name**	**Exemplar Species**	**UK**		**Fr**	
			1	2	1	2
Syrphid Social Wasp Mimics (Cont.)	VBrightYell	*Xanthogramma*			●	●
Hornet Mimics ?	VZone	*Volucella zonaria* *Volucella inanis*			●	●
Non Mimetic Syrphids	Leucozona	*Leucozona glaucia*		●		
	Ferdinandea	*Ferdinandea cuprea*		●		
	Pellucens	*Volucella pellucens*	●	●		
	Rhingia	*Rhingia campestris*	●	●		
	Platycheirus Grey	*Platycheirus albimanus*	●	●	●	
	Blank Cheilosa	*Cheilosa variabilis*	●			
	Black Eristalis	*Eristalis sepulchralis*			●	●
	Dull Orange Band	*Xanthandrus comptus*			●	●

Table 5.1 c Species Pattern Categories used during Visual Censuses of British and French Sites. (Uk 1 Refers to Bunny Wood, UK 2 to Owston, Fr 1 and 2 to Massane Sites 1 and 2).

single species, or by a group of species which share a virtually identical pattern, for example where several members of a genus are effectively inseparable. An exemplar species is named in the Table for each category, though this is intended for reference purposes and is not necessarily the species encountered. A shaded circle is used to denote the presence of at least one category representative at the two British and two French sites. For clarity, and for the purposes of some later calculations, categories are further combined into a series of Groups. For example, "Honey Bees", "Honey Bee Mimics" and "Solitary Wasp" each represent different Groups of categories.

5.3.2. Is the absolute abundance of hoverflies greater in disturbed sites than in undisturbed sites ?

As mentioned in section 5.2.2., it was immediately obvious that the absolute abundance of hoverflies at both French sites was substantially lower than that observed on most occasions at the two British sites, hence the revised census technique.

Owston wood was censused eight times during August 1987, and a total of six censuses were carried out across both Massane sites during the same month of the following year. For each individual census, the total number of syrphids (ie syrphids in any category from Table 5.1) encountered was divided by the measured or estimated census distance, to yield an estimate of absolute abundance for all syrphid species. Similar calculations were repeated for all individuals falling into the syrphid social wasp mimic Group to separately estimate their absolute abundance. The eight pairs of estimates for Owston wood and the six pairs for the Massane Sites were then separately averaged to obtain estimates of the mean absolute abundances at each location. Corresponding means were calculated for the two censuses of Bunny wood in August 1988. All results are recorded in Table 5.2.

	Owston (n=8)	Bunny (n=2)	Massane (n=6)
All Syrphids mean individual/m ±se	1.34 (0.307)	0.424	0.056 (0.011)
Wasp Mimics mean individual/m ±se	1.21 (0.298)	0.352	0.024 (0.008)

Table 5.2 Mean (± s.e.) Absolute Abundances of all Hoverflies and Apparently Social Wasp-Mimicking Hoverflies at British and French Survey sites in August 1987/88.

The very clear differences in the mean values for the different sites could be construed as consistent with the hypothesis that British sites do contain a higher abundance of all syrphids, including apparently social wasp-mimicking syrphids as a result of some form of ecological disturbance. However, further attributes of the data indicate that it may be misleading to draw conclusions from surveys of hoverfly abundance performed over a short period. For instance, Figure 5.1 plots the eight pairs of estimates of absolute abundance used to produce the above means for Owston Wood.

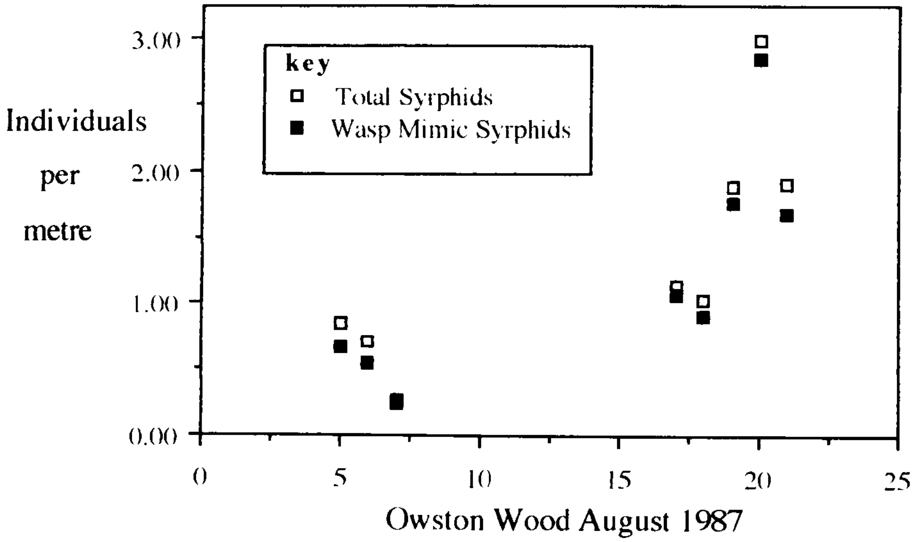


Figure 5.1 Absolute Abundance of all Hoverflies and Apparently Social Wasp-Mimicking Hoverflies in Eight Censuses of Owston Wood 1987.

This data emphasizes that local hoverfly abundances can undergo large and very rapid change, in this instance approaching a threefold increase within a single calendar month. It is probable that the size and timing of such peaks in abundance differ between sites and between years at the same site. This immediately attaches a qualification to any conclusions about the abundance of hoverflies in two locations if no data is available to demonstrate that the two populations have been compared at corresponding points in their seasonal fluctuation. In this case, these long term data are not available for the Massane, but data from Bunny Wood through the 1988 season indicate that the disparity in abundances between British and French sites may not be as great indicated in Table 5.2. Figure 5.2 depicts the change in absolute abundance of, again, all syrphids and of apparently wasp-mimicking syrphids. The results for all censuses in the same month, between May and September 1988, have been averaged.

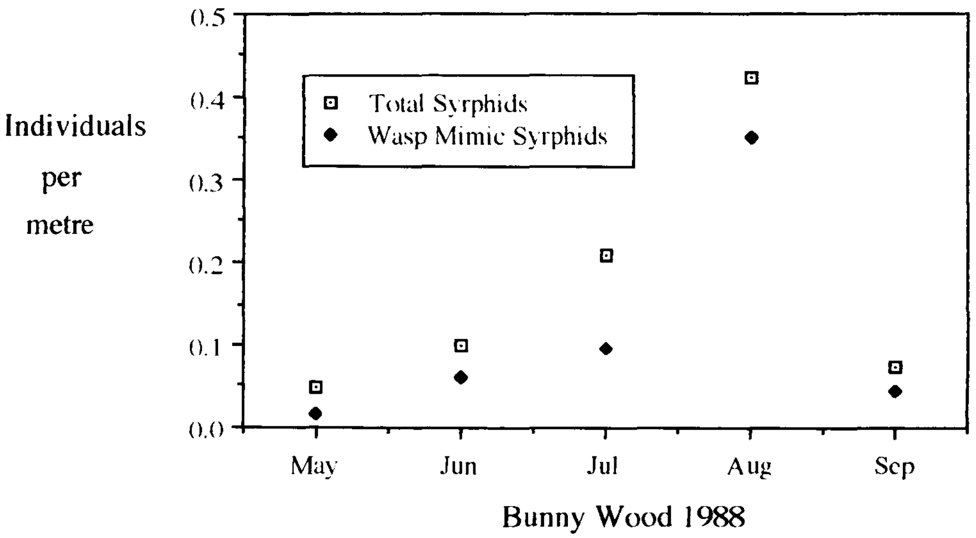


Figure 5.2 Mean Monthly Abundances of all Hoverflies and Wasp-Mimicking Hoverflies at Bunny Wood between May and September 1988.

This Figure demonstrates that the absolute abundances at the Massane sites, of all syrphids and of the wasp mimicking subset, are not dissimilar from those encountered at either side of the late summer peak in Bunny Wood in 1988. Alternatively, the Massane populations may show a bimodal distribution in abundance, thus avoiding the summer drought, and the community may have been censused just at the beginning of the second peak.

The implication is clearly that the Massane site may have been sampled at a point when the mean values for abundance may not be representative of those which can occur at these sites at other times.

Consequently, while the mean results described in Table 5.2 above may transpire to be an indication that there are significant and consistent differences between disturbed and undisturbed sites, such a conclusion cannot be reliably drawn from the data available here.

5.3.3 Do hoverflies represent a greater proportion of flying insects in disturbed sites ?

In addition those defined in Table 5.1, a further category named "Other Flies" was maintained for the purpose of recording the availability of apparently palatable, innocuous, inconspicuous, non-syrphid (but of the same approximate range of sizes) flying insects, primarily diptera. The category notionally corresponds to the "palatable alternatives" known to be a key determinant of the effectiveness of mimicry. Table 5.3 records the number of insects scored in this category relative to the total number of hoverflies and to the number of apparent social wasp Mimics at Bunny Wood and Massane Sites.

	Bunny Wood			Massane Forest		
Estimate	Date	Syr:OF	Mim:OF	Date	Syr:OF	Mim:OF
1	14.5.88	0.25	0.08	19.8.88	1.60	0.86 [1]
2	07.6.88	0.20	0.05	24.8.88	1.38	0.82
3	07.6.88	0.33	0.09	25.8.88	0.64	0.24
4	12.6.88	0.50	0.14	26.8.88	1.18	0.58
5	14.6.88	0.74	0.16			
6	21.6.88	0.69	0.01	23.8.88	0.78	0.25 [2]
7	14.7.88	0.78	0.44	27.8.88	1.31	0.21
8	21.7.88	2.74	1.13			
9	02.8.88	3.00	2.73			
10	06.8.88	2.89	1.89			
11	09.9.88	0.71	0.43			
Mean		1.16	0.65		1.148	0.493
s.e.		0.34	0.27		0.15	0.12

Table 5.3 Estimates of the Ratio of All Hoverflies (Syr:OF) and Apparently Wasp-Mimicking Hoverflies (Mim:OF) to the Number of Individuals in the "Other Flies" category at Bunny Wood and Massane (1 and 2 denote Massane Sites 1 and 2 estimates).

The data indicate that the ratios of Total Syrphids to other flies and of Wasp Mimic Syrphids to other flies are not significantly different (Syr:OF Two-Tailed U=22.5, p>0.05, Mim:OF Two Tailed U=24, p>0.05) This is consistent with the suggestion that hoverfly abundance is not different in disturbed and undisturbed sites, relative to the number of apparently palatable alternative flying insects.

5.3.4. Are supposedly mimetic hoverflies more common in disturbed sites, relative to their putative Models ?

5.3.4.1. Wasps and Wasp Mimics.

The data from some censuses of British sites are such that it is impossible to calculate an informative Model:Mimic ratio. The eight censuses of Owston Wood in August 1987 recorded in excess of 2600 potential social wasp Mimics, but not a single wasp.

The surveys of Bunny Wood during summer 1988 produce only slightly less extreme results; social wasp Mimics were present in all eleven censuses, but social wasps in only four. Within these four, the most extreme Model:Mimic ratio was recorded on 2.8.88, which falls within the late summer peak of abundance and scores a ratio of 1:28. The other three values outside this peak give a mean ratio of 1:2.88. Taking into account all census results, including those within the late summer peak and the censuses where social wasps were not recorded, gives an overall mean ratio of 1:19.3. The results from the Massane indicate a more balanced ratio. Summing across all cenuses at both Massane sites gives a mean Model:Mimic ratio of 1:1.94. On this basis the Model-Mimic ratio for the wasp sub-complex is significantly different British and French sites (Two-tailed U=4, p<0.01)

5.3.4.2. Hive Bees and Hive Bee Mimics.

Census data from Bunny Wood during summer 1988 suggest that apparent honey bee Mimics do not exhibit the extreme fluctuations in numbers evident in the apparent social wasp Mimics. However, the bias in Model:Mimic ratio is almost as extreme, with only two bees being recorded in 11 censuses, against 39 apparent Eristaline Mimics (ratio 1:19.5). The 8 August surveys at Owston in 1987 recorded only a single bee versus 124 apparent Mimics. Again the Massane data indicate a less extreme ratio; both bees and their apparent Mimics were present in all surveys at both sites and summing all totals yields a mean ratio of 1:4.46.

Again using the broader base provided by the 11 Bunny Wood censuses, the Model-Mimic ratios for Honeybees and their Mimics are significantly lower in the British sites (Two-Tailed U=2, $p<0.01$) than in the six surveys of the Massane.

5.3.4.3. Bumble Bees and their Mimics.

The bumblebees and their Mimics occur at frequencies more in accord with conventional expectations about the structure of mimetic systems. Combining all categories of bumblebee and bumblebee Mimic, and summing the results for all 11 Bunny Wood surveys gives a Model:Mimic ratio of 1.7:1. Similarly, summing all Owston surveys produces a ratio of 14.6:1.

No informative Model:Mimic ratio for bumblebees and their Mimics can be calculated for the undisturbed sites; no appropriate Mimics were recorded at the Massane.

All of the Model:Mimic ratios observed here are consistent with the hypothesis that ecological disturbance may have caused a decrease in the number of Models relative to their putative Mimics.

5.3.5. In terms of relative abundance and Model-Mimic similarity, is the hoverfly community signficantly different in disturbed and undisturbed sites ?

Three factors complicate the analysis of actual similarity in the two locations. Due to an oversight, similarity estimates were not obtained for four Model-Mimic combinations. This does not substantially compromise the results presented here because three of the four species concerned represent only very low frequency component of the British and French communities. In the fourth case, *Episyrphus balteatus* , actually the most common species, estimates are obtainable elsewhere. Parker (1991) has used *Simpack* in another context and reports an *Episyrphus-Vespula* similarity of 15.1±3%.

This difficulty is somewhat compounded by what the other similarity ratings indicate about the structure of the French community. Table 5.4 records similarity ratings for 7 Mimic and 3 Model categories censused at Massane Site 1.

	Models		
Mimic	Vespula vulgaris	Polistes	Amblyteles
Xanthogramma	70.6	73.4	70.4
Scaeva	62.3	68.3	76.5
Platycheirus	60.7	66.4	71.3
Myathropa	65.4	71.5	67.8
Syrphus	62.3	60.1	59.1
Chrysotoxum	70.7	69.0	67.8
Metasyrphus	69.1	77.8	72.1
Mean	65.87	69.5	69.28

Table 5.4 Similarity ratings for representatives of three Model categories and seven Mimic categories recorded at the Massane. (See Table 5.1 parts a-c for category and species names.)

If, for each Model species, the mean similarity across all 7 Mimic categories is calculated, as shown at the bottom of Table 5.4, the result indicates that on average, apparent Mimics are more similar to the social wasp *Polistes* than to the species which is the supposed Model in British communities, *Vespula vulgaris* . That *Polistes* is also the most common hymenopteran in the Massane indicates that in this locality, *Polistes* acts as the primary Model. It seems biologically more appropriate to compare the structure of the British and French communities on the basis of the most probable Model in each case.

That the similarity data has emphasized that there may be different Model species for the same basic group of Mimics is interesting in its own right.

It might also suggest that Mimic patterns represent a "compromise" which optimizes mimetic protection through a simultaneous resemblance to more than one Model. It does, however, present another small problem in that no substitute similarity estimate is available for the *Episyrphus* - *Polistes* pairing. However, such a measurement is estimable from the data in Table 5.4. On average, the estimates for Mimic-*Polistes* similarity are some 5% higher than the corresponding Mimic-*V. vulgaris* estimate. A calculated estimate of some 20% is therefore adopted for *Episyrphus* - *Polistes* and the structure of the French community is assessed with respect to *Polistes* , while British communities are described in terms of similarity to *V. vulgaris* .

The total number of individuals in each of the Social Wasp Mimic categories was summed over four Massane Site 1 surveys; each category total was then expressed as a percentage of the total Social Wasp Mimic community. These percentages were then plotted against the similarity estimate for each category to obtain the "Similarity Profile" shown in Figure 5.3 below.

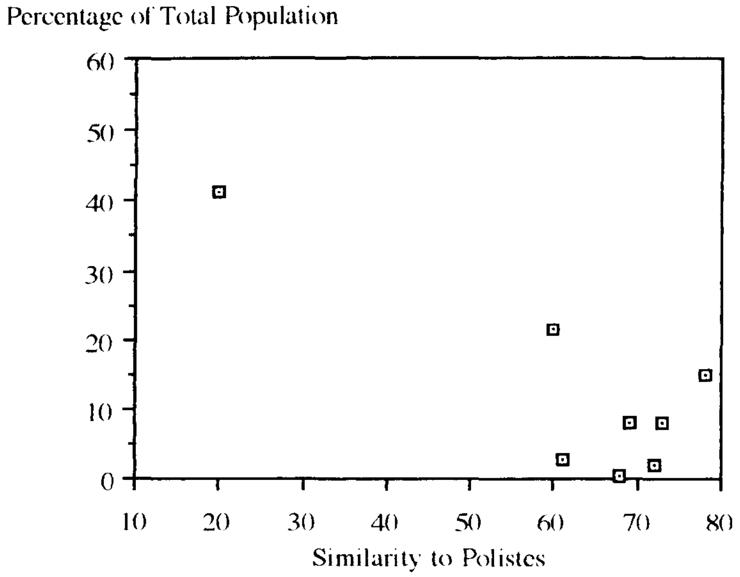


Figure 5.3 Mimic Frequency versus Mimic Similarity to the putative Model *Polistes* averaged over four surveys of Massane Site 1.

As previously mentioned, similarity estimates were not obtained for some low frequency categories in the community (eg *Dasysyrphus*) and these are not represented on the profile. Nevertheless, the profiles do describe 98.5% of the total Social Wasp-Mimic population censused.

For comparison, a corresponding calculation was made for three randomly selected surveys of Owston Wood in 1987. The resulting similarity profile is depicted in Figure 5.4. Again similarity estimates for some low frequency categories (eg *Helophilus*) were not obtained; the profile does, however, describe all but 1.07% of the total Social Wasp Mimic population.

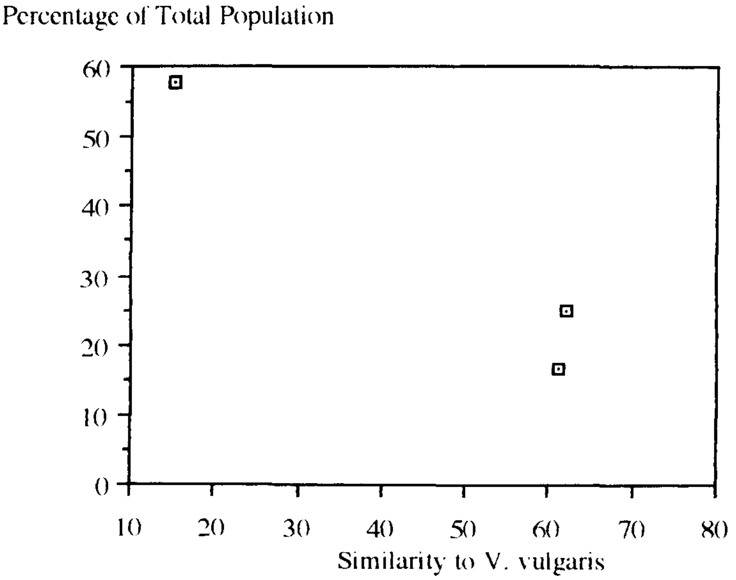


Figure 5.4 Mimic Frequency versus Mimic Similarity to the putative Model *V. vulgaris* averaged over three days in Owston Wood 1988.

The Disturbed Ecology hypothesis proposes that the apparent paradox of mimicry in the hoverflies is a product of an increase in the number of "poor" Mimics, relative to their more accomplished counterparts, caused by large-scale ecological activity. The contrast in these two profiles provides only partial support for this hypothesis. Relative to the supposed undisturbed site at the Massane, the British sites do lack Mimic species which score *actual* similarity ratings in excess of 65%. This may indeed transpire to be indicative of the loss of "good" Mimic species at disturbed sites, though the issue is, as will be discussed shortly, complicated by the possible non-equivalence of actual and perceived similarity. It is, however, equally clear that both communities are numerically dominated by a species with a low similarity value. Although no conclusive judgement can be drawn from the above data, the suggestion is that while agricultural activity may have perturbed the composition of "natural" hoverfly communities, such a perturbation will have exaggerated, not created, the paradox of apparent mimicry in the hoverflies.

5.4. Discussion.

5.4.1. Bumblebee Mimics.

Before proceeding with the discussion of the primary concerns of this chapter, the testing of the Disturbed Ecology hypothesis and the use of similarity profiles to describe community structure, the opportunity will be taken to record some observations about Syrphids which mimic bumblebees.

The remainder of this thesis will omit any further consideration of species such as *Merodon equestris* and *Volucella bombylans* , which appear to be accomplished bumblebee mimics. The reason for this exclusion is primarily that these Mimics are markedly less abundant than their apparently wasp-mimicking counterparts, as is indicated in the above data. There are also some minor problems in performing image analysis on these species; often they depend on body hair coloration rather than cuticular colour for their resemblance to bumblebees. In some test image captures using pinned specimens, the heavy artificial side-lighting did not reveal the patterns visible in natural outdoor light. When image analyses are carried out on these species, it will be necessary to first obtain good quality photographs in lighting which does not obscure the patterning created by the hair colours.

In the field, the impression is that these species represent a significant contrast to the apparent wasp Mimics. Generally, the quality of mimicry is much higher in bumblebee Mimics, their identification often requiring more than the cursory glance that is usually sufficient to discriminate between the apparent wasp Mimics and their Models. In addition, there are a number of specific adaptations in some species. *Volucella bombylans* , for example, occurs in more than one colour form; the typical form closely resembles the white-tailed bumblebees, such as *Bombus terrestris* , while the variety *plumata* is thought to Mimic red-tailed bees (eg *Bombus lapidarus*); Gabritchevsky (1924) suggests that the most dominant mimetic colour form varies across Europe according to which bumblebee is most common. Conn (1972) describes a similar pattern of colour form variation in *Merodon equestris* .

Overall, the suggestion is of a mimetic system more closely constrained than the putative wasp-centred complex, and one that is more in accord with conventional expectations about the structure of mimicry complexes. The Model:Mimic ratio calculated here certainly re-inforces this impression since, in contrast to the apparent wasp system, the Mimics do not vastly outnumber their Models.

The census data presented above does provide one intriguing, if scant, indication that bumblebee mimicry is indeed more constrained. Combining all bumblebee and bumblebee Mimics, Figure 5.5 depicts the number of Models and Mimics encountered on each census of Bunny Wood in summer 1988.

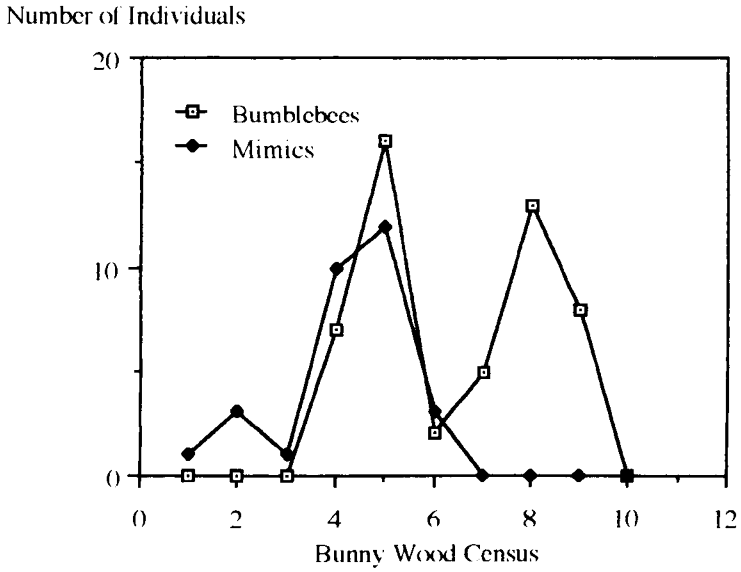


Figure 5.5 Temporal Synchrony between Bumblebees and Syrphid Bumblebee Mimics ? (See Table 5.3 for census dates, note that data for two censuses on the same day in June have been combined.)

There is an obvious suggestion of synchrony between emerging bumblebee and bumblebee Mimic species, a pattern which is in accord with mimicry theory and one which is certainly deserving of further attention.

5.4.2. Changes in Hoverfly Abundance.

Figure 5.1 above clearly indicates rapid and short-term changes in hoverfly abundance. The available data do not permit a conclusive demonstration that the British and French sites were sampled at corresponding points in their respective seasonal cycles, and this must attach a general qualification to any conclusions drawn in this chapter. It may further suggest that future assessments of abundance and community structure should be undertaken with survey methods such as Malaise trapping which make it easier to assess long term trends. However, such fluctuations should *not* be regarded as a troublesome confounding factor. If we are to suggest that effective mimicry is commonplace among the hoverflies, such changes in abundance must be reconciled with, and understood in the context of, the predictions of mimicry theory.

5.4.3. Similarity Profiles.

5.4.3.1 The Success of Similarity Profiles.

In themselves, the similarity profiles presented in Figures 5.3 and 5.4, represent the fulfilment of a central aim of this chapter, and indeed this thesis. Were this chapter to achieve nothing more than to produce these profiles, it would still have demonstrated the potential of *Simpack* to contribute to our understanding of mimicry by illustrating that it is possible to describe the actual Model-Mimic similarities in a natural mimicry complex, and that it provides a description of community structure which is independent of species identities.

From this perspective, the unfortunate failure to obtain some estimates of similarity is not particularly significant, and, despite the minor difficulties this presents, the resulting profiles are revealing about mimicry complex structure and the role of actual similarity in mimicry.

5.4.3.1. A Partial Basis for the Apparent Paradox.

Even if the substituted and derived values for *Episyrphus* similarities represent a substantial under-estimate, it is clear that the distribution of objective similarity corresponds to the subjective, and paradoxical, assessment of mimetic quality in the hoverflies. Both hoverfly communities are numerically dominated by a species with a low objective similarity to the apparent Model, while in the French community at least, *Chrysotoxum* , usually considered to be an accomplished Mimic, registers a high similarity rating, but occurs only at a low frequency. Broadly then, these results suggest that there is an objective basis to the apparent paradox of mimicry in the hoverflies and that, therefore, there is a general, positive correlation between actual, objective similarity and perceived similarity.

5.4.3.2. Actual and Perceived Similarity.

Other aspects of the results, however, suggest that if there is a broad correlation between actual and perceived similarity, there must in individual cases be substantial deviations from this relationship. While it is true that an apparently accomplished Mimic such as *Chrysotoxum* has registered a high actual similarity score relative to an apparently mediocre Mimic such as *Syrphus* , it is also the case that some other apparently unremarkable Mimics such as *Metasyrphus* , also achieve a high similarity score. This indicates that there are at least some instances where actual similarity predicts perceived similarity only very poorly. These contradictory suggestions are inconclusive, but nonetheless intriguing in what they may indicate about the relationship between actual and perceived similarity, and mimetic status. If there is a consistent positive correlation between actual and perceived similarity, and if the perceptual systems of human observers and natural predators operate in a broadly similar fashion, the apparent paradox of mimicry in the hoverflies would be evident to natural predators, and still therefore requirs reconciliation with current mimicry theory. If there is not an even vaguely linear relationship between actual and perceived similarity, what *is* the nature of the relationship ? How can it be that a species with a high similarity score is not perceived as being similar to a Model ? What is it, for instance, about the structure of *Metasyrphus* patterns which makes them "fail" to be perceived by observers as similar to wasps despite a high actual actual similarity rating ? It is not possible to resolve these intriguing questions here, but the implication is that there can be some particular structural pattern attribute which determines perceived similarity. This suggestion that some Mimics could in some sense be "exploiting" idiosyncracies of predator perceptual and cognitive systems is an underlying theme of this thesis; reference is repeatedly made to "mechanisms" (which may be enhanced by Mimic behaviour) which transform actual similarity into a quite different degree of perceived similarity. The final corollary of this suggestion is that if different perceptual systems operate under different constraints, the paradox which is apparent to human observers may not be apparent to the biologically relevant predators: Mimics which are "poor" to our eyes may be entirely capable of perpetrating successful mimicry in presence of natural predators.

5.4.3.3. The Effect of Size Correction.

It is important to re-iterate that the similarity profiles presented in Figures 5.3 and 5.4, are independent of size; initial image capture is such that, as far as body shape allows, all pattern images fill the same samplin space. There is therefore a more trivial sense in which these profiles do not necessarily directly indicate mimetic status. One high-similarity component of the Massane community is *Myathropa florea* , a species which is significantly larger than the putative Model. Were these results to be size corrected, so that the final similarity rating was adjusted to reflect any disparity in Model-Mimic body size, *Myathropa* would certainly slip down the similarity scale. However, the most significant species (*Syrphus* , *Metasyrphus* , *Chrysotoxum* and *Xanthogramma*) are all much the same size; size correction of the above profiles would probably not significantly alter the similarity relationships these species exhibit, nor therefore, undermine the discussion about the relationships between actual and perceived similarity.

5.4.4 Practical Constraints.

The estimates for *Episyrphus* similarity are substantially lower than those for other species. This is actually in accord with subjective expectation; *Episyrphus* is perhaps the most implausible of wasp Mimics. There is, however, reason to believe that the disparity between the *Episyrphus* estimates and all others, has been exaggerated. Unlike the test images in the previous chapter, the images used here were obtained from pinned samples, resulting in relatively smaller images. The use of smaller images reduces the total number of match scores which can be registered when comparing any Mimic pattern with the Model. In turn, this will compress the *range* of similarity estimates which describe all Mimic patterns. It is not clear if, or how, this compression effect can also shift the similarity estimates relative to those obtained with full screen images, as is the case with the substituted *Episyrphus* estimate used here. It is impossible to estimate such an effect without further experimentation, but it is unlikely to disrupt the general distribution of similarity values observed here; *Episyrphus* also registered the lowest similarity score recorded by Parker (1991) in an analysis of four hoverfly species. In addition, many of the most interesting issues raised by the use of these profiles, for example the possible contrast between actual and perceived similarity, rely on the *relative* similarity values of species such as *Chrysotoxum* , *Syrphus* and *Metasyrphus* , rather than the disparity between these species and *Episyrphus* .

5.4.5 The Disturbed Ecology Hypothesis.

If one assumes that the British sites are relatively less disturbed than their French equivalents, what do these results indicate about the adequacy of the Disturbed Ecology hypothesis as an explanation for the paradox of mimicry in the hoverflies ?

The data on absolute abundances are not conclusive. The absolute abundance in the undisturbed site may be lower, but this may be attributable to the time of sampling. On average, the abundance of hoverflies relative to other flying insects is not different in disturbed and undisturbed sites. These two conclusions indicate that ecological disturbance does not affect syrphid community structure.

Other aspects of the data contradict this conclusion. The similarity profiles indicate that some species with a high actual similarity to the putative Model are largely absent from disturbed sites. This pattern of change is certainly in accordance with Bankowska's (1984) overall conclusion that ecological disturbance reduces the species diversity of hoverfly communities, and enhances the numerical dominance of the most common species. The discussion of the possible non-linearity of the relationship between actual and perceived similarity should make it obvious, however, that it is not clear how a reduced diversity and increased dominance of common species will affect the perceived distribution of mimetic quality.

The most obvious difference in the complex structure in undisturbed and disturbed sites is a much lower abundance of the supposed Models in the latter. While it is possible that ecological disturbance may have accentuated the apparent paradox of mimicry in the hoverflies, it seems unlikely that it alone can explain it. The most significant effect of ecological disturbance on the success of mimicry in the hoverflies may be mediated through Model rather than Mimic abdundances.

5.5 Conclusion.

The work reported in this chapter has revealed some indication that large-scale ecological disturbances may have affected the wasp-based component of the apparently mimetic hoverfly community. While the abundance of hoverflies, in absolute terms and relative to other flies, is similar in the supposed undisturbed and disturbed sites, there is a suggestion of a decline in the abundance of Models in the latter. The use of similarity profiles suggests that disturbed British sites may have seen a reduction in the abundance of relatively rare species with high actual similarities to the apparent Model of the complex.

In addition, those profiles have revealed that there is an objective basis for the apparent paradox of mimicry in the hoverflies and provided the first, intriguing indication that there is not a simple relationship between actual and perceived similarity.

There are some unfortunate practical constraints to these conclusions, but this is only to be expected in the first experimental application of a new technique. The real purpose and success of this chapter has been to demonstrate that *Simpack* provides a totally unique method of comparing different examples of the same mimetic complex.

Acknowledgements

This Chapter is dedicated to M. J.Trave of the Laboratoire Arago, Banyuls-sur-mer, France, who provided a great deal of assistance during the work in the Foret de Massane, and who has dedicated much of his personal time and effort to protecting the Reserve. Particular thanks are extended to him, his wife and family for their memorable hospitality. The visit to the Massane was supported by a University of Nottingham Carr scholarship.

Chapter Six

Simpack Between-Complex Analyses.

6.1 Introduction.

In the previous chapter, *Simpack* was used to compare different examples of the same putative mimicry complex. It was possible to perform such an analysis because the objective measurement of similarity permitted all hoverfly abdominal patterns to be compared on a common basis, so that the "similarity profile" of each hoverfly community was independent of the constituent species. There is another obvious potential advantage of this species independence - it may permit wholly different mimicry complexes to be subjected to direct comparison. This facility would open up the phenomenon of mimicry to a previously impossible form of comparative analysis. Such analyses would certainly contribute to our understanding of mimicry by revealing broad trends and differences in objective similarity across many examples of the phenomenon. A thorough and comprehensive comparative analysis of similarity is a substantial task in its own right, one which is not undertaken here. A single comparison between the hoverfly complex and another example of mimicry will be sufficient to demonstrate the validity of the method and should provide further information on the mimetic status of the syrphids.

Which single between-complex comparison would be the most fruitful ? In Chapter One, it was argued that the close resemblance between the abdominal and thoracic patterns of some hymenopteran and syrphid species, and the presence of some very specialized morphological and behavioural adaptations in the latter, indicated that conventional Batesian mimicry must account for the appearance of at least some hoverflies. The purpose of this thesis became to determine whether, and at what point, Batesian mimicry ceased to become tenable as an explanation of the coloration in a range of hoverfly species. Given this intention, an obvious strategy is simply to compare the degree of Model-Mimic similarity in a series of hoverflies with that in a more widely accepted, less ambiguous example of visual Batesian Mimicry.

6.1.1. Selecting an Appropriate Comparison.

In seeking such a comparison with the hoverflies, there can be no more obvious candidate than the Viceroy butterfly, *Limenitis archippus* and its Model, the Monarch butterfly, *Danaus plexippus* . The Monarch has been the subject of systematic research for in excess of thirty years, so that it must now represent the most thoroughly researched example of an "aposematic basis for mimicry" (Brower 1988). It is well known that individuals in many Monarch populations sequester substantial quantities of cardenolides (cardiac glycosides) from their larval food plant, the Milkweed (*Asclepias* spp.) (Brower and McEvoy 1972). The presence of this substance renders the butterfly distasteful and emetic to a number of natural predators (Brower 1958, Brower *et al* 1968 and

Brower 1988). This sequestration process appears to represent part of a specific anti-predator strategy. Rothschild *et al* (1984), for example, report the presence of further substances, pyrazines, which might provide predators with scent cues to the presence of cardenolides prior to any physical contact, indicating that cardenolides represent one tier of a well adapted defensive mechanism. It is for this reason that patterns of cardenolide incidence in the larval food plant, the adult Monarch population and even within individual Monarchs, are often interpreted in terms of their significance for the foraging behaviour of predators (Brower 1988). Brower and Glazier (1975) report significant variation in the concentration of cardenolides between different body parts of Monarch individuals and suggest that this distribution is an adaptation which maximizes the long term impact of the predator's initial taste or emetic reaction to an encounter with a Monarch. Similarly, Brower *et al* (1968) (see also Brower and McEvoy 1972, and Malcolm *et al* 1989) propose that variation in cardenolide concentration in the food plant creates a spectrum of palatability in the adult Monarch population, a concept which has received much subsequent attention in the context of predator foraging strategies.

The potential intricacy of this defensive mechanism is made only more intriguing by the presence of the apparently mimetic Viceroy butterfly. The early indications that captive predators which had not experienced Monarchs were more likely to consume Viceroy butterfiles than those that had (Brower 1958), have meant that the Monarch-Viceroy system has come to be accepted as the definitive example of visual Batesian mimicry (Vane-Wright 1991). The recent report by Ritland and Brower

(1991) that the Viceroys from a representative Florida population were actually as unpalatable to some predators as their supposed Batesian Models therefore has a signficance not merely for those concerned with the status of the Monarch-Viceroy system. In re-assessing this complex as essentially Mullerian, Ritland and Brower have deprived mimicry theory of its classically cited instance of Batesian mimicry. The impact of this revision is such that there are now some suggestions that Batesian mimicry represents an idealised mechanism only rarely approached in nature (Vane-Wright 1991). This may be an early indication of a more general re-assessment of current theory and past data, as researchers examine the implication that only rarely can the fundamental simplicity of the Batesian mechanism be expected or assumed.

What is apparent from this revised status of the Viceroy is that the original aim of this Chapter, that of comparing Model-Mimic similarity in the hoverfly -wasp complex with that in a less ambiguous example of Batesian mimicry, cannot now be fulfiled with a comparison to the Monarch system. At this preliminary stage in the history of between-complex analyses, this is not catastrophic; given the novelty of the method, almost any between-complex comparison of similarity is likely to be fruitful. In Chapter One, for example, there was some suggestion that the hoverfly complex is also essentially a Mullerian system, so that in comparing it to the Monarch system we are comparing two products of the same selective process. Alternatively, if the hoverfly complex is regarded as essentially Batesian, the comparison is between the two most significant forms of mimicry.

6.1.2. Model-Mimic Resemblance in Batesian and Mullerian Systems.

The literature contains apparently well-founded predictions about the degree of Model-Mimic resemblance in Batesian and Mullerian systems. It is widely accepted that the pattern of costs and benefits to the parties in the two mimetic relationships are fundamentally different (Owen and Owen 1984). In classical Batesian systems, the Mimic enjoys a reduced risk of predation at the expense of both the predator and the Model; predators obviously lose potential palatable prey as a result of the deception, while Models suffer a higher rate of predation than they otherwise would as the Mimic disrupts the establishment and maintenance of the predator's learned avoidance of the Model pattern.

In contrast, in Mullerian systems, all parties appear to benefit from the interaction; predators are able to efficiently reject a range of unpalatable prey items through learning and generalizing from the pattern of a single co-mimic species, which in consequence effectively spreads the predation load across all species and individuals in the complex. This dissimilar pattern of costs and benefits is reproduced in a number of mathematical models of mimicry systems (Owen and Owen 1984, Huheey 1976, Turner *et al* 1984) and is likely to be manifested in differences in the degree of Model-Mimic resemblance in the two types of system. In classical Batesian systems there is a clear selective advantage to predators with enhanced perceptual and cognitive systems which enable them to discriminate between Models and Mimics on at least some occasions. In response, Batesian Mimics are likely to evolve enhanced resemblance to their Models in order to mitigate this heightened risk of predation. In Mullerian systems, however, there will usually be no selective advantage to predators in discriminating between the species specific variations of the basic Mullerian pattern and, consequently, a limit to the selection pressure on co-mimics to converge on a common pattern. This prediction that the Model-Mimic resemblance will be lower in Mullerian than in Batesian systems now represents an established aspect of mimicry theory (Huheey 1988).

This chapter will continue to compare Model-Mimic similarity in the hoverfly-wasp complex with that in the Monarch-Viceroy system, but with the revised aim of determining what the comparison with a Mullerian system might imply about the status of apparently mimetic hoverflies. The estimates of hoverfly-wasp similarity gained in the previous chapter will be used as a basis for this comparison.

6.2 Method.

Five preserved *D. plexippus* and five *L. archippus* individuals were obtained from a collection[1]. Each pinned sample was photographed against a white foam background using a 35mm print film, from a fixed distance using a 50 mm standard lens and extension tubes. Subjects were lit with a microscope cold light source. The digitized images of the ten resulting standard prints were obtained using *Simpack* 's image capture program. Framing criteria were adopted in order to standardize these images; the vertical cross hair of the image capture screen passed through

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[1] Royal Museum of Scotland Collection. Particular thanks to Dr. G. E Rotheray for his assistance.

the anterior-posterior axis of the thorax and abdomen and the image was captured from a distance such that the wings exactly filled the vertical axis of the screen.

These images were edited to remove lighting high spots and redefine poorly captured pattern and edge features. Monarch and Viceroy patterns are obviously similar, consisting of dark brown wing borders, forewing tips and venation. Between veins the colour is a bright orange-brown, while the wing borders are punctuated with white spots, particularly on the forewing tips. The digitizing process rendered the wing borders and other dark brown features black, the background digitized as white, orange wing areas digitized red and the white spots were manually filled with yellow to distinguish them from the background. The antennae, head and abdomen were edited out of all images since they represented trivial chance variation between images which could obscure the result.

Primary data files were generated from each of the ten images and stored on disc. From each Primary file a blocked file series was generated according to the Master List of dimensions adopted in previous chapters. These files series were then analysed to yield a mean match rate within the *D. plexippus* (Model) pattern type and then between Model and Mimic (*L. archippus*) pattern types. The matching program used to calculate match rates was modified to accommodate three significant colours, black, red and yellow; this is in contrast with the previous analyses of hoverfly patterns which consist of just two significant pattern colours, black and yellow. When dealing with these patterns, red and yellow pixels were previously treated as the same logical colour, the modification permitted them to register as different logical colours. The inclusion of this additional colour does not affect the method of the analysis. The following comparison will employ data on Hoverfly-Wasp similarities obtained as part of the previous chapter; reference should be made to that chapter for details of the image capture and editing procedures adopted.

6.3 Results.

The mean Model-Model and Model-Mimic match rates are tabulated in Table 6.1 below.

		Monarch vs. Monarch		**Viceroy vs. Monarch**	
Level	Blocks	Match Score *(n=10)*	se	Match Score *(n=25)*	se
Primary	81920	24722.5	742.27	22483.7	969.10
1	5120	1595.6	48.60	1495.4	33.22
2	3264	1003.8	35.46	938.8	21.95
3	1280	431.9	15.19	393.1	9.15
4	800	268.1	11.73	237.5	7.87
5	320	70.7	4.13	54.5	1.51
6	180	48.6	2.77	37.0	1.91
7	80	24.2	1.45	24.1	0.73
8	42	16.4	0.97	15.2	0.5
9	20	7.8	0.47	6.6	0.23

Table 6.1 Monarch-Monarch and Monarch-Viceroy match rates versus *Simpack* Master List Level.

Adopting an identical method of analysis to that used in Chapters Four and Five, Model and Mimic mean match rates are regressed on Block numbers and an index of similarity calculated, as shown in Table 6.2.

	Co-efficient of Regression	Difference from Model Regression	Index of Similarity	% Similarity
Monarch	0.302	0.000	1.000	100%
Viceroy	0.274	0.028	0.972	97.2%

Table 6.2 Regression co-efficients and calculated index of similarity for Monarch and Viceroy butterflies.

Figure 6.1 below depicts these regressions, excluding data on the Primary level of the Master List in the interests of clarity, though these data were used in calculating the regressions.

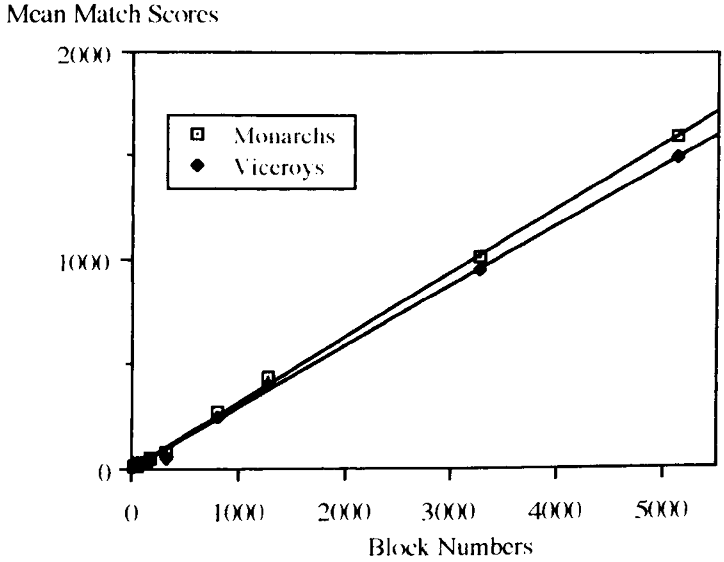


Figure 6.1. Monarch-Monarch and Monarch-Viceroy Mean Match Rate Regressed on Block Numbers.

Using the analysis of covariance outlined in Snedecor and Cochran (1972), there is no significant difference in residual variance about these regressions (F8,8=2.172, p>0.05), but the slopes do differ significantly (F1,16=2221.86, 0.05>p>0.01). The ratio of the two slopes is 0.274/0.302, yielding a *Simpack* similarity rating of 97.2%.

For comparison, Table 6.3 reproduces the estimates of Model-Mimic similarity obtained in the previous chapter for a series of hoverfly and wasp species.

	Models		
Mimic	Vespula vulgaris	Polistes	Amblyteles
Xanthogramma	70.6	73.4	70.4
Scaeva	62.3	68.3	76.5
Platycheirus	60.7	66.4	71.3
Myathropa	65.4	71.5	67.8
Syrphus	62.3	60.1	59.1
Chrysotoxum	70.7	69.0	67.8
Metasyrphus	69.1	77.8	72.1
Mean	65.87	69.5	69.28

Table 6.3 Estimates of Model-Mimic similarity in a French hoverfly community.

The estimates of Model-Mimic similarity in the hoverfly community range between 60% and 80%, substantially below the estimate obtained for the Monarch-Viceroy system.

6.4 Discussion

The preceding analysis provides a clear indication that the degree of Model-Mimic similarity is substantially lower in the studied example of the hoverfly-wasp complex than in the Viceroy-Monarch pairing; two aspects of this analysis warrant further discussion. Careful consideration of this single cross-complex analysis reveals some pre-requisites for a valid, more extensive comparative analysis of similarity, and suggests some constraints in interpreting comparative data. Secondly, the direction of the obvious disparity in similarity values between the two systems is apparently not consistent with the theoretical prediction that the degree of Model-Mimic resemblance will be lower in Mullerian than in Batesian systems. The following sections address these two issues.

6.4.1. Constraints on *Simpack* Cross-Complex Analyses.

The particular constraints and qualifications to the use of *Simpack* in the comparative context are inherent in the fundamentals of its method. As such, they apply equally well in principle to within-complex analyses of the kind demonstrated in the previous chapter, and might legitimately have been dealt with earlier. However, for all practical purposes they are more likely to be encountered in cross-complex analyses, or are more easily discussed with reference to the patterns involved in this particular comparison, and it is for this reason that they are discussed here.

6.4.1.1. Image Complexity.

Chapter Five reported that the initial images of the French hoverfly abdomens were obtained directly from pinned specimens rather than from the photographic enlargement method described in the tests of the *Simpack* system. This resulted in unfortunately small images which, as discussed in the previous chapter, probably has the effect of compressing the range of values which described the hoverfly species analysed. Detailed comparison of the image size and match rate data for the hoverflies and butterflies illustrates that there is a further property of images which determines absolute rates of matching. Image size is calculable from *Simpack* 's match scoring module output, which includes match and mis-match data for the pairwise image comparison. Adding match and mis-match values for the Primary level of the Master List indicates the number of pixels occupied by one or other of the images. This represents the "image space" occupied by the various examples of each pattern in *Simpack* 's sampling area. If this calculation is done for each of the seven patterns representing the categories in Table 6.2, and the result averaged, the mean value representing the shared image space is 17,898 pixels, to the nearest whole pixel. This represents approximately 22% of Simpack's total sampling space of 81920 pixels. Additionally, the match rate for each pairwise comparison can be expressed as a proportion of the sum of match and mis-match values. If this is done for the seven pattern types, the estimates range from 51.3% to 67.6%, with a mean of 57.9%. The larger size of the butterflies and the return to using photographic enlargements for image capture enabled large, good quality images to be obtained and similar calculations for the Monarch-Viceroy pairings reveal a contrasting situation. Here the average space occupied by the Monarch-Viceroy matches is 51,436 pixels, which represents 62.8% of the total sampling area, obviously indicating a much larger mean image size. The mean match rate for Monarchs and Viceroys at the Primary level, 22,484 pixels, therefore represents approximately 44% of the average occupied space. Clearly, while the total space occupied by the butterfly images is much larger than that occupied by the wasps and flies, the average proportion of that space which matches between images is much smaller in the former than in the latter case.

This relatively lower rate of matching does not make cross-complex comparisons invalid and is not necessarily indicative of low similarity between the patterns; there *is* a low rate of matching between the average Monarch and Viceroy patterns, but so too is there between different examples of the model Monarch pattern. The obvious first explanations are that Monarch and Viceroy patterns exhibit a high degree of natural variation and are poorly aligned within *Simpack* 's frame of reference. Both of these suggestions may be correct, but they are trivial inasmuch as they are symptomatic of a more fundamental effect, that of pattern complexity. There are many more individual features, bands, spots or stripes, in the Monarch pattern than in any hoverfly pattern. The absolute rate of matching between patterns is clearly influenced by pattern complexity, not merely image size. More complex patterns provide greater scope for natural variation to cause mis-matches between the compared images. Of course, this effect of pattern complexity does not mean that it is invalid to compare the degree of Model-Mimic similarity in a system with complex patterns with that in one with much simpler pattern structure. *Simpack* 's final index of similarity is a ratio of two absolute match rates and it is this independence from the absolute match rates that allows different patterns to be compared on a common basis. However, any such comparison of similarity in different systems is only as reliable as the similarity estimates for each Model-Mimic pairing and to this extent there may be some circumstances where pattern complexity effects become significant. The implication is that where comparisons of similarity involve complex patterns, large sample sizes may be required to offset the complexity effect on absolute match rate. Here, despite the complexity of the Monarch and Viceroy patterns, just a few individuals have been sufficient to achieve statistical separation. Other species which bear complex patterns may provide fewer alignment cues and hence require larger sample sizes.

Given these complexity effects, it may seem a serious liability that estimates of hoverfly similarity are based on a single individual; restrictions on the removal of specimens from the field site imposed this pratical limitation, though museum samples could have been used to supplement sample size. It is unlikely, however, that larger sample sizes would radically alter the broad result obtained here; most hoverfly patterns are rather simple in structure and display little obvious intra-specific variation relative to differences between syrphid species. Larger samples may require revision of some hoverfly-wasp similarity estimates by one or two percentage points but this would be insignificant compared to the magnitude of the disparity in similarity values for the hoverfly and butterfly systems.

6.4.1.2. Floor Effects in Comparative Analyses.

In addition to these complexity effects, there are other reasons to be aware of the absolute match rate. *Simpack* measures the degree of co-incidence between patterns which are wholly described by three logical colours in a strictly defined space. It is not a feature-based analysis capable of identifying and matching corresponding features in different pattern structures. Consequently, any random object or pattern will exhibit some residual rate of matching with the Model pattern and this effectively imposes a floor effect on *Simpack* analyses which may become significant if the interpretation of a large comparative analysis attaches significance to small differences in similarity values. The residual floor effect match rate can be regarded as a form of background noise, and where image complexity, size and alignment conspire to produce low absolute match rates, there may be some doubt as to the relative contribution of the "signal" of actual pattern co-incidence and "background noise" to the final estimate of similarity. If background noise is significant, *Simpack* may produce misleadingly high estimates of similarity and the possible consequence is that in a wide ranging comparative analysis, high levels of similarity may have a higher than expected incidence among relatively complex patterns than among simpler ones. If such circumstances arose there would presumably be some difficulty in achieving statistical separation of some Model-Mimic pairings. The ease with which the Monarch-Viceroy pairing was separated suggest that this potential problem was not realised in this instance, and only further experience of the method will indicate whether the floor effect will impose a significant limit on the application of

Simpack in a comparative context. Initially, it would seem an appropriate precaution to regard *Simpack* as sensitive to inadequate image size and poor alignment, particularly when analysing complex patterns.

6.4.1.3. Selectivity in *Simpack* Analyses.

It has already been emphasized that *Simpack* provides an index of pattern similarity and repeated reference has been made to behavioural mechanisms capable of transforming a given level of objective similarity into a quite different degree of perceived similarity. This issue will be returned to shortly and will not therefore be laboured here, except to make obvious one general point. In between-complex analyses of Model-Mimic similarity, differences in the size, shape and behaviour of the species and differences in their predators, make it possible that there is significant variation in the relationship between actual and perceived similarity across a very wide range of species. This relationship may be reasonably consistent within a group, such as the hoverflies or the butterflies, but may well differ between them. This qualification must be remembered when assessing what the data from a comparative analysis of Model-Mimic similarity might imply about the structure and dynamics of mimicry systems. However, a slightly more subtle point must also be considered.

The application of *Simpack* is clearly selective. In the Monarch and Viceroy patterns, the head and abdomen were edited out of the image before generation of the Primary file; purely chance variation in the positioning of such features in preserved specimens may contribute appreciable variation to the match scores. This may obscure any trend in match rate data for wing patterns which are undoubtedly, in this case, the most significant visual signal to predators. For much the same reason of trivial variation, analysis of hoverfly similarity considers only abdominal patterns. In most hoverfly species, the thorax is uniformally dark, but in some of the apparently more accomplished wasp Mimics (eg *Xanthogramma* and *Chrysotoxum* species), the bright abdominal patterning extends onto the thorax, and in apparently bee-mimicking hoverflies (eg *Pocota personata*), the colour of the thoracic pilosity enhances the resemblance. In selecting only the abdominal pattern, this analysis may be discounting the contribution of other body parts to the overall resemblance to the Model. Inevitably, there will be a trade-off between the ideal of including all of a species' potentially mimetic features, and the need to minimize the effect of trivial variations between images caused by body features which are not significant in mimicry. This trade off is likely to be different for different types of body structure and in a comparative analysis the result may be a non-uniform pattern of selectivity across all groups in the comparison.

6.4.1.4. Image Sampling Density.

Another obvious source of non-equivalence in a wide ranging comparative analysis is simply subject body size. The potential limitations outlined above clearly make it advantageous to obtain the largest representation of the compared patterns. Where a comparative analysis includes species with a wide variation in body size, and image capture routines are such that image size is broadly standardized, the result is that species patterns are effectively sampled at different densities. For reasons discussed above this will not be significant in estimating the similarity in each Model-Mimic pair, or for the purposes of comparing different complexes. It becomes pertinent only when interpreting the significance of comparative similarity data in terms of mimetic interactions. If one assumes that the relevant predators respond to the size and variation of pattern features on an absolute scale, the variation in sampling density may be regarded as attributing, in the analysis, equal significance to pattern features of different absolute sizes. The most obvious circumstance for this is where a small Model and Mimic species are effectively magnified to fill *Simpack* 's image capture screen; the similarity estimate for this pair will incorporate the effect of pattern variations which are insignificant in terms of the predator's perceptual and cognitive performance.

6.4.2 The Disparity in Viceroy-Monarch and Hoverfly-Wasp Similarities.

Nothing in the preceding discussion of the qualifications to the use of *Simpack* in the comparative context was sufficient to invalidate the particular comparison described in this chapter. Such limitations as there are either did not apply, or were likely to be insignificant compared to the magnitude of the disparity between the Monarch-Viceroy and Wasp-Hoverfly systems. There is, then, nothing to suggest that the result obtained is an artifact of the method, and we are free to consider the biological significance of the observed difference in similarity in the hoverfly and butterfly systems.

If one assumes that the hoverfly-wasp system is predominantly Batesian and accepts the Viceroy's revised status as a Mullerian Mimic, the observed result appears to falsify the prediction that Model-Mimic resemblance should be higher in Batesian than in Mullerian systems; there are a number of alternative explanations for this apparent falsification.

6.4.2.1. The Viceroy as an Atypical Mullerian Mimic.

The subsequent chapter on mathematical models of mimicry describes the theoretical investigations by Brower *et al* (1970) and Pough *et al* (1973) into the properties of automimetic systems, where unpalatable or noxious individuals are effectively mimicked by palatable members of the same species. Their model incidentally yields some predictions about the expected natural incidence of Batesian mimicry and unpalatability. They suggest that unpalatability enhances individual fitness only in common species and therefore that for unpalatability to evolve in a rare dispersed species, that species must first pass through a phase of successful Batesian mimicry. A species which had arrived at a state of Mullerian mimicry via such a route would therefore appear as an exception to the general prediction of a relatively low degree of resemblance in Mullerian systems. As yet, the predictions made by Brower and Pough *et al* have not been reproduced by any other model and have not been corroborated by any report on the incidence of unpalatability and Batesian mimicry in natural mimetic assemblages. In the context of that prediction, the result obtained here could explain the apparent paradox of higher similarity in the Mullerian Viceroy system, if one assumes that the Viceroy has indeed secondarily evolved unpalatability. Investigating the current abundance of the Viceroy to determine whether it fulfils the condition of rarity may not provide an adequate test of this proposition; it is the historical abundance that is relevant, there being no obvious mechanism to prevent greater abundance once the Mullerian state has become established.

A different explanation for the observed result also identifies abundance as a key factor. The prediction of lower similarity among Mullerian Mimics might hold only for common species; where Mullerian Mimics exist in a rare, dispersed but stable state, the absolute rate of encounter with predators might begin to co-incide with a limit on the predator's capacity to retain the noxious associations of the co-mimic pattern. Here, there may be a selective advantage in co-mimics closely converging on a common pattern in order to maximize the benefit from the predator's avoidance behaviour. This hypothesis is similar to that of Brower and Pough *et al* in excepting rare, dispersed species from the general expectation of relatively low resemblance between co-mimics in Mullerian systems.

Other explanations also invoke special circumstances which may produce exceptions to this general rule. If a Mullerian mimicry complex is itself mimicked by a palatable species, the co-mimics will effectively act as composite Batesian Model. As such they may be subjected to a selection pressure both to strongly converge on a common pattern and, jointly, to diverge from the pattern of their Batesian mimic in order to "escape" its deleterious effect (see the following chapter).

6.4.2.2. Hoverflies as Atypical Batesian Mimics.

All of the preceding hypotheses effectively assume that the hoverflies occupy the range of similarity which is quite normal for a Batesian mimic, and explain the paradox of higher similarity in a Mullerian Viceroy system by speculating on those special circumstances which could produce high resemblances in a Mullerian complex. There is a quite different approach.

The Monarch and Viceroy may, for instance, fall within the range of similarities normally occupied by Mullerian systems and it may be the hoverflies which have a similarity which is atypically low for a Batesian mimic. This hypothesis again implies that hoverflies exploit some behavioural mechanism or particular limitation in the predator's perceptual system which effectively transforms their low actual similarity into a much higher degree of perceived similarity.

6.4.2.3. Hoverflies as Mullerian Mimics.

One final interpretation is simply that the hoverflies actually constitute a Mullerian system and that their similarity values, and those of the Monarch and Viceroy, fall within the normal range for Mullerian systems. Chapter One reported that there are some slight indications in the literature that hoverflies may have access to substances in larval food plants which render the adult distasteful to predators. While this evidence is not particularly strong, a lack of unpalatability would not necessarily preclude hoverflies from Mullerian status, if an attribute such as their agility reduced their potential profitability to predators, and if low profitability is a sufficient basis for Mullerianism.

6.4.3. Predicting Mimic Attributes.

Clearly, there is a wide range of alternative hypotheses to explain the apparent contradiction between the observed result and the prediction that resemblance should be higher in Batesian than in Mullerian systems. *Simpack* is, of course, a novel observational technique and in itself is incapable of discriminating between these alternatives. If, however, the result obtained here is not an exception, the evolutionary trend to which it belongs is likely to emerge from a more extensive comparative analysis of mimicry. The purpose of this chapter has been to demonstrate that, subject to some constraints, such comparative analyses are possible, but there is one further issue to which the whole concept of *Simpack* should have alerted us.

In essence, this chapter would appear to test the apparently well-founded hypothesis that Model-Mimic resemblance should be higher in Batesian than in Mullerian systems, but what precisely *is* the prediction? In developing and using *Simpack* , a very clear distinction has had to be drawn between actual and perceived similarity, and recognition given to mechanisms which determine the relationship between these two properties of patterns. In this context, it is obvious that aspects of mimicry theory which make predictions about the appearance of Mimics can no longer easily rely upon vaguely defined concepts such as "resemblance". Unless a comparative analysis does reveal largely unambiguous trends (for example in the similarity of Mullerian and Batesian mimics) it is difficult to envisage how predictions about the "appearance" of Mimics can be tested against field observations unless and until the relationship between actual and perceived similarity is elucidated.

6.5. Conclusion.

The potential significance of this chapter is perhaps belied by the simplicity both of its aims, and of the result it reports. Applying *Simpack* or a similar image analysis technique to between-complex analyses of similarity immediately makes the phenomenon of mimicry amenable to a powerful and novel comparative approach. The single comparison performed here is sufficient to demonstrate that, with some qualification, such analyses are perfectly valid.

With regard to the specific purpose of this chapter, that single comparison cannot alone definitively establish the status of mimicry in the hoverflies. However, it strongly suggests that if one assumes that there is a simple, direct and consistent relationship between actual and perceived similarity across a range of pattern types, one must invoke some sort of special circumstance to explain a paradoxically high similarity value for the Monarch-Viceroy system, or a paradoxically low similarity value in the hoverfly-wasp system. Relatively minor variations on basic mimicry theory are able to provide such circumstances.

Finally, this single comparison has further demonstrated that with the advent of objective measures of similarity, aspects of mimicry theory which make predictions about the appearance of Mimics in visual mimicry systems, must acknowledge the distinction between actual and perceived similarity.

Chapter Seven.

A Review of Mathematical Models of Mimicry.

7.1 Introduction.

The preceding two chapters have demonstrated that *Simpack* has the potential to generate a new diversity of data to describe the structure and dynamics of mimetic systems; some similarly novel methods would presumably have the same potential. While welcome, this new information in isolation is likely only to compound a problem evidenced in Chapter Two. Part of the appeal of mimicry is that even from very simple definitions of it, it is possible to draw a variety of plausible conclusions about the factors that are likely to affect the behaviour of mimetic systems. The difficulty lies not in identifying the significant factors, but in assessing their precise effect and relative importance in governing mimicry complexes. Mathematical models represent the most obvious method for integrating the identified factors into a cohesive, comprehensive, predictive description of mimicry systems. This chapter reviews the published mathematical models to assess which, if any, provide the most suitable basis for a model capable of exploring the apparent persistence of poor mimicry in the hoverflies.

The review will concentrate on three main aspects of the available models: the techniques used to represent the components of mimetic systems, the assumptions made for each and the type of predictions that they yield. The structure of the review therefore entails some disadvantage in the first section, where the mechanics of each model are described in isolation from their results, but it is hoped that this is more than offset when, in the second section, common predictions are distilled from a variety of model types.

To avoid the obvious confusion, "Model" will, for the rest of this thesis, be used to describe the species which is the aposematic basis of mimicry, while "model" will refer to mathematical representations or simulations of mimetic systems. For consistency, those species which gain protection from a resemblance to a Model will be referred to as Mimics.

7.2 Modelling Techniques.

7.2.1. *n*- parameter models.

Huheey (1964) represents the earliest effort to derive a formal mathematical description of mimicry. This model assumes that a single encounter with a Model individual causes a predator to avoid the subsequent *n* available prey items, be they Models or their perfect Mimics. At the end of this avoidance sequence, the noxious associations of the Model are forgotten and the random series of Models and Mimics are re-sampled until a further Model encounter re-establishes the avoidance behaviour. The single parameter *n* is seen as summarizing the effect of Model noxiousness and the persistence of the predator's reaction, and this approach has inspired a series of mathematical models of mimicry. Figure 7.1 below illustrates the concept of avoidance sequences, the basis of all *n*- parameter models.

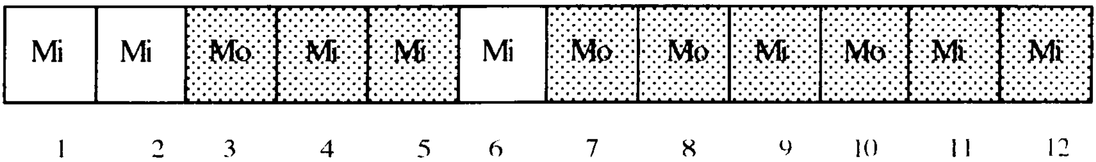


Figure 7.1 Illustration of Avoidance Sequences. (After Huheey 1988).n =3, and. 1-12 are prey items, Mo refers to Models, Mi to Mimics. Shaded prey are protected by avoidance behaviour.

The sequence 1-12 presented in Figure 7.1 represents the series of prey items which become available to the predator; "Mo" indicates a Model, "Mi" a Mimic. In this illustration, the value of *n* is 3 and the shaded items are protected by the predator's avoidance behaviour. Prey 1 and 2 (Mimics) are unprotected, but prey 3, a Model, initiates an avoidance sequence, protecting Mimics 4 and 5. Mimic 6 is unprotected as the avoidance sequence ends and is attacked. Model 7 re-establishes an avoidance sequence sustained until prey 10 which, being a Model, immediately re-establishes the avoidance sequence.

From the logical consequences of this simple conceptual model, Huheey derives the relationship

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

where P is the proportion of unprotected Mimics in a population, q and p represent, respectively, the frequency of Models and Mimics in the population, and where n is the average length of the predator's avoidance sequence.

This basic n parameter model was later extended by Huheey (1976) to produce a model of Mullerian mimicry, such that p and q represent the frequencies of two species with closely similar appearance, but differing levels of unpalatability. Both species initiate avoidance sequences, but of differing length. Although our primary concern is not with Mullerian mimicry, this model incidentally produces some general predictions about Batesian systems, and these are dealt with in a subsequent section.

Much the same is true of the enhanced n parameter models produced by Brower *et al* (1970) and Pough *et al* (1973) to account for automimetic systems, where, as in some Monarch butterfly populations, a single species exhibits a range of palatabilties. These authors retain the basic concept of an avoidance sequence but include a slight re-definition of the n parameter as the number of prey a predator would eat in a fixed time period, were it not to encounter an unpalatable item. The purpose of this modification was to produce an association with a further parameter m which describes prey availability as the number of prey per predator individual. In situations where $n > m$ there are insufficient prey items of the automimetic species to satiate the predator, though the model implicitly assumes that alternative palatable prey are always available. Conversely, where $n < m$, more prey are available per time period than the predator can consume. A subsequent section will describe how the predictions of the model vary with the different n/m ratios.

7.2.2. Markov Sequence Analysis.

Two models extend Huheey's *n* -parameter approach by incorporating a Markov chain analysis. These analyses involve conditional probabilities of encounter, for example the probability of encountering a Mimic given that the preceding prey item was a Model. Estabrook & Jespersen (1974) proposed this form of analysis as a means of accounting for the effect of the spatial distribution of the two prey types. The purpose of their model was to determine the most profitable strategy for predators which have the opportunity to include a Model-Mimic complex in their diet, but which are not obliged to do so because, it is assumed, profitable alternative prey are always present. As in Huheey's model, it is further assumed that Models and Mimics cannot be discriminated by predators until eaten, and that a single encounter with a Model is sufficient to establish predator avoidance behaviour. In addition, they assume no short term changes will occur in the abundance or distribution of the two prey types, assumptions which Estabrook & Jespersen suggest will be approximately true in large, stable prey populations with season-long generation times and where predators are active only for a short period during the season. Further, they incorporate a term *b* which summarizes the noxiousness of the Model in the same units as the profitability of Mimics and which is assumed to be uniform throughout the Model population. By manipulating their model parameters, Estabrook and Jespersen derived a number of predictions about the foraging strategy which should be adopted by a well-adapted predator over a range of prevailing conditions; these will be summarized in section 7.4.1 below. The Markov chain enhanced *n* -parameter model was also adopted by Bobisud & Potratz (1976) who sought to determine the effect of the assumption of single-trial learning. In their extended model, predators were able to accumulate *j*, a memory of the number of Mimics encountered, and to use this "memory" to condition their reaction to an encounter with a Model. Specifically, they assumed that the predator established maximal avoidance behaviour only when two Model individuals were encountered consecutively and that the Mimic series length *j* could be used to modify the length of the avoidance sequence *n* .The effect of these modifications is to simulate multi-trial predator learning and again the consequences that this revised assumption has for the predictions made by Estabrook & Jespersen are discussed in section 7.4.2.

Luedeman *et al* (1981) used Markov-chain enhanced *n* -parameter models to account for the effect of alternative prey types on predator strategies. They introduce a further set of conditional probabilities to accommodate the presence of alternative prey and additional parameters to define their profitability and the cost of the Model. Again, the object of the model was to determine, for a range of given conditions, the predator foraging strategy which maximized profitability per encounter.

Owen & Owen (1984) present the most recent and perhaps most advanced elaboration of the basic *n* -parameter approach. These authors suggest that conventional summaries of Mullerian and Batesian mimicry imply that two distinct selective processes obtain, depending on whether one or both species in the incipient mimicry complex are unpalatable. Owen & Owen (1984) wished to explore the effect of relative unpalatability on the evolution of mimetic complexes and to determine whether the palatability spectrum was reflected in a spectrum of evolutionary mechanisms. The repeated predator sampling assumed by the basic n -parameter model appeared to provide a plausible mechanism for investigating the effect of relative unpalatability, except that, these authors insist, this model cannot accommodate the evolution of anything other than mimicry which is essentially Batesian in nature. Consequently, they reject Huheey's (1976) conclusion that the evolution of a Mullerian complex is actually characteristically Batesian in that the less palatable species benefits from its resemblance to a more noxious species, at the latter's expense. Owen & Owen (1984) suggest that this inability to accommodate the evolution of truly Mullerian systems, where both unpalatable species enjoy a nett gain from the association, can be rectified by expanding the model to include the effect of absolute as well as relative prey abundance. The conclusions drawn from an n -parameter model expanded to account for absolute abundance are briefly discussed in section 7.5.

Despite its simplicity, the basic n- parameter construct has yielded a family of models theoretically capable of accounting for many factors known to be important to the evolution and dynamics of mimetic systems: relative and absolute prey abundance, patterns of spatial distribution, Model noxiousness, variation in predator strategies and so on. In this much, the n -parameter class of models represent the most established approach to modelling mimicry systems.

7.2.3. Monte Carlo Simulations.

Turner, Kearney & Exton (1984) and Turner (1987) present a simple alternative to the *n* -parameter class of models described above. In their simulation, predators maintain a fluctuating probability of attack for each of four distinct prey types. The patterned, distasteful MODEL and its palatable MIMIC are indiscriminable. NASTY has a different pattern, but is as distasteful as MODEL, while SOLO is as palatable as MIMIC but has no protective pattern. Prey individuals from these four types are made available to the predator in a random order and in proportion to their simulated abundance. As each individual becomes available, the predator may or may not elect to attack. If the predator has no prior experience of the type, its probability of attack is an arbitrary fixed value representing a naive state. Attack probabilities for subsequent encounters are determined by the predator experience which results from the attack. Attacks on palatable MIMICS and SOLOS cause attack probabilites for subsequent prey with the same appearances to be increased by a fixed factor. Similarly, attacks on unpalatable types reduce future attack probabilities by a constant factor. Repeated attacks on either palatable or unpalatable prey types therefore cause, respectively, an asymptotic increase or decrease in attack probabilities for the type. Of course the most interesting equilibrium concerns the attack probabilities for MODEL and MIMIC. Since these two types are indiscriminable, there is a single probability of attack for both species. An attack on a MIMIC will enhance the attack probability for subsequent MIMICS *and* MODELS.

In each encounter, the attack probability is compared to a randomly generated number to determine whether an attack occurs. The simulated predator therefore displays at least some superficial similarity to observed predator behaviour in tests with artificial prey; known, distasteful Models are usually avoided but sometimes eaten, while palatable prey are occasionally rejected (Turner *et al* 1984). At the end of each encounter, the predator's probabilities of attack for each type are reduced to simulate the process of forgetting the associations between appearance and palatability, such that without re-inforcement, all attack probabilities would decline asymptotically to the naive state. Over a sufficient number of simulated encounters, the attack probabilities for each type arrive at an equilibrium which represents a balance between forgetting and re-inforcement.

Through very simple manipulations to relative and absolute effect of the four encounter types on predator attack probabilities, this model structure is capable of representing a wide range of mimetic systems. In particular, it has been used to explore the effect of the "spectrum of palatability" that prey species often appear to exhibit, on the evolution and classification of Mullerian and Batesian mimicry. This is not of immediate interest here, but the model incidentally confirms predictions made by other models, as will be discussed shortly.

7.2.4. Information Theory Model.

The majority of mathematical models of mimicry, including all of the above, account for predator behaviour through simple learning and forgetting rates for unpalatability. Emlen (1968) , argues that this approach ignores the significance of predator mis-identification of prey at the time of the encounter. Emlen suggests that prey identification could be modelled by a series of predator "yes/no" questions about particular aspects of the prey species' phenotype. Where mimicry evolves, the predator has to compensate for the possibility that the answers to some questions in this series are in error. Emlen is concerned with those instances where the number of questions required to reliably identify Model and Mimic exceed the number of "questions" sustainable by the predator. The framework of this model permits the calculation of the probability of correct identification at the completion of the inadequate question set, and, subsequently, the frequency of predation on the Model and Mimic species. The initial use of this model was to predict how the effectiveness of mimicry is influenced by the relative abundance of Models, but, as will be discussed shortly, this approach also yields a number of predictions about the circumstances which permit mimicry to evolve, and calls into question the adequacy of simple learning and forgetting models of predator behaviour.

7.2.5. Signal Detection and Optimal Foraging Model.

Getty (1985) addresses the issue of imperfect prey discrimination in the context of Optimal Foraging models. Predators are usually confronted with a range of potential prey types, each of which typically represents a particular nutritional benefit to the predator at an associated cost of acquisition; optimal foraging models are used to predict how predators should select a diet which optimizes the gain from its foraging effort. Such models often assume that predators can reliably discriminate and identify the available prey types, but where the potential diet includes a mimicry complex, predators are unable to reliably correlate prey type and value with prey appearance for a potentially significant proportion of the available prey.

Getty's model extends the conventional optimality algorithm to account for imperfectly discriminable prey types by incorporating Signal Detection theory. The latter is discussed in greater detail in the subsequent chapter, where it is proposed as a means of calibrating the performance of models of predator cognition against behavioural observations of real predators. Briefly, however, Signal Detection theory has been widely used to describe the performance of diagnostic systems (Swets & Pickett 1982, McNicol 1972) in discriminating a signal from associated background noise. In the current context, this enables a predator's ability to discriminate Mimics (signal) from Models (disruptive background "noise"), to be described by a single parameter which is a product of both the predator's perceptual performance and the similarity of the Model and Mimic. This parameter effectively describes the constrained relationship between the probability that a predator will correctly identify a Mimic and the probability that it will erroneously assign a Model to the Mimic category. Predators are regarded as being free to "select" the most appropriate operating point along this constrained relationship; robust predators might elect, for example, to incur a high probability of misidentifying Models as Mimics because this permits a similarly high probability of capturing Mimics. This freedom to select an appropriate operating point is referred to as the predator's "selectivity".

The union of signal detection and optimality theory produces a model where predators which have the opportunity to include a mimicry complex in their diet, may maximize their nett gain per prey encounter by varying their selectivity, and by adding or deleting particular alternative prey types from the optimal diet. The model's basis in optimality theory permits it to account for a variety of factors thought to be important in the dynamics of mimicry systems, including prey densities (though a random distribution is assumed), predator search speed and the particular profitabilities of alternate prey types. In many ways, Getty's model represents the most accomplished mathematical model of mimicry to date, though its most obvious prediction may be rather marginal to most discussions of mimicry. However, in the current context, this model is particularly significant because it illustrates a powerful technique for modelling imperfect mimetic resemblances. This almost unique approach gives rise to predictions sometimes at odds with the predictions from earlier models.

7.3 Predictions from Mathematical Models.

The models described above represent efforts to explore the theoretical properties of mimetic interactions. Rigorous attempts to compare model predictions with observed data are rare; authors more commonly make general, sometimes superficial reference to the empirical literature. Huheey (1988) achieves an impressive fit of the predictions of the most basic *n*- parameter model with the observed behaviour of captive predators in Avery's (1983) experiments using an artificial mimicry complex; despite the apparently improbable assumptions of this model, it appears to explain 98% of the variation in observed predation rates in Avery's data. Huheey (1988) reports that few further data sets of the correct type have since been generated and this is indicative of a lack of enthusiasm for comparing model predictions with real data, an issue which will be discussed at some length later. However, it is *not* the purpose of this chapter to assess the success of mathematical models in confirming predictions derived from other approaches or in explaining empirical results. No attempt is made below to discuss model predictions in the context of the literature review in Chapter Two, though general relationships should be obvious. The primary purpose in summarizing model predictions is to illustrate the type of prediction made by the current models and how consistent these predictions are between different model classes. For clarity the following summary is divided into three sections. The first concerns the attributes of Model and Mimic species, the second deals with the behaviour of a predator encountering a Model-Mimic complex, while the final section briefly addresses predictions relating to the properties of Mullerian and Batesian mimicry complexes.

7.3.1. Model and Mimic Attributes.

7.3.1.1. The Evolution and Incidence of Batesian Mimicry

As in Huheey (1988), this review omits the population genetic models about the evolution of mimetic systems in favour of "ecological" models which make relatively short term predictions. Nevertheless, some of these latter models incidentally yield predictions about the conditions under which mimicry is most likely to evolve and these legitimately fall within the remit of this section.

Emlen's (1968) Information Theory model represents prey identification as a series of yes/no questions about particular prey features. Where mimicry evolves, the number of required questions exceeds the number sustainable by the predator, resulting in a residual ambiguity from which Emlen is able to estimate prey mortality rates. When the relative mortality rates of a mimetic and non-mimetic morph of a single prey species are compared, the model predicts that the mimetic morph enjoys an advantage only when the predator's rate of correct decision-making falls below a critical threshold. Emlen suggests that the necessary low rates of predator success are most likely to occur when the mimicry complex is pre-disposed to being a relatively insignificant part of the diet, so that the predator is not subject to strong selection pressure to enhance its capacity to discriminate between Model and Mimic. Similarly, the condition of low predator success will also occur if the adoption of a mimetic strategy does not lead to a significant increase in conspicuousness and the consequent increase in risk of predation. These two predictions appear to imply that mimicry should be regarded as a low-cost strategy for reducing an already low rate of predation to zero, and not as a strategy for reducing high rates of predation.

Where mimicry does evolve, models of several types support the conclusion that being mimicked is costly to the Model species in Batesian systems. The simulations by Turner *et al* (1984) illustrate this well since the MODEL species suffers higher rates of predation than the equally unpalatable and conspicuous but un-mimicked NASTY. The presence of a Mimic clearly increases the Model's risk of predation if naive predators are in a phase of learning to discriminate and as experienced predators make identification errors or deliberately re-sample the complex to detect changes in relative frequencies. Over evolutionary time, Models in Batesian systems should be selected for dissimilarity to their Mimic to reduce this predation. However, Huheey (1964) emphasizes that Models which are dissimilar from a close Mimic will also be dissimilar from the typical Model population and therefore sustain a higher risk of predation as a novel prey type. The evolutionary "escape" of Models from Mimics is likely to be slow and ultimately unsuccessful, though there may be continuous shift in the shared Model-Mimic pattern even in "stable" mimicry complexes.

Though apparently rather specialized, the *n*- parameter models of automimicry (Brower *et al* 1970, Pough *et al* 1973) do yield predictions about the evolution of Batesian systems. These models examine "automimetic advantage" (the reduced risk of predation enjoyed by an individual in an automimetic population) over a range of prey abundances. This advantage was found to be greatest when the abundance was such that every available prey could be eaten without satiation of the predator population. Departing from this condition in either direction, so that prey are insufficient to satiate predators or exceed the predator's requirement, caused a decline in automimetic advantage. However, the decline is assymmetric, with the rate of loss being lower when prey are too common. These authors suggest that this makes the evolution of unpalatability easier in common species than in rare and dispersed species and that this should affect our expectations about the incidence of Batesian mimicry and unpalatability. Rare species may not, they suggest, be able to evolve unpalatability without passing through an intermediate stage of Batesian mimicry of an established unpalatable species. This argument appears to assume that the evolution of unpalatability is a fate common to most species in any form of mimetic relationship, but there is a general plausibility in their suggestion that we should see complex mimetic assemblages in nature centered around a single Model and resulting from a mix of selective processes. In such situations, their prediction is that purely Batesian mimicry is more likely to occur in the rare, dispersed species of the assemblage.

7.3.1.2. Model and Mimic Frequency and Model Noxiousness.

Huheey's (1964) original *n*- parameter model was developed in response to Brower's (1960) experimental confirmation that a Batesian mimetic system did not break down if the Mimic became more common than the Model. The most favourable conditions in this original model permitted a maximum Mimic:Model ratio of 3:1, though there is no reason to suppose that this is a genuine upper limit in real complexes. This prediction has been confirmed by further models (Estabrook & Jespersen 1974) and it is now generally accepted that the early assumption that Mimics must be rare relative to their Models is incorrect. Several models confirm the obvious assumption that noxiousness of the Model is a key factor in determining the sustainable Model:Mimic ratios, but Pough *et al* (1973) emphasize that noxiousness interacts with Model frequency; a common, moderately noxious species may be more likely to be mimicked than a more noxious but rarer one.

Getty (1985) suggests a more specific effect of Model noxiousness which is best understood in the context of his wider prediction that the behaviour of predators may have a density-dependent regulatory effect on Mimic populations. The behaviour which produces this effect will be discussed in a later section on predator attributes; for the present it is sufficient to accept that in some instances the relationship between (what is effectively) probability of attack and Mimic density is as shown in Figure 7.2 below.

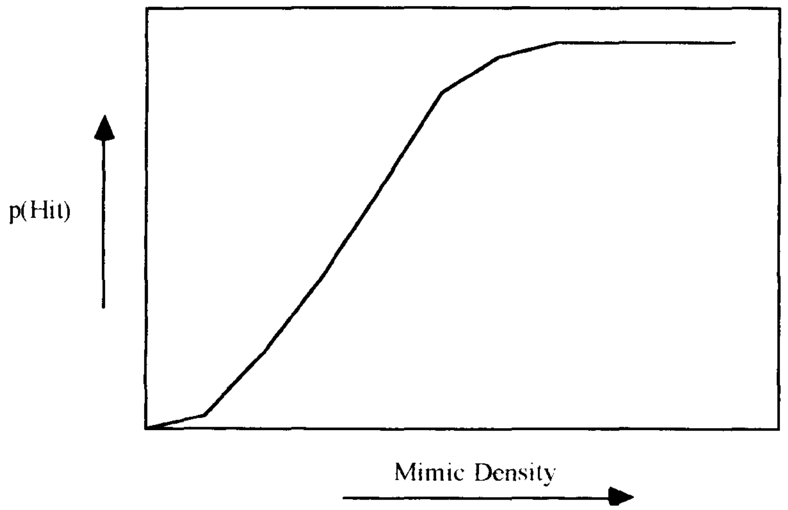


Figure 7.2 The relationship between p(Hit) (a value related to probability of attack) versus Mimic Density.After Getty (1985) Figure 4.

This relationship is clearly similar to the Holling type-III functional response familiar to population biologists for being a factor that theoretically can exert a density-dependent regulatory effect on population size (although in practice it does not). Getty suggests that where predatory pressure is the limiting factor in mimicry complexes, the foraging behaviour of predators may regulate Mimic populations at, or at almost any point below, their maximum un-regulated population size. In view of the general failure of type III functional responses to regulate prey populations, this seems rather unlikely, but it will depend upon the actual shape of the curve in Figure 7.2. The effect of increasing Model noxiousness is to flatten out the sigmoidal relationship shown in Figure 7.2, shifting the maximum probability of attack to higher Mimic densities.

7.3.1.3 Palatable Prey

Getty's (1985) Signal Detection model also illustrates the significance of alternative palatable prey in determining predatory pressure on mimicry complexes. It will become obvious in the subsequent section how the availability and profitability of alternative palatable prey affects an optimally foraging predator's decision to include an available mimicry complex in the diet. The nett effect of increasing the profitability of alternatives in Getty's model is closely similar to the effect of increasing Model noxiousness, i.e. a flattening out of the sigmoidal relationship in Figure 7.2, delaying the maximum probability of attacks on Mimics to higher Mimic densities.

In adopting the general assumptions of an optimal foraging model, Getty has derived the most rigorous theoretical account of the effect of palatable prey to date. However, Luedeman *et al* (1981) have extended the n- parameter model to include the effect of alternative prey in relation to patterns of prey spatial distribution. The importance of spatial distribution is discussed shortly in the context of optimal predator strategies, but briefly the suggestion is that mimicry may be sustainable only when prey are concentrated to produce patches of Models and Mimics in the environment. Luedeman *et al* (1981) predict that the effect of alternative prey is to relax the requirement for patchy prey distribution.

7.4. Predator Behaviour.

A surprising proportion of the predictions produced by mathematical modelling relate not to the attributes of Models and Mimics, but to the optimal learning and foraging strategy for a predator which has the opportunity to include a Model-Mimic complex in its diet.

7.4.1. Foraging Strategy.

The apparent success of the original n- parameter model in predicting some observed experimental predation rates has already been described. This model makes no provision for any form of long-term memory and its apparent success despite this leads Huheey (1964) to suggest that long term factors are insignificant. Emlen (1968), however, disputes that any learning-forgetting model is adequate to describe the behaviour of predators of mimetic systems because such models do not yield the low rates of predator success that his own model requires to sustain mimicry. Nevertheless the majority of models concerned with predator behaviour retain the learning-forgetting assumption and, together, they yield some surprising predictions about the predatory behaviour we should expect to observe.

Estabrook & Jespersen (1974) incorporated conditional probabilities of encounter into their model as a means of accounting for the effect of prey spatial distribution on the optimal predator strategy. Under the majority of values for prey abundance, conditional probability of encounter and Model noxiousness, their model predicts that the optimal predator strategy is to unconditionally reject or unconditionally accept both Models and Mimics; only a very narrow range of parameter values supported positive, finite values of *n* (the length of the avoidance sequence, *n* =0 corresponds to unconditional inclusion, *n* =infinity corresponds to unconditional exclusion). Where unconditional inclusion of the complex would represent the optimal predator strategy, mimicry offers potential prey no protection and should not be sustained; conversely, where unconditional exclusion is optimal, mimicry may be sustainable with very few Models. Estabrook & Jespersen argued that unconditional exclusion was most likely to be optimal in conditions where Models were concentrated into patches to produce high Model-Model transitional probabilities (probability of encountering a Model, having just encountered a Model) while Mimics were well dispersed, giving a low Mimic-Model transitional probability. Arnold (1978) raises some doubts about this analysis, suggesting that the mathematics of the model do not allow for independent Model and Mimic distributions; where Models are clumped into patches, the model permits only patchy Mimic distributions. Assuming these matched patterns of distribution, Arnold re-examined the significance of spatial distribution for the optimal predator strategy and also concluded that a very simple pattern of predator behaviour was optimal. For most transition probabilities "non-modifiable" predators, which unconditionally accepted or rejected the complex, were superior to a predator which accepted a fixed, randomly selected proportion of available prey; which of the non-modifiable strategies was optimal depended on an interaction of Model noxiousness and Model:Mimic ratio. Modifiable predators, which were able to adopt intermediate values of *n* (avoidance sequence length) became more successful than non-modifiable predators when the prey distribution became clumped, resulting in increased Model-Model and Mimic-Mimic transitional probabilities, and therefore reduced environmental uncertainty. In these circumstances, selection favours strategies which skipped clumps of Models to exploit intervening Mimic patches. The length of *n* should increase as a function of patch size and the noxiousness of the Model since these factors reduce the advantage of, and increase the risks from, re-sampling the environment soon after an encounter with a Model. Rather intriguing in the context of mimicry in hoverflies, is the prediction that where the environment contains large or particularly noxious Model clumps, favouring large *n* strategies, a predator which is able to discriminate between Model and Mimic has little advantage over one which is not. This may indicate that there may be conditions where there is nett profitability in including the complex in the diet and an advantage in large re-sampling times, but where there is little selective advantage in discriminating between Model and Mimic.

This consistency between models in predicting a simple pattern of predatory behaviour does not necessarily indicate a robust prediction, since the preceding models all share the same basic structure and many of the same assumptions. However, the Signal Detection model (Getty 1985) represents an entirely different model structure which, in some circumstances, also predicts the unconditional inclusion in, or exclusion from, the predator's diet. Earlier, it was suggested that an optimally foraging predator encountering a Model, an imperfect Mimic and a range of palatable alternatives, should show a density-dependent preference for including the Mimic in its diet, leading to the sigmoidal relationship shown in Figure 7.2. At low Mimic densities, only those Mimics with a very poor resemblance to the Model should be included in the predator's optimal diet. As Mimic density increases, they represent a more profitable component of the potential diet and the model predicts a decline in predator selectivity so that progressively more Model-like Mimics become acceptable. (Initially these predictions of partial preferences in prey types in the diet and the decrease in predator selectivity with increasing density appear to contradict conventional optimality theory. In fact, they are entirely consistent with the latter if it assumed that the predators are defining prey types by appearances). It was explained earlier that this density dependent functional response could result in Mimic populations being regulated at a stable point by predator behaviour. Factors such as increasing Model noxiousness or alternative prey density flatten out the sigmoidal curve which described this response, but decreasing the discriminability of Models and Mimics has the reverse effect, accentuating the sigmoidal function into a stepwise one. In these circumstances, the overlap of Model and Mimic appearances is sufficiently complete that the predator is required to regard the complex as a single species of variable profitability but relatively uniform appearance. The predator has little or no opportunity for varying its selectivity and the whole pseudo-species constituted by the complex must be unconditionally included or excluded from the diet, depending upon its overall nett profitability and that of alternative prey; this pattern of behaviour is identical to that predicted by some *n* - parameter models.

Given the range of significant determinants of mimetic success and the potentially complex interaction between them, it might be supposed that sophisticated predator strategies will be optimal. There is a degree of consensus between models that at least in some circumstances, observed predator behaviour may be very simple, approximating to unconditional acceptance or rejection of Models and Mimics, with the concomitant predictions that successful Mimics should suffer low rates of predation and that relatively few Models may be required to sustain them.

7.4.2. Predator Learning.

Most of the preceding predictions are derived from models which assume single-trial learning, that is, that the avoidance behaviour is established as the result of a single encounter with a Model. Bobisud & Potratz (1976) examined several thousand combinations of values for Model and Mimic encounter rates and Model noxiousness using their modified *n* parameter model. Multi-trial learning, where a succession of Model encounters were required to establish the avoidance, was found to be less profitable than single-trial learning in almost all conditions. Arnold (1978) has revised this prediction somewhat, suggesting that multi-trial learning may be advantageous where the spatial distribution of Models and Mimics is such that the environment cannot be described by the simple, fixed transition probabilities assumed in the simplest Markov-chain analysis. This may be the case, for example, where Models are predominantly clumped, but where some well-dispersed Models also occur. Here, predators may benefit from the sampling effect of multi-trial learning, which makes them "aware" of the heterogeneity in Model distribution.

7.5 Batesian and Mullerian Systems.

Mathematical models have, finally, been used to explore the differences in the evolution of Batesian and Mullerian mimicry systems. Again, these are issues which are not of direct interest here, but these models do illustrate the type of predictions that mathematical models of mimetic interactions can yield.

Both extended n- parameter models (Owen & Owen 1984) and simulations (Turner *et al* 1984) have been used to compare the selective processes which are active in the evolution of the two types of mimicry. These two groups of authors recognise that the conventional distinction between Mullerian and Batesian systems is not immediately reconcilable with the observation that prey species vary in palatablility, producing a "palatability spectrum", rather than a division into palatable and unpalatable types. Both groups use their respective models to assess the costs and benefits to the species involved in the interaction and conclude that despite the spectrum of palatability, there is no corresponding spectrum of selective processes. Mullerian and Batesian mimicry represent the outcome of different selective processes, the essential difference being that all species in a Mullerian system derive some benefit from the interaction, while in Batesian systems one species suffers a nett loss due to the presence of its Mimics. This conclusion does not necessarily contradict the suggestion by Huheey (1976, 1984) that the dynamics of Mullerian systems have some Batesian attributes in that the most unpalatable species in a Mullerian system is in some respects similar to the Model in a Batesian complex.

7.6 Discussion.

Mathematical models have provided a formal theoretical framework for exploring and describing the effects of factors, such as Model noxiousness, which intuition and observation have suggested to be important in the evolution and regulation of mimicry. They have also been successful in emphasizing the significance of factors such as prey spatial distribution which are less immediately obvious. Some of the predictions they produce appear robust to different mathematical or logical representations of mimetic systems, while others are as yet unique to one model type. Any simplification of an imperfectly defined, complex natural phenomenon will be open to criticism of its basic assumptions and approximations, but it is a valid general criticism of mathematical models that they have exceeded our capacity to provide convincing tests of their predictions. This has resulted in an increasingly sophisticated theoretical appreciation of mimicry, while the most basic tenets of mimicry have only modest empirical support. As will be discussed shortly, this theoretical bias may be understandable given that the events which make up mimicry are not open to direct observation, but one obvious disadvantage is that this sophistication diverts attention away from basic issues and perpetuates complex debates on, for instance, the definition and classification of Mullerian and Batesian mimetic systems.

The apparent paradox of poor Mimics outnumbering the good in the mimetic hoverfly complex represents one opportunity to test how well the developed body of theory can be extended to explain one specific, naturally occurring observable attribute of a mimicry complex. Which of the previous mathematical models is the most appropriate basis for a model which might explain the persistence of apparently poor mimicry ? It is naive to expect any existing model to prove suitable without some modification, but the basic assumptions made by most models, and the type of predictions they yield raise doubts about their fundamental capability for testing the persistence of poor mimicry.

7.6.1. Model Assumptions.

Almost all models assume perfect mimicry and provide no opportunity for predators to discriminate between Model and Mimic prey; this immediately discounts all of the *n*- parameter models from any analysis of imperfect mimicry without radical alterations to their basic approach. In assuming perfect mimicry, most models make the implicit assumption of perfect Model-Mimic resemblance. The success of a Mimic is determined by its resemblance to the Model, but also by the ability of predators to make discriminations between similar patterns. Were the predator is sufficiently constrained, a Mimic could in principle achieve perfect mimicry, in the sense that they are always identified by predators as Models, despite imperfect resemblance. (For this reason, hoverflies labelled "poor Mimics" in this thesis ought more properly be referred to as having poor resemblance.) It is likely that an accomplished model of "poor mimicry" would have to accommodate these related issues of resemblance and mimetic success. Getty (1985) acknowledges this distinction, though his model describes the interaction of both factors using a single parameter.

This inability of predators to exploit available sensory information is just one respect in which the models assume only very elementary predator abilities. As was suggested earlier, the diversity and interaction of factors which determine mimetic success might suggest that a sophisticated foraging strategy would be the most profitable, yet most models predict a very simple pattern of predator behaviour. However, this predicted simplicity may derive from the assumptions of immediate acquisition and loss of noxious Model associations made by *n*- parameter models. Again Getty's (1985) model is an advance in incorporating a relatively sophisticated optimality model for foraging behaviour, but he does not consider the effect that naive predators have on a mimetic complex as they learn Model associations.

A further but less widespread inappropriate assumption is that alternative palatable prey are not present or that they have no consequent effect on predation on the mimicry complex. Given the consensus about the significance of alternative prey, this omission will probably not be repeated, though there are some relatively recent models (Turner *et al* 1984) which include palatable alternatives but take no account of their effect on predator foraging behaviour

7.6.2. Model Predictions.

A second reservation about currently available models concerns the type of predictions that they yield. There is little doubt that mathematical models are a rich source of predictions about the evolution and dynamics of mimetic systems, but two features of the set of predictions described above re-emphasize that many existing models are inappropriate for the current purpose.

Firstly, surprisingly few predictions directly refer to the attributes of the Model and Mimic species. The largest group of predictions relate to the optimal learning and foraging strategy for a predator which encounters a mimicry complex. Another group of predictions are concerned with the conditions in which mimicry is most likely to evolve, with the gain in fitness of Mimics relative to non-mimetic morphs and the costs and benefits to species in the evolving complex. Those predictions which do relate directly to prey attributes, such as the Model:Mimic ratio and the expected patterns of spatial distribution are rather general, and have invited few attempts to compare them with field data. It has already been implied that many of the predictions produced are inherently difficult to test convincingly. For many insect visual-mimicry complexes, for instance, the most likely predators will be small birds; collecting an appreciable number of comparable field observations of encounters between these predators and their prey is unlikely to be practical. More substantial bodies of data are likely to be derived from wild or captive predators preying upon on artificial mimicry complexes, but, as discussed in Chapter Three, such an approach will always be limited in its ability to reproduce natural encounters. Similarly, the substantial number of predictions about the prerequisites for the evolution of mimicry and the course of its early evolution are open only to indirect testing through a comparative analysis of the properties of extant mimetic complexes.

This difficulty in testing predictions is effectively inherent in the phenomenon of mimicry and it has forced our theoretical appreciation to advance with only sparse empirical support. "Mimicry" consists of a long series of rare and brief events, making direct observation effectively impossible. The key to a full understanding of mimicry is an accomplished model of predator perception and cognition, and even a reasonable body of such observations would have limited value in determining how predators arrive at particular decisions. "Mimicry" is endowed with a fundamental intractability which precludes any direct approach to its most essential basis. New, more detailed information about mimetic systems can only come from a diversity of more tangential approaches, and formal models will have a critical role in the synthesis of a complete and cohesive account of mimicry. Despite the intractability of the phenomenon, and concerns over the basic assumptions and predictions of current models discussed earlier, it *is* possible to conceive of a mathematical model which yields predictions that are testable against field observations. I believe that the pivotal attribute of such a model is that the sub-model of predator cognition should determine the stability of particular prey characteristics. While the observation of natural, individual encounters between predator and Mimic may be impossible, the outcome of a long series of predator decisions will be evident in the structure of a mimicry complex, providing that one assumes that predation is the key limiting factor for prey abundance. The structure of a mimetic complex, in terms of the relative and absolute abundances of Models and Mimics is one of the very few aspects of mimetic systems which is readily and reliably observable in the natural situation. Predictions produced by mathematical models can be tested against field data, providing they are predictions about the stability of patterns of prey abundance. A model concerned with the persistence of apparently poor Mimics must additionally account for the degree of resemblance between Models and Mimics; it must explore the stability of the complexes both in terms abundance and Model-Mimic similarity. The significance of a pattern comparison technique such as *Simpack* is obvious in this context; Chapter Seven has already demonstrated how natural mimic populations can be described in terms of similarity and abundance, independent of the constituent species. While the relationship between objective and perceived similarity has yet to be elucidated, the facility for describing a complex in terms of abundance and similarity represents a novel mechanism for comparing model predictions with field observations, so making a comprehensive, testable model of mimicry systems a feasible objective. The following chapter describes the practical work undertaken to develop a mathematical model of mimicry which exploits some of the techniques of the reviewed models, and which possesses the attribute of predicting the structure and dynamics of a mimetic complex which would result from a given pattern of predator behaviour.

Chapter Eight.

Developing a Mathematical Model of Mimicry.

8.1 Introduction.

This chapter continues the discussion of mathematical models of mimicry. The following Method section describes the design and development of a model with some of the properties which, as argued in the previous chapter, may provide a rare opportunity to test theories of mimicry against field observations. The Results section reports on the outcome of a series of tests of one version of this model. The discussion suggests how such a model might be employed, and closes with some brief speculation on the future development of mathematical models of mimicry.

From the literature review reported in the previous chapter, it was evident that none of the available models possessed the properties argued for; none simulated an evolutionary context to the interaction between predator and prey, and without this property, it would be impossible to test the stability of simulated mimetic strategies. Initial modelling work sought to reproduce existing models to determine which was most suitable for extending and enhancing. It is the techniques used in these models, rather than their results and conclusions, that were of primary interest.

Getty's (1985) Signal Detection model was successfully reproduced in Fortran on an IBM mainframe computer. This model excited particular interest because it explicitly included potential imperfection in mimicry and provided a means for describing the perceptual performance of predators making Model-Mimic discriminations. The model also incorporated an optimal foraging theory approach to the role of alternative, non-mimic prey items. Other than the omission of a simulated evolutionary time scale, this model probably represented the most accomplished and realistic model of mimicry available, and as such represented the most attractive candidate for development. Its chief disadvantages were the degree of computational complexity and the long simulation times which resulted. These factors protracted the cycle of testing, modifying and re-testing and thus limited the practicality of the model as a research tool, particularly in the mainframe environment where processor time must be shared between many users.

The Monte Carlo model of Turner *et al* (1984) was investigated as an alternative which would be feasible in a personal computer environment. This model, described in greater detail in the previous chapter, offered less sophistication in its representation of predator foraging and decision making, and of prey populations. Its advantages were primarily practical ones, in that its computational and mathematical simplicity offered low simulation times and facilitated enhancement. The model did, however, demonstrate some degree of biological realism in as much as the pattern of predator behaviour it predicted exhibited some similarity to observations of real predators (Turner 1984). There were few difficulties in reproducing this type of model in BASIC on a BBC micro computer and it proved easy to extend and modify; it was therefore selected as the basis for developing a model that possessed the properties required to test the stability of alternative mimetic strategies.

8.2 Method.

8.2.1. Extending the Turnerian Model of Mimicry.

The most obvious shortcomings of the basic Turnerian model for the current purpose were that it did not include the required simulated evolutionary time scale and that it assumed perfect mimicry in all instances. The model did not include a mechanism which permitted a prey species to modify its protective strategy over a number of simulated generations and the modelling of predator decision making omitted the use of sensory information available at the time of the encounter with a potential prey item. The first original modelling work sought to include these enhancements in the basic Turnerian framework and resulted in a model written in Fortran to run on an IBM PC compatible computer, which offered speed advantages over the BBC microcomputer used for earlier work. The Fortran source code for this model, named *Complex*, can be found in Appendix Three. The development and testing of *Complex* accounted for the majority of the modelling effort. Despite this, a detailed discussion of *Complex* and its results is passed over in favour of a description of a subsequent and simpler version, *MacComplex* , designed for the Macintosh computer environment. *MacComplex* and *Complex* share the same fundamental structure but differ in the manner and sophistication of modelling predator decision making, and predator and prey population dynamics.

The reason for this simplification was that *Complex* exhibited a great deal of instability despite the progressive approach taken to its development. Manipulating the parameters of a *Complex* simulation sometimes produced results which were consistent with expectations based on simple assumptions about the behaviour of mimicry complexes. However, these responses were inconsistent, and replicates of the same simulation usually exhibited only poor reproducibility. Despite a long series of modifications, the source of this variation was never properly isolated and it is possible that chance events early in a simulation had significant effects on the remainder of the run. Alternatively, it is possible that prey responses to predatory pressure were too intricate to become evident over the time span simulated. Though it is not being suggested that mimicry complexes are genuinely chaotic systems, it is conceivable that this lack of reproducibility is of some biological significance. Nevertheless, it was decided that even were this true, it represented an aspect of mimicry complexes that was too advanced for current purposes. It was for these reasons that the decision was taken to create a less sophisticated, but perhaps more stable, version of *Complex* ; the result, *MacComplex* , is available in Appendix Four and will be the subject of the majority of this chapter.

8.2.2 *MacComplex.*

8.2.2.1 *MacComplex* Structure.

MacComplex maintains simulated predator and prey populations. Up to four predator and four prey species can be sustained and the numbers of each species can be varied independently. Each of these simulated populations are comprised of discrete individuals, each capable of having a unique history. One of the prey species can be designated as a Model (though it ought more properly be referred to as an aposematic species if a mimicking species is not present). Each predator and prey species has particular attributes which are discussed in greater detail later.

A *MacComplex* simulation is organized into a series of Seasons (generations), and within each of these Seasons a number of Encounters occur between individual representatives of the predator and prey populations. During each of these Encounters, a prey individual is selected at random from the total prey population; the relative abundance of each prey species can therefore be simulated by specifying a different population size for each; and the same is true for predator populations.

8.2.2.2. *MacComplex* Prey.

The appearance of each prey individual is represented on a continuum of similarity to an idealized representative of the Model species, on a scale of 0.0 to 1.0, such that a prey species which closely resembles the Model species will have a value approaching 1.0. This method of describing Model-Mimic similarity is derived from the *Simpack* method of pattern similarity assessment which is discussed in the first part of this thesis. Prey populations are not homogeneous in their similarity values; at the initialisation of a simulation, a seed similarity value is specified for each prey population, this value then has a small random value within the range 0.0 to 0.1 added or subtracted to it before being assigned as the similarity value of an individual within that prey population. Each species therefore exhibits within-species variation in similarity values. Prey species may overlap with each other to any degree, while remaining discrete, independent populations. Model populations are also seeded with variation, at a point slightly below the idealised value of 1.0.

8.2.2.3 *MacComplex* Predators.

At initialisation, each predator individual possesses two species-specific attributes, a basic probability of attack and a tolerance value. Each individual has a further attribute, initialised at zero, which is used to represent the predator's memory of past encounters with individuals of the Model prey type. The way in which these attributes are used to model predator decision making is described in a later section.

Unlike the prey populations, predator attributes are simply seeded at the species-specific value, no variation is added and the population is therefore uniform at the beginning of the simulation. As is explained shortly, within-species variation arises as a result of the history of encounters which an individual predator may accumulate.

8.2.2.4 Predator Decision Making.

The predator's decision to attack or ignore the available prey is simulated by a simple two stage process. The first stage yields the individual's estimate of the lowest similarity value which could represent a Model individual; it will shortly be apparent how this estimate is based on the particular history of the predator individual. Recall that at initialisation, each predator is seeded with two species-specific attributes, one of which was referred to as its "tolerance", and the other a "memory" attribute used to record an experience of the Model species. The memory attribute is simply set to the similarity value of the last Model individual that was attacked. The tolerance attribute, seeded at 0.2 in the simulations presented here, is subtracted from this "memory" to yield an estimate of the lowest likely limit of Model similarity. The difference between this estimate and the similarity value of the currently available prey item is calculated and tested against a randomly generated number. The object of this stage of the process is for the predator to assign the prey item to a Model or Non-Model class. If the difference between current prey item similarity and the lowest estimate of Model similarity is small, it is likely to be lower than a random number. The predator will therefore in effect "decide" that the current prey is a Model. The use of a random number imparts the predator with the properties of a statistical decision maker; even where the difference between the estimate of

Model similarity and the similarity of the current prey is small, there is still small probability that the predator will not assign the prey to the Model class.

If the predator has not previously encountered a Model individual, the result of these calculations is that all prey items are assigned to the Non-Model category.

In the version of *MacComplex* described here, the model of predator decision making is complete once this allocation to Model and Non-Model classes has occurred. Apparent Non-Model prey are attacked and killed, Models are ignored.

In some test versions, a further species-specific attribute was used to simulate the difference between specialist and non-specialist predators. The inclusion of this attribute and a further test against a random number was used to determine the outcome of an additional stage of decision making wherein the predator may elect to attack a prey item despite a Model-like appearance. The object of this further stage was to simulate the greater tolerance to handling the Model type that specialist predators are likely to have. No results from this version of the model are reported here.

8.2.2.5. Encounter Events.

During an Encounter, the attributes of the randomly selected predator and prey individuals are used in the simple model of predator discrimination and decision making described above, in order to determine whether the predator attacks the prey item. Prey items which are attacked cannot escape and are usually deleted from the prey population. The only exception to this is provided if the Model population is fixed. The purpose of *MacComplex* is to permit prey populations to respond to predatory pressure by "evolving" their protective strategy, as described by their mean similarity value, and in principle this opportunity is also available to the Model population. Current mimicry theory agrees that the Models in Batesian systems should show an evolutionary "escape" response to reduce the deleterious impact of being mimicked. For simplicity, however, the simulations presented in this chapter fix the Model population at its initial similarity value. This constancy is achieved by not deleting Model individuals from the population if they are attacked, though the post-attack revision of predator attributes described in 8.2.2.6. still takes place. The similarity value of Models therefore appears as a straight line in the plots which result from *MacComplex* runs which include a Model species.

8.2.2.6. Post Encounter Revisions.

The results of an attack on a prey individual are used to revise the attributes of the individual predator. If the prey transpires to be from the Model species, and the predator has not previously attacked a Model, the predator's memory attribute is set to the similarity value of the Model individual. Irrespective of whether or not the predator has previously encountered a Model, every attack on a Model individual causes the predator's tolerance attribute to be multiplied by a small constant value, greater than 1.0 (1.2 in the simulations presented later), effectively lowering the predator's minimum estimate of Model similarity for the next encounter. This revision is intended to simulate the extent to which a predator generalizes from its experience of a Model.

Conversely, an attack on a Non-Model prey item causes the predator's tolerance to be lowered by multiplying it by a factor below 1.0 (0.8 here), which raises the lower estimate of Model similarity.

8.2.2.7. Post Season Prey Revisions.

The outcome of a series of Encounters is the deletion of individuals from the prey population. As explained above, the single exception to this is where Model populations are fixed by preventing the deletion of Model individuals. It is through the restoration of the prey populations over a large number of Seasons that prey species are permitted to modify their protective strategy.

In the original version of this model, *Complex* , this restoration included inter-specific competition for the free spaces created during the preceding Season. The number of spaces allocated to each species was calculated from their survivorship in the previous Season. The model then simulated intra-specific competition for the allocated spaces at the point where survivors reproduced to restore their populations. The simulated reproduction introduced a small degree of variation in terms of the similarity value of offspring, such that parents and offspring were similar, but not identical. Over a number of Seasons *Complex* prey populations were therefore capable of responses to predatory pressure which involved changes in population size and individual similarity values. However, it was evident that changes in population size were unrealistically rapid relative to the changes in the population similarity values. This complex response may have been the source of the apparent instability of *Complex* and as a consequence, despite a number of advantages, it was abandoned for the writing of *MacComplex*. In *MacComplex* , prey population sizes are fixed so that prey responses to predatory pressure occur solely in terms of population mean similarity values. The element of intra-specific competition has also been removed and the restoration of prey populations therefore proceeds as follows.

For each free space in each prey population, a survivor of the appropriate species is selected at random to act as a parent. An offspring individual is then created, with its similarity value being calculated from the parental similarity, plus or minus a small amount of variation (parent similarity ±0.05).

8.2.2.8. Post Season Predator Revisions.

At the end of each season, the model simulates the recruitment of naive predator individuals by returning the attributes of a fixed proportion of the predator population to their species-specific seed values. Memory attributes are returned to zero for all of these individuals, thus erasing any "experience" those individuals had accumulated during previous Seasons. The predator population at the beginning of the following Season therefore consists of a mixture of naive and experienced individuals. This recruitment is performed simply on a fixed, randomly selected proportion of the population; there is no limit to the number of seasons which an individual predator might survive.

8.2.2.9. Summary.

A *MacComplex* simulation consists of a number of Seasons, within which a series of Encounters takes place. Each encounter requires the random selection of a predator and prey from the total population pools and it is the attributes of these individuals which are used to decide whether the prey item is attacked or ignored. The outcome of attacking encounters is used to revise individual predator attributes so that its behaviour in subsequent encounters is modified. At the end of each Season, prey populations are restored to their original size through a form of reproduction which maintains intra-specific variation in prey similarity values. Predator populations are subject to a recruitment process which returns a proportion of the population to species-specific attribute values. Over a large number of Seasons the "evolutionary" response of each prey species to the prevailing predator behaviour may become evident as shifts in the population mean similarity value. Manipulation of the initial parameters of a *MacComplex* population make it possible to simulate a wide range of predator-prey interactions.

As with the *Simpack* similarity package described earlier in this thesis, *MacComplex* requires a test of functionality to ensure that there are no coding errors. The following Results section reports on a number of replicates of four *MacComplex* simulations which demonstrate that manipulating the model parameters results in prey population responses that are consistent with simple assumptions about the mechanics of mimicry complexes.

8.3 Results

8.3.1. Initial Parameter Values.

Each *MacComplex* simulation requires a set of parameters to be defined at initialization and this section describes the parameter values used for the first simulation, described in section 8.3.2. The simulations reported in sections 8.3.3 to 8.3.6. are achieved by manipulating one or a few of these parameter values. All simulations involve 1000 Seasons, with 10 Encounters occuring per Season. Small populations are specified to facilitate prompt evolutionary responses. Consequently the number of Encounters per Season was kept low to ensure the continued survival of prey populations; in other simulations the entire prey population was predated, ending the simulation.

The initial simulation includes a single, Non-Model prey species, with a population of 10 individuals; no Model prey are included. At the initial construction of this population, the seed value for Similarity is 0.5, to which is added or subtracted a random value between 0.0 and 0.1. The similarities in the population therefore represent a random sample from the interval 0.4 to 0.6. At the end of each Season, when the depletions in the population are restored, offspring are allocated a similarity value by selecting a random value between 0.0 and 0.05 and adding it to, or subtracting it from, the similarity value of the selected parent.

The Predator population consists of five individuals from a single species. The initial tolerance value is set at 0.2 for all individuals; recall that this value is subtracted from the similarity value of the last Model individual attacked to yield the predator's estimate of the lowest likely limit for Model similarity values. When the attacked prey item is a Model, the tolerance value of the predator individual is multiplied by 1.2; when Non-Model prey are attacked, the tolerance value is multiplied by 0.8. The nett effect of these manipulations is to make predators more likely to assign a prey item to the Model class if they have recently attacked a Model, and less likely to do so if they have attacked a Non-Model.

At the end of each Season one fifth of the Predator individuals (ie. one individual in this case) are returned to their species-specific tolerance value and have all "experience" of previous Encounters erased in order to simulate the recruitment of naive predator individuals.

8.3.2. Neutrally Costed Similarity in the Absence of Models.

It is certainly a safe assumption that a mimetic protective strategy cannot be sustained in the *complete* absence of a suitable Model species. In this first *MacComplex* simulation, the prey population is made up of just one species, not of the Model type, seeded with a similarity value of 0.5. In this simulation, there is no cost or benefit to any particular similarity value and it can be assumed that the prey population will not demonstrate any repeatable pattern of change over a large number of Seasons.

The results of five replicates of this simulation are depicted in Figure 8.1. The vertical axis of these plots represents the scale of similarity from 0.0 to 1.0, while the horizontal axis describes the number of simulated Seasons. The line of the plot indicates changes in the population mean similarity for the prey species over the Seasons. Close inspection of the plots may seem to indicate that more than one mean value is being reported for each Season, but this is a result of the compression required to accommodate 1000 Seasons; throughout this section it is the overall pattern of change which is significant. Though the simulation has only been run over 1000 generations, there is no indication of any trend appearing within any replicate or of any repeatability between replicates. Changes in mean similarity appear random, which is consistent with the prediction made earlier.

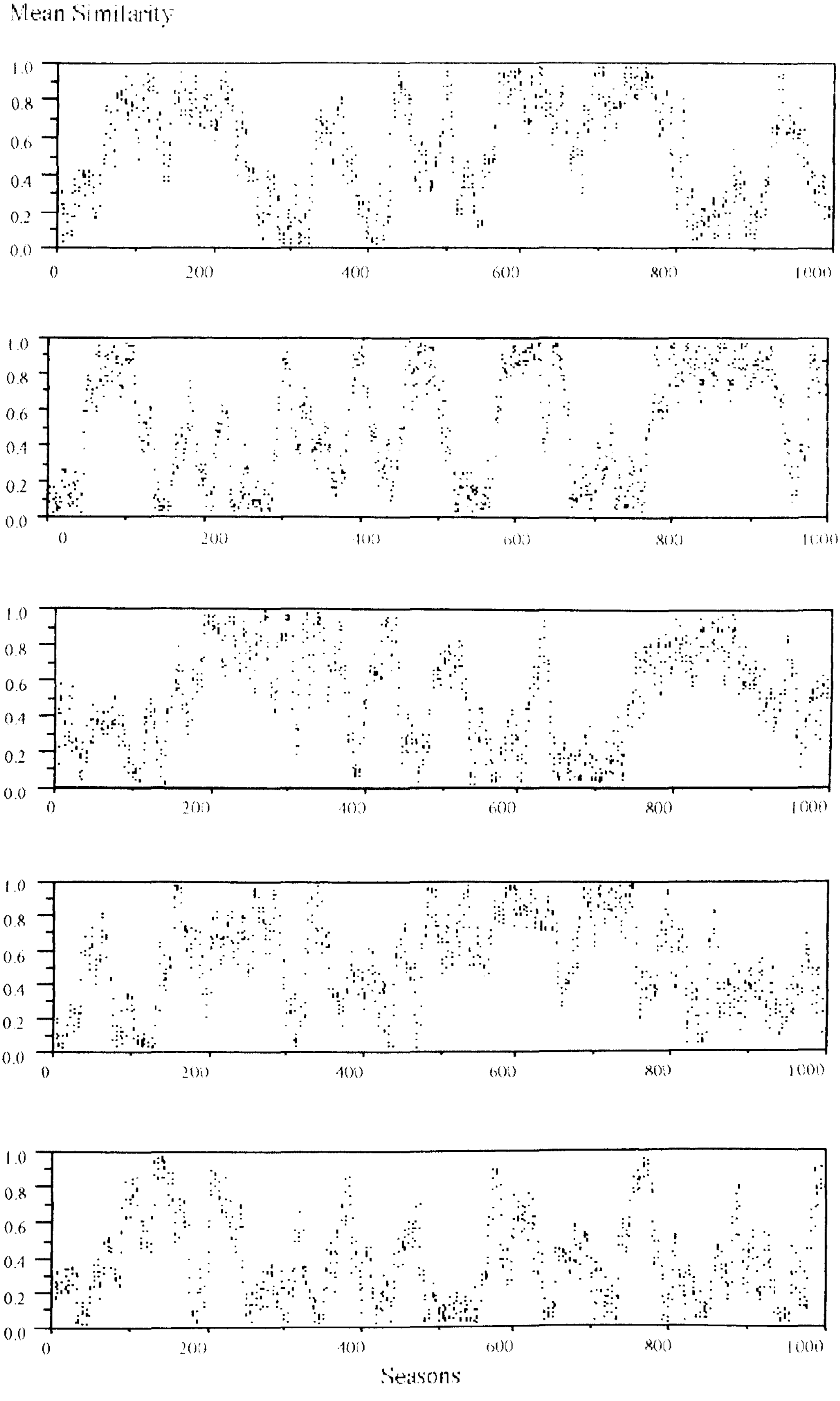


Figure 8.1. Five replicates of a MacComplex simulation with no models and neutral costs to similarity. See text for parameter values.

8.3.3. Neutrally Costed Similarity in the Presence of Models.

The second simulation retains the same parameters as that reported in the previous section, except that 10 individuals of the Model type seeded at 0.97 are introduced. High similarity values should now acquire a benefit because predators should reject prey items with the same or similar appearance to the Model type. Non-Model species with high similarities can be regarded as Mimics of the Model type. Since a mimetic similarity has no cost, it can be predicted that the Non-Model species should evolve to a mimetic strategy because mimetic individuals are more likely to survive and reproduce.

Figure 8.2a and 8.2b show the results of four replicates of this simulation. (The different formats of Figure 8.1 and Figure 8.2 a and b again results from a limitation of the graphing software used and has no other significance). The predicted shift towards a mimetic strategy is evident in all four replicates.

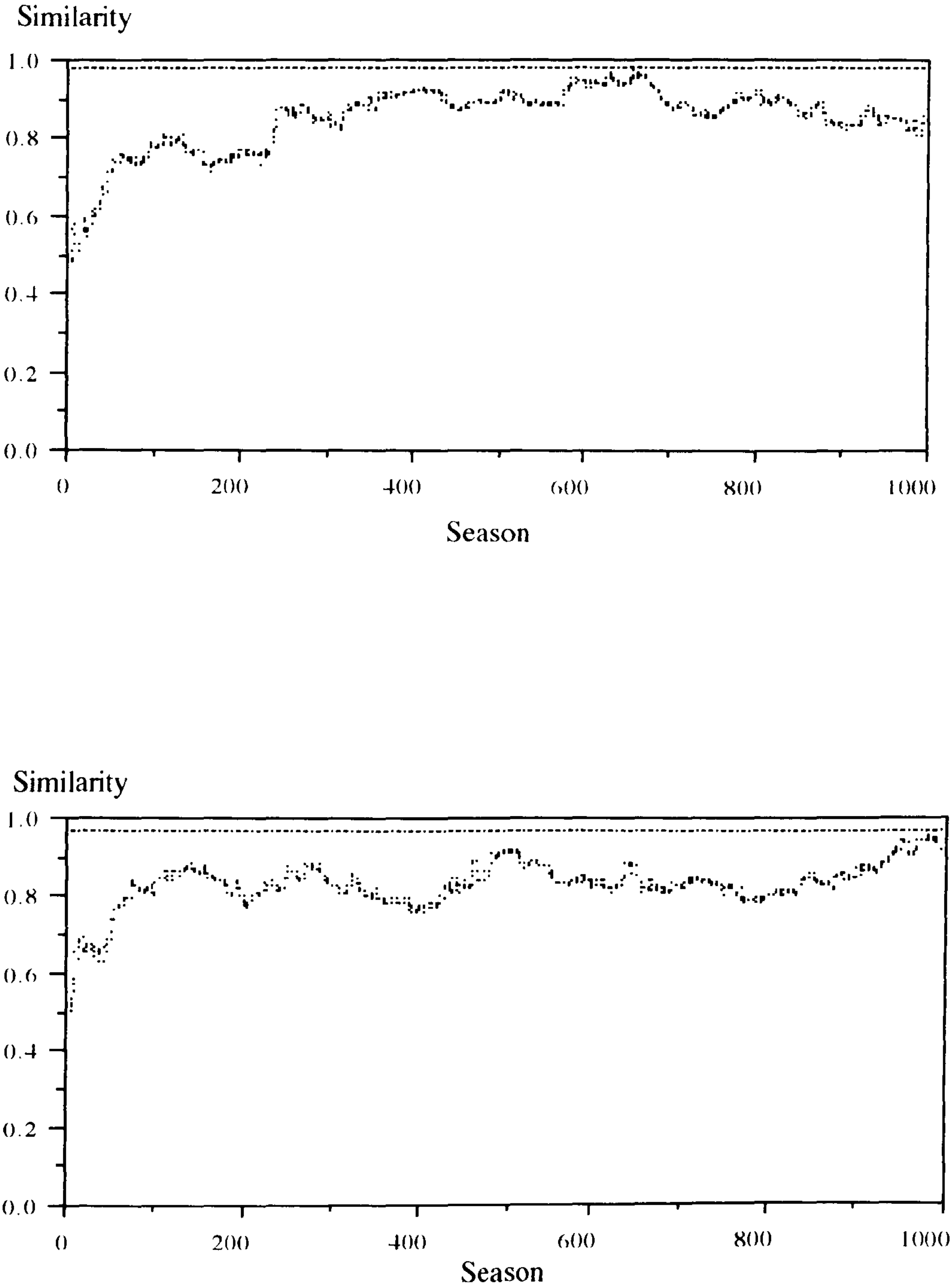
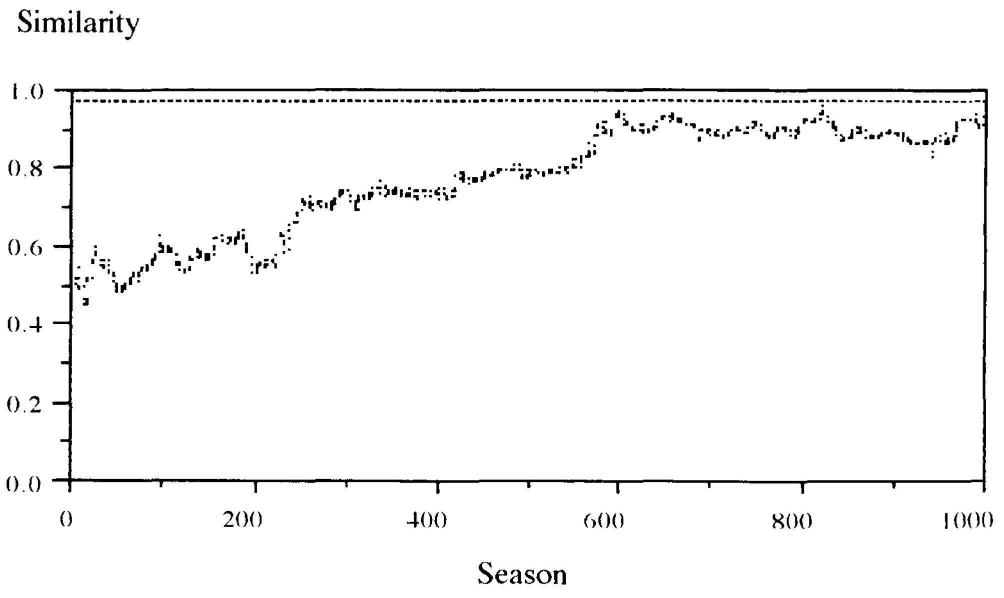


Figure 8.2 a. Two replicates of a MacComplex simulation with neutrally costed similarity in the presence of a Model species. See also Figure 8.2b. See text for parameter values



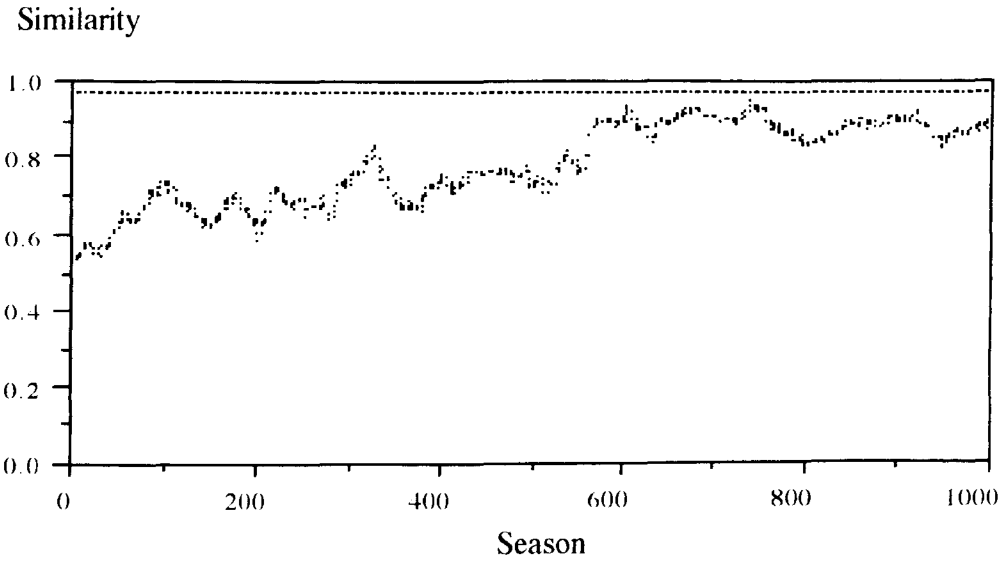


Figure 8.2 b. Two replicates of a MacComplex simulation with neutrally costed similarity in the presence of a Model species. See also Figure 8.2a. See text for parameter values

8.3.4. Adding a Cost to Mimetic Strategies.

A model in which prey species always evolve to a state of high quality mimicry is clearly unrealistic; an enhancement to the model is required to provide an alternative protective strategy. In effect, mimicry should retain its current benefit, but it must also incur a cost to offset this advantage.

The real costs of mimetic strategies are largely a matter of speculation. Certainly there will be some form of "genetic" and energetic cost over evolutionary time which results from changes to the phenotype and the required accumulation of resources, such as pigmentation compounds, needed to "implement" the strategy. The original *Complex* attempted to capture these costs through the medium of intra-specific competition which penalized large changes in phenotype. The intention was to maintain a stability at a given strategy and cost to changing to a new strategy. *MacComplex* omits this "evolutionary" perspective to costs but retains a proposed short term cost to mimetic strategies. The argument for this cost is based upon the assumption that a Model species has evolved to advertise its low profitability through bright, warning coloration. It is further assumed that this advertisement increases the probability of initial detection by a predator. Since the appearance of Mimics converges on that of Models, they are likely to incur the same cost of high initial probability of detection. The precise shape of the relationship between similarity to the Model pattern and probability of detection is again largely speculation except that relationship is unlikely to be linear. Models may represent an optimum signal for detection and as prey appearance converges on that of the Model, they are likely to have similar probabilities of detection in a given circumstance. However, any arrangement of bright pattern features are likely to result in an increased probability of detection and even very poor Mimics are likely have a probability of detection approaching that of the Model, despite their relatively low degree of similarity. *Complex* incorporated a sigmoidal similarity/detection relationship, but the inflexion points of these curves caused rapid and irreversible switches between protective strategies due to minor random fluctuations in population similarity. For *MacComplex* a very different, but functionally similar, and smoother, relationship was adopted.

The functional relationship between similarity values and probability of detection is modelled by simple power law, as used in Getty's model to describe the discriminability of Model and Mimic types (note that the use of this relationship in the two models is entirely different). Figure 8.3 below shows the power law relationship:

$$\textbf{probability of detection} = \textbf{similarity}^{\,0.3}$$

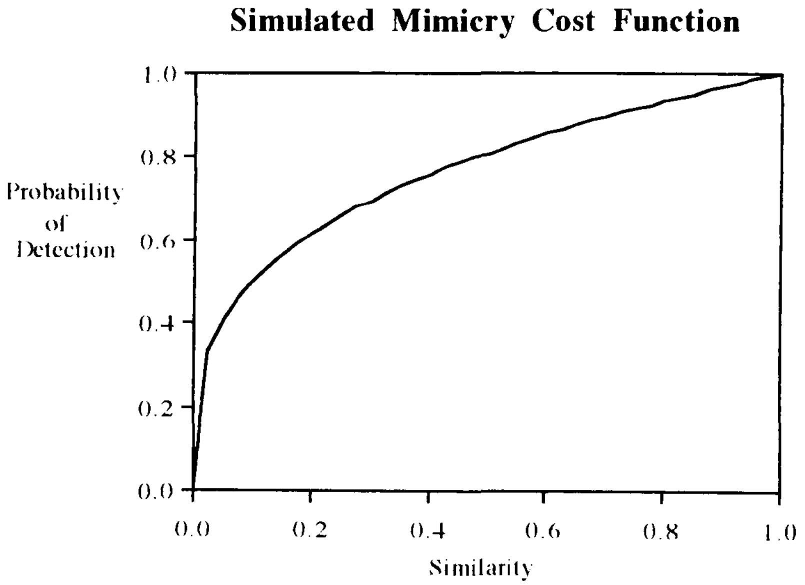


Figure 8.3 Simulating a Cost to Mimicry. Probability of detection during an encounter is determined by Similarity to the Model.

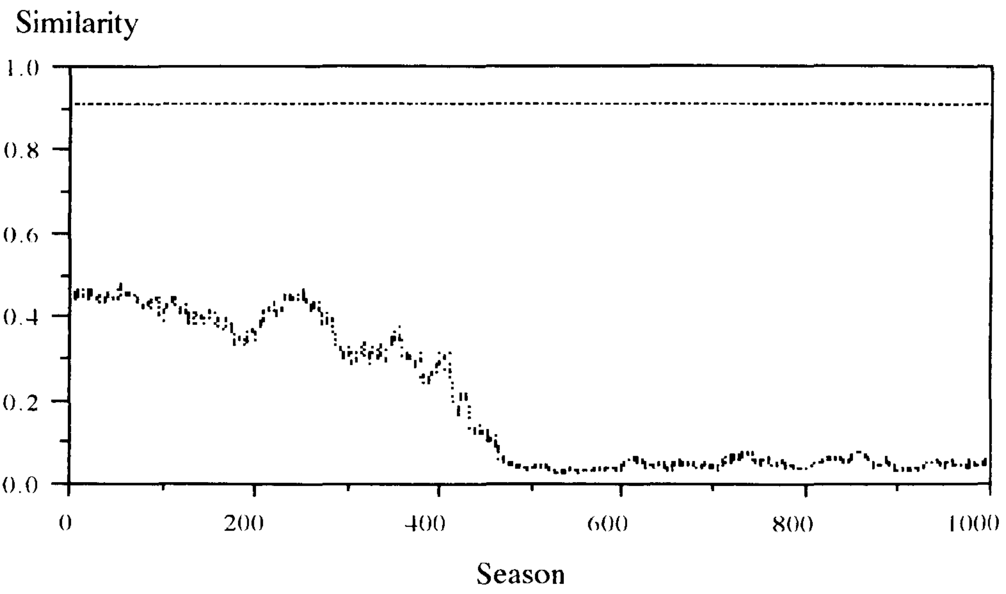
This relationship broadly divides available similarity values into representing alternative protective strategies. High similarities incur high probabilities of detection which may be offset by the protection to be gained from evolving a close resemblance to the Model type. As an alternative to mimicry, prey species may occupy lower similarity values which offer a rapid decline in probability of detection resulting from the loss of all conspicuous pattern features. For the purposes of this thesis, that lower region will represent cryptic strategies.

While it probably is the case that real mimics do incur the cost of a higher initial probability of detection than similar non-mimic prey, it is not being suggested that the relationship depicted above is a particularly realistic representation of those costs. The intention is simply to provide *MacComplex* prey species with alternative protective strategies and to ensure that prey evolving towards a mimetic strategy pass through a phase of "bad mimicry" where there is a high probability of detection consequent of conspicuous signals, but where Model-Mimic similarity is not high.

8.3.5. Simulated Evolution of Crypsis.

The costs of mimicry discussed above can be incorporated into the model by using the relationship described in Figure 8. 3 above to determine the probability that the randomly selected prey item becomes "visible" to the predator during the Encounter. The prey individual's similarity value is used to calculate its probability of appearance and this probability is again tested against a random number such that individuals with a low probability of detection are unlikely to become available to the predator. It is thus now the case that no prey become available to the predator during some Encounters.

In the presence of this cost it should be possible to lower the utility of the mimetic strategy developed in the previous *MacComplex* simulation, so that the prey species evolves to the cryptic alternative. One means of achieving this is by decreasing the relative abundance of Models in the prey population to a point where a mimetic strategy cannot be maintained. In the following simulation the ratio of Models to Non-Models is lowered by reducing the number of Models to 2, while the Non-Model population is increased to 30 individuals. All other parameters remain the same. Figure 8.4 a and b depict four replicates of



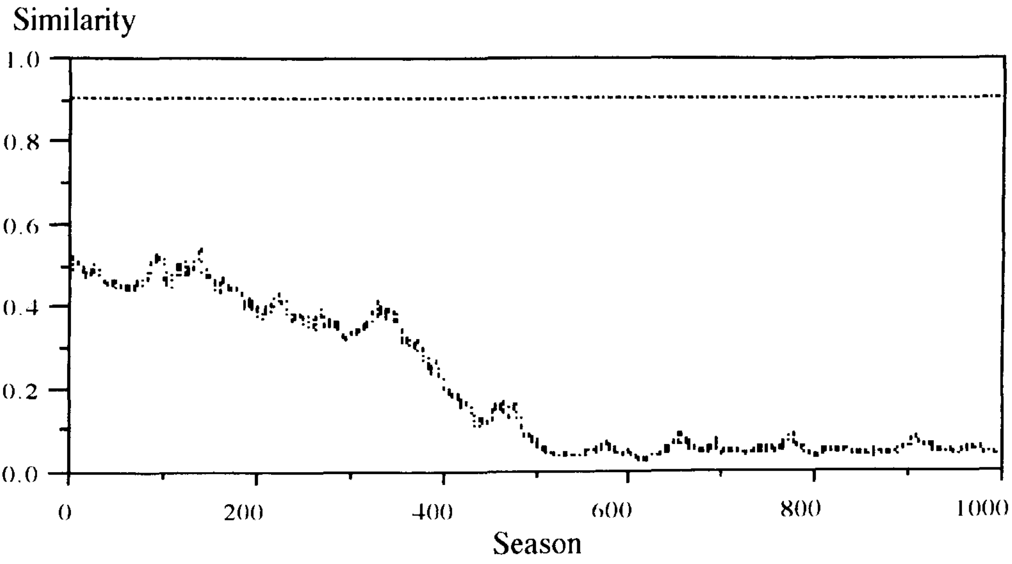
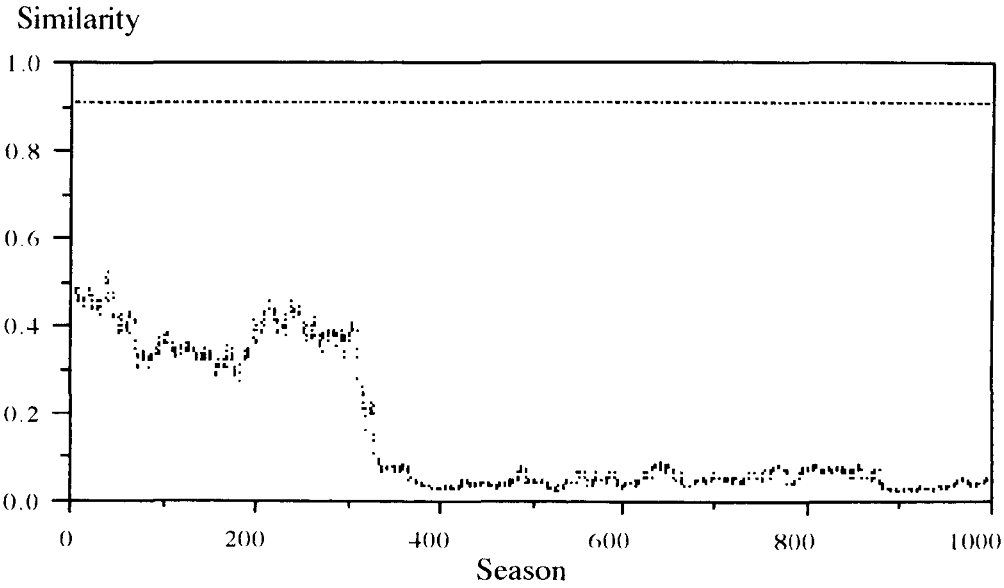


Figure 8.4 a. Two replicates of a MacComplex simulation which includes a cost to high similarity values. See also Figure 8.4 b. See text for parameter values.



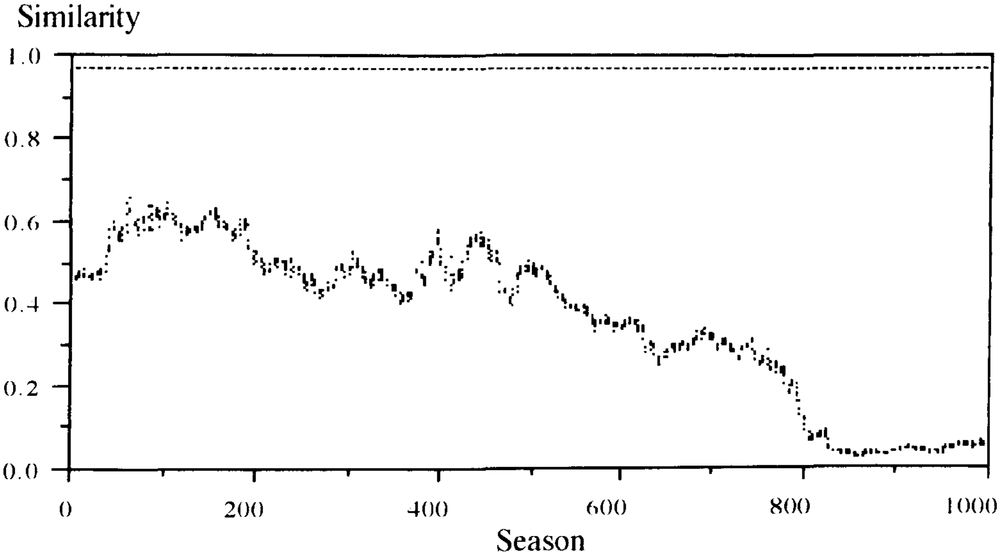


Figure 8.4 b. Two replicates of a MacComplex simulation which includes a cost to high similarity values. See also Figure 8.4 a. See text for parameter values.

this simulation and all show a decline to low similarity values analogous to a cryptic strategy.

8.3.6 Restoring the Mimetic Strategy.

It should be possible to reverse the evolution towards crypsis, evident in the previous simulation, by improving the ratio of Model to Non-Model prey. When the number of Models and Non-Models are restored to their original values, the evolution of mimicry re-appears when the simulation is repeated, as depicted in Figure 8.5 a and b; again all other parameters remain at their original values.

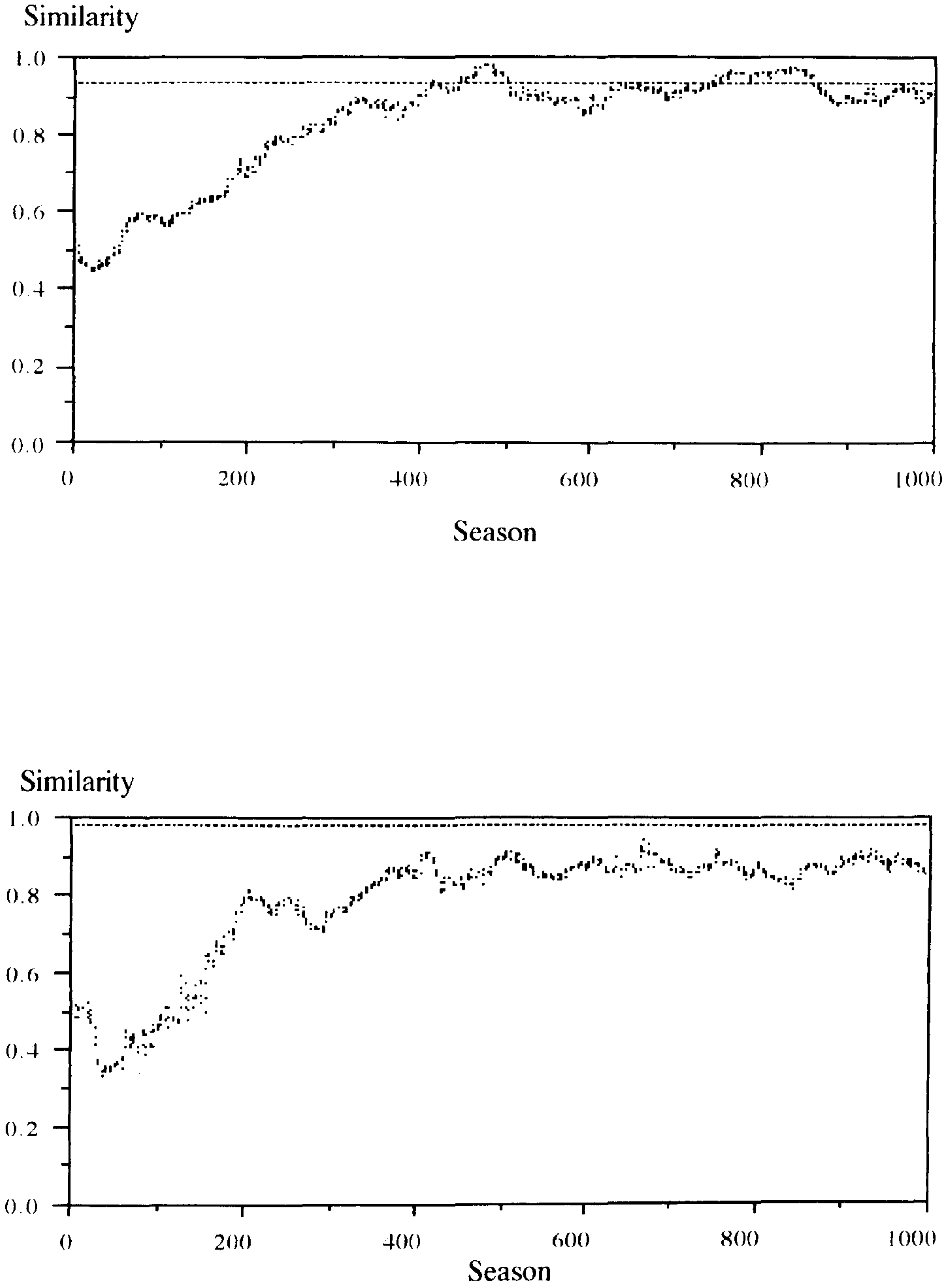
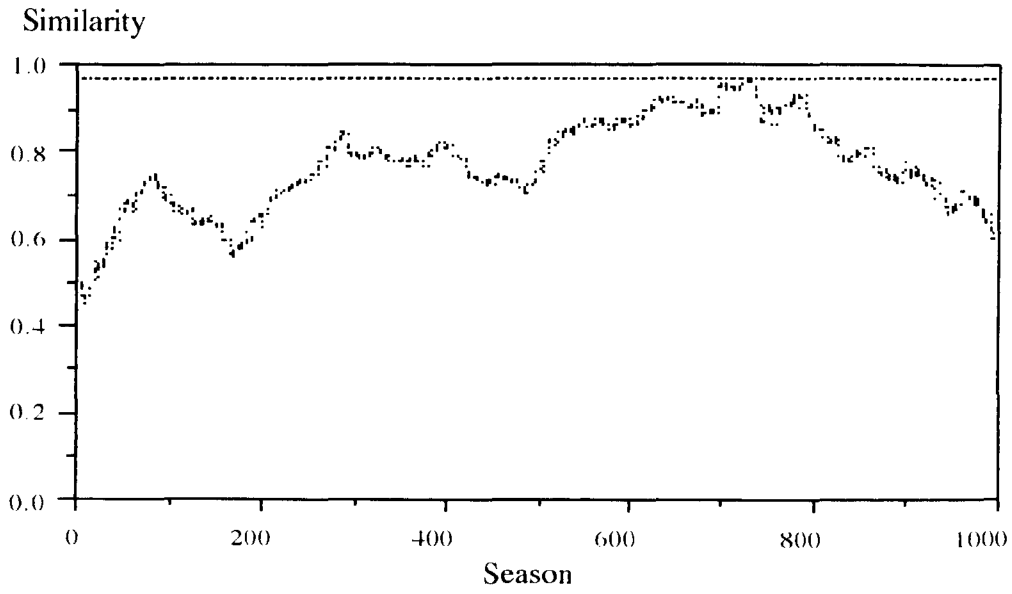


Figure 8.5 a. Two replicates of a MacComplex simulation where high similarities are beneficial despite their attendant costs. See also Figure 8.5 b. See text for parameter values.



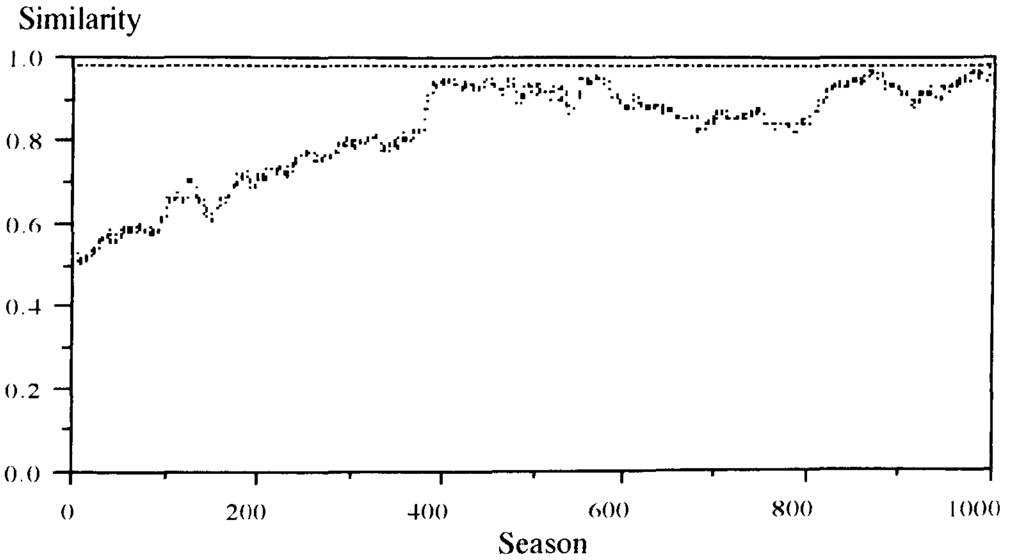


Figure 8.5 b. Two replicates of a MacComplex simulation where high similarities are beneficial despite their attendant costs. See also Figure 8.5 a. See text for parameter values.

8.4. Discussion.

8.4.1. MacComplex Successes.

The previous section demonstrates that the responses of *MacComplex* populations to a range of predatory regimes are wholly in accord with predictions which logically follow from simple definitions of the phenomenon of mimicry. These successes are not at all informative about mimetic systems; their significance is that they demonstrate that *MacComplex* has been correctly coded to provide a framework wherein the outcome of a succession of simulated predator-prey encounters translates into a change in the characteristics of the prey population. *MacComplex* is therefore a success in that it represents an elementary example of the class of models argued for in the preceding chapter. No claim is made for the realism of the model; there is no suggestion that the changes in population mean similarity value represent *realistic* responses to *realistic* predatory pressure. Nevertheless, *MacComplex* does have potential as a comparative model of mimicry.

8.4.2. Modelling the Costs of Mimicry.

It is obvious that the prey responses evident in the preceding simulations are heavily dependent on the particular mimicry cost function adopted. Indeed, it is only when an evolutionary context is added to simulations of mimicry systems that the costs of a mimetic strategy require explicit consideration, so models of this type are of value even in this general sense. It is likely that a higher probability of detection is a cost imposed on Mimics, and in principle the use of variously patterned artificial prey placed in the field could reveal the shape of this cost function. However, the major cost to mimicry is more probably the energetic and genetic cost of developing the appropriate pattern. These costs are likely to remain a highly theoretical aspect of models of this type and may therefore be the most significant limiting factor in achieving realistic representation of actual mimetic systems.

8.4.3. Using *MacComplex.*

In developing the original *Complex* model, the intention was to represent as many discrete aspects of real mimetic systems as was practically possible. It was this approach that, as discussed later, led predator decision-making to be represented as a multi-step process in an attempt to approximate each of the components of real decision making. *MacComplex* resulted from a different approach. It too, for instance, sought to simulate the outcome of predator decision making, but it did so not by representing individual components of decision-making, but by a simple, single process.

Some aspects of *Complex* simulations were, and would probably always remain, purely speculative, such as the evolutionary costs of mimicry discussed above. Other aspects, the relative abundance of different Mimic species for example, could be modelled using census data from real populations. What made *Complex* an exciting prospect was that a third class of factors, which were previously impractical or impossible to estimate, could with the aid of *Simpack* and similar aids, become estimable in real populations. *Complex* could, then, have formed the basis of a model which although theoretical in some respects, permitted field data to be used to simulate real mimicry complexes. Such a model has the potential to improve our understanding of mimicry even in the context of a single mimetic system since it can demonstrate the likely effect of particular manipulations on the dynamics of a real complex. The simpler approach taken with *MacComplex* has the obvious advantage that it has produced repeatible prey responses, but the attendant cost is that some of the potential power and flexibility of *Complex* is lost. The various simplifications incorporated into *MacComplex* could probably be manipulated to contrive almost any response desired, and were it used in this way it would rightly be viewed with some scepticism. However, there is reason to suppose that *MacComplex* could legitimately be used as a comparative model of mimicry systems. The basic theoretical parameters of *MacComplex* could be manipulated so that it produced a stable representation of a known mimicry complex. In a restricted sense, this would represent a realistic model of mimicry. With the basic parameters remaining fixed, data from novel complexes could be submitted to the model and the "responses" of the prey population compared with the state of the established complex. This comparative approach of "calibrating" the model with data from one complex, then analysing its behaviour when used on data from another, focusses attention on which aspects of the two complexes differ significantly. It represents the only way in which *MacComplex* , in its current form, could be used to test our understanding of mimicry theory against observation; further work is required to achieve a complete, general description of mimicry systems.

8.4.4. Future Models

The success of *MacComplex* , at least compared to its predecessor, may indicate that simplicity is the key to producing a usable model of mimetic systems. Any suggestion that future models might continue to require such simplification is less than encouraging if one accepts the argument, developed in the previous chapter, that modelling will have an increasingly critical role in the understanding mimetic complexes. The following sections close the discussion of model development by exploring some new approaches to various aspects of mimetic systems

8.4.4.1 Sub-models of Predator Behaviour.

Complex was abandoned largely because of the apparently unstable and erratic response of prey populations to the prevailing predatory pressure. *MacComplex* prey began to exhibit similar instability when, in some test versions of the program, the predator decision making process was made more elaborate than that described in section 8.2.2.4. above. The purpose of these elaborations was to arrive at a more complete, more realistic model of predator behaviour, which is essentially what determines the structure of a mimetic complex. It seems improbable that the best model of a predator's perceptual and cognitive system is a repeatedly enhanced and degraded estimate of the lowest threshold for Model type similarity values; the decisions of real predators are likely to be much more subtle and sophisticated integrations of past experience and available sensory information. The attempts to simulate this process in *Complex* and *MacComplex* may simply have resulted in inconsistent predator decision-making, which in turn contributed to erratic prey responses. A model which incorporates a realistic representation of predator behaviour is likely to offer a much more detailed understanding of the structure and dynamics of mimetic systems. Are such models a realistic hope ?

The apparent requirement is for nothing less than a model of predator cognition, and it is the fields of cognitive psychology and artificial intelligence that yield some indications that a realistic model of predator behaviour may be achievable. It has long been appreciated by cognitive psychologists and artificial intelligence researchers, that for the human brain to perform a multiplicity of complex tasks, such as pattern recognition, with such alacrity, it must be processing its input in parallel (Johnson-Laird 1988). In order to investigate the properties of parallel systems, techniques were developed to simulate parallel processing on serial computers. Some of the products of that approach are termed Parallel Distributed Processors, or, more widely, Neural Networks. The properties that these networks exhibit are so unlike those most expect of computers that they have been greeted with near euphoria in some circles and are seen uncritically by some as a computing panacea. While some do overstate the case for the potential of networks, there is no doubt that some networks have achieved remarkable feats.

Neural Networks simulate the behaviour of a large number of highly interconnected processing units, somewhat analagous to nerve cells, which handle their input in parallel (Feldman and Ballard 1982, Rumelhart and McClelland 1986, McClelland and Rumelhart 1986, Crick 1989). The units in the network are richly interconnected, each unit affecting the behaviour of a number of other units through a series of excitatory and inhibitory connections. As a result of this interconnection, these networks are capable of "learning". A pattern of stimulation presented at the top of such a network is modified by its internal activity before being produced at the bottom as an output pattern. For a given input pattern, the output pattern is initially little more than random, bearing no obvious relationship with the input. However, the disparity between the current output pattern and the desired output pattern can be used as a basis for calculating modifications to the strength of connection between units, such that the desired output becomes more likely when the input pattern is next presented. Over a series of such "tutoring" sessions, a stable relationship of interconnection can (but does not always) emerge so that the input pattern consistently produces the desired output.

This capacity to respond correctly to the input pattern comes, not from the application and progressive refinement of a restricted set of rules, programmed into the network, but from its "experience". A trained network has effectively succeeded in extracting the correct rule for tranforming input into output, from an analysis of its performance over a set of specific, discrete presentations.

Trained networks are said to have a "distributed representation" of the "knowledge" that these rules represent. The capacity to respond appropriately to input is not located in any one specific part of the network: it is distributed throughout the processing units in the form of a stable pattern of interconnection. One product of this distribution of knowledge is termed "graceful degradation" and it too is a property shared with the brain. Networks are said to degrade gracefully because they can continue to produce the correct output even if part of the input pattern, or the network itself, is removed; the pattern of mutual excitation and inhibition is such that the internal activity of the network "restores" the missing parts of the pattern. This means that should an inferior quality copy of the tutor pattern be presented, it may be that the network will be capable of restoring the missing or incorrect parts of the input and of continuing to give the correct output response. In effect, this means that rule extraction can represent a "generalization" if the tutoring consists of the presentation of a set of slightly differing patterns rather than the repeated presentation of the same pattern. In such cases, the extracted rule reflects the shared features of the patterns and the network effectively becomes capable of categorizing an input as belonging, or failing to belong to, the class established during tutoring. A novel variation of the tutor pattern will succeed in producing the correct output only if it possess sufficient likeness to the set of patterns used to tutor the network and those that do not, could legitimately be described as being part of a different class.

Neural networks are not merely illustrative models: they are capable of reproducing the behaviour of real cognitive systems. One of the earliest models was that of Kohonen *et al* (1981), a network which, having been tutored on series of human faces, proved capable of recognising those faces at novel angles. Sabbah (1985) reports on models which are capable of recognising outline ("origami") shapes. McClelland and Rumelhart (1986) describe a number of network models of psychological and biological systems. One of the most encouraging properties of these models is that they are capable of making errors similar to those made by real cognitive systems. Seidenberg *et al* (1987) desribe a network capable of recognising and pronouncing words, having learned by example. The errors this system made during training corresponded to those made by children in phases of word acquisition. By denying this network some of its "neurones" it proved possible to produce behaviour typical of poor readers, and when parts of the full network were destroyed, the results were similar to a type of acquired dyslexia.

The potential benefits of using a neural network as a model of predator cognitive behaviour should be obvious. While neural networks are not necessarily proposed as a model of predator *learning* , their tutoring phase could establish classes of input pattern analagous to the "Model" class that a predator might establish during learning. A successful Mimic is one which, in the given circumstances of the encounter, is sufficiently similar to the Model species to prompt the predator to mistakenly assign it to the Model class, and in principle it would appear that a network may make similar errors. More detailed work would be required to establish whether any similarities between networks and real predators were more than superficial; if they were, the potential benefits are substantial.

A network would be a tireless subject, capable of endless training sessions and experimental trials. In a field hampered by the difficulty of acquiring and maintaining naive predators, an adequate network represents an endless pool of naive model predators, the "experience" of each of which could be manipulated with great finesse and recorded in great detail. In short, if networks did prove to have a significant predictive value then they offer the degree of experimental manipulation and the sample sizes which the study of mimicry has so sorely lacked.

The technique of neural networking is not, however, without its own particular limitations, so while there is clearly great potential, it remains uncertain how much of that potential can be realised. For some applications, it proves impossible to construct a neural network capable of learning the required input pattern, and where it is possible, network construction represents a substantial undertaking in its own right, requiring some computing expertise, a grasp of the underlying algebra of neural networks and access to suitable hardware and software.

8.4.4.2. The Signal Detection Approach.

A neural network which behaved with some general similarity to a real predator represents only a partial solution to the problem of producing a realistic model of predator cognition. Some means must also exist for comparing and calibrating the behaviour of a network against that of a sample of real predators. The previous chapter reported on mathematical models of mimicry which incorporated a body of theory which might provide such a mechanism.

Getty (1985) describes the perceptual problem faced by a predator encountering a mimic as one of signal detection. Signal Detection Theory has been developed and applied in a variety of fields, such as radar and telecommunications analysis and medical diagnostics, and it now stands as a complex field in its own right. Fundamentally, it relates to those situations where a perceiver must discriminate a positive signal from unwanted or distracting background "noise". Swets and Pickett (1982), for instance, provide a detailed analysis of a signal detection task where practitioners are required to discriminate potentially harmful abnormalities appearing on mammograms from benign tissue concentrations. Signal detection theory provides a theoretical framework which describes the strategy and performance of observers dealing with such situations, and of particular interest in the current context is the method it may provide of describing the perceptual performance of predators. Getty correctly sees a predator's problem as being the discrimination of the Mimic signal from the unwanted background (visual) "noise" of the Model's signal.

A predator which correctly identifies and attacks a Mimic is described as having made a "hit", and one that mistakenly attacks a Model as having suffered a " false alarm". Since, by definition, Models and Mimics are not perfectly discriminable, the relationship between the probability of making a hit and the probability of a false alarm is a constrained one; a predator cannot vary its probability of a hit independently of its chances of suffering false alarms. The relationship between p(Hit) and p(False

Alarm) for a given perceiver is referred to as the Receiver Operating Characteristic or ROC curve. This constrained relationship can be modelled to a good approximation by a simple power law relationship, p(Hit) = p(False Alarm) ^{k}. An illustration of this model relationship is presented in Figure 8.6, for several values of the exponent K.

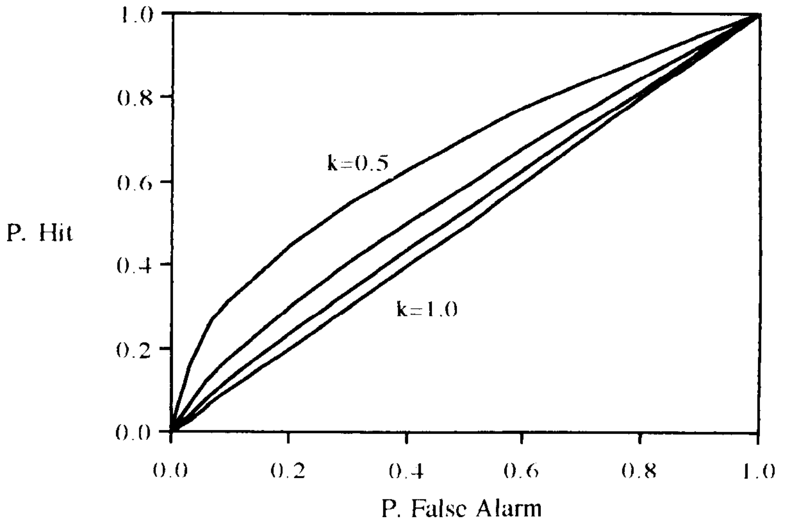


Figure 8.6. Power Law Approximations to ROCcurves, for four values of the exponent K, 1.0, 0.9,0.75 and 0.5.

K describes the constraint on the predator when making the discrimination between Model and Mimic. Where K = 1.0, the predator is incapable of making any discrimination and p(Hit) is always equal to p(False Alarm). Where K = 0.0, a predator is capable of achieving a perfect Hit rate with no probability of False Alarms, which is not possible in the case of mimicry. Predators in real mimetic systems are likely to be described by intermediate K values. The value of K effectively places an upper limit on the perceptual performance of the predator, an upper limit on the p(Hit) it can achieve for a given p(False Alarm) cost. Predators have freedom to operate at or below this limit and may have some freedom as to where they operate along this curve; a predator may, for instance, elect to operate at the lower end of the curve where p(False Alarm) (and therefore p(Hit)) is low because of the costs of encountering a particularly noxious Model. Alternatively, a robust predator might operate higher up the curve where its tolerance to a high p(False Alarm) enables it to achieve a high p(Hit).

In effect, signal detection theory could be used to describe the performance of a predator discriminating between states. If the value of K could be determined for real Predator-Model-Mimic relationships it would provide a concise means of comparing the behaviour of neural networks and real predators.

There are, however, substantial difficulties. K describes the upper limit upon the ability of a predator to discriminate between Models and Mimics, and this limit is really the product of two factors, the degree of discrepancy between model and mimic patterns, and, secondly, the capacity of the predator's perceptual system to assess that discrepancy. Both of these factors were considered of crucial importance to any formal model of hoverfly mimicry complexes, but, clearly, an assessment of K does not provide an indication of the partial effects of these two factors. While it would be possible to use K as an index of, for instance, the similarity of hoverfly and wasp patterns, the value of that index would be dependent upon the properties of the perceiver of those patterns. Similarly, K as an assessment of the perceptual abilities of the predator will be contingent on the particular pattern types presented. It was partially for this reason that efforts to devise an index of pattern similarity were directed toward producing an index of similarity which was perceiver independent.

There are also a number of practical difficulities associated with assessing the value of K. McNicol (1972) describes the design and execution of a rating scale experiment which yields a data set from which a ROC curve can be plotted (see also Swets and Pickett (1982)). These experiments usually involve a human subject providing judgements about the presence of signal or noise over a long series of presentations, along with a rating which describes their confidence in each assessment they make. This method is intended to make the perceiver simultaneously hold a number of different decision criteria so that the path of their ROC curve can be estimated from a series of points; the situation is analagous to a predator simultaneously tolerating several levels of risk and operating at different points on their ROC curve (Swets and Pickett describe methods of estimating perceiver characteristics from just a single point, but there are limits to the reliability of this method). Even with human perceivers, undertaking a rating scale experiment is no small task. Nevertheless, it would be appropriate to adopt operant conditioning techniques so that a laboratory avian model predator has the opportunity to make judgements about the presence of the signal and noise conditions over a series of visual presentations. It may also be possible to provide an estimate of the predator's confidence in making the judgement by, for example, timing the delay in its response. Though this laboratory based approach still suffers some of the constraints discussed in Chapter Four it is in principle possible to conduct a rating scale experiment with an avian model predator; the major difficulty lies in the number of trials that are required to provide a reliable ROC trajectory. McNicol (1972) recommends a minimum of 250 signal-noise pair presentations (therefore some 500 presentations per individual plus control presentations). Providing an estimate of K for a reasonable number of predatory individuals and for a reasonable number of hoverfly species therefore represents a very considerable logistical effort.

8.4.4.3. Prey Sub-Models.

Two obvious simplifications in the representation of prey populations could be overcome by the adoption of a simple model for a "genotype" of each prey individual. Currently the "appearance" of a prey individual is described simply by a value which indicates its similarity to the Model species, much as a *Simpack* analysis would describe the similarity of two patterns. A prey individual in *MacComplex* does not have a pattern it is similarities, not patterns which *have* similarity, which evolve through *MacComplex* time. This first simplification could be overcome if each individual was described by a code which generated a phenotypic pattern. A simulation could then describe the evolution of simulated patterns, not just similarity values. It is possible that such a sophistication would add little to the realism of the model: what makes it fascinating are the possible properties of the neural network models of predator behaviour described in section 8.4.1.1. above. If the code which represents the patterns of individuals is sufficiently adaptable and the behaviour of the neural networks really can be made similar to that of real predators, it is possible that a model like *MacComplex* could see the "evolution" of artificial, hoverfly-like patterns. This possibility is intriguing because it may indicate that some features of the Mimic pattern are more significant than others in the task of deceiving the predator, and it may reveal that some Mimics appear bad only because they reproduce only the critical features of the Model pattern.

A simulated genetic code for each individual would improve on the other key simplification, the model of prey reproduction. Currently, offspring are created by adding random variations to a randomly selected parent individual. A simple genetic model would permit the simulation of sexual reproduction and spontaneous mutation to achieve stability and variation in the prey populations. Such a model may exhibit speciation events and polymorphism within prey populations.

This kind of extension to the basic model may not be a purely theoretical exercise. The idea for a simple genetic model was inspired by Dawkins' (1988) *Biomorph* model which indicates how simple pattern coding rules subjected to a form of cumulative selection, can evolve intricate and unexpected patterns. It is possible that a similar set of coded drawing rules could be created to generate a whole diversity of hoverfly-like patterns, and it may prove possible to relate these simple models to the real genetic basis of hoverfly patterns (Heal 1979, 1982).

8.5. Summary

This Chapter has reported on the development of elementary models of mimicry which permit the outcome of interactions between predators, Model and Non-Model prey to modify the characteristics of the prey populations. Difficulties with some versions of these models indicate that simulating complex processes such as predator decision-making is not straightforward. However, the behaviour of simplified models is consistent with the basic predictions of mimicry theory, and there is a possibility that the current model will be productive if used as part of a comparative approach to a variety of mimicry complexes. There are a number of exciting developments in other fields which might be used to extend simple models of this type into more realistic and sophisticated mathematical models of mimicry.

Conclusion.

The hoverflies : a case of poor mimicry? From the outset, it was obvious that a complete explanation for the paradox of mimicry in the hoverflies could not be achieved in the term of the project. The decision to explore how far conventional mimicry theory could explain the coloration of hoverflies represented simply the most appropriate first step towards a complete understanding of a complex and intriguing natural phenomenon.

Establishing how much protection a Mimic enjoys in its natural state is a problem so intractable that it has prevented anything more than the most basic empirical advance in a field that may have a unique role in understanding evolution. The traditional method of testing mimetic success by presenting a series of Model and Mimic individuals to a captive predator seemed particularly inappropriate in the case of these fast, agile flies. However, the assertion that such tests inevitably introduce a bias in favour of the predator, seemed partly applicable to many similar tests of mimetic success. The underlying purpose of the thesis therefore became to develop novel empirical approaches to supplement these conventional techniques. Primarily, the intention was to explore the mimetic status of the hoverflies, but it was hoped that this could be done in a way that might benefit other studies of mimicry. One specific attribute of hoverfly patterns, their diversity, suggested that one particular facility would be invaluable to the research. Human judgements about the similarity of hoverflies to their supposed Models appeared to be heavily dependent on prior experience and preconception, and seemed to shift with time and familiarity. The need to bring order and constancy to this complex, fluid situation suggested that an objective method of measuring pattern similarities was an essential prerequisite for success in this study. The vast majority of the practical work undertaken during this project was dedicated to developing an objective index of pattern similarity, demonstrating its reliability, and exploring some of its most obvious applications.

Adopting the conventional approach to testing mimicry, as reported in Chapter Three, did make specific contributions to the list of possible determinants of mimetic success. It suggested that factors such as social learning and dominance hierarchies in group-feeding predators may have some minor qualitative and quantitative effects on the predatory pressure imposed on some mimetic complexes. It also emphasized that in some circumstances, predators may operate simple "attack all" rules which preclude any degree of mimetic protection.

How has an objective index of similarity supplemented these conventionally derived ideas ? It has made possible the direct comparison of different examples of a mimetic complex. Such a comparison revealed both differences and similarities in the structure of two widely separated hoverfly communities. There were some indications that the differences might be attributable to the effect of man's agricultural activity, which may reduce the diversity of hoverfly species and exaggerate existing patterns of abundance. Simultaneously the similarities in community structure revealed an objective basis to the perceived paradox: the most common "Mimic" does indeed have the lowest actual similarity to the supposed Model. However, the use of an index of objective similarity also provided the first indication that the perceived similarity of hoverfly patterns may not be directly predictable from their actual similarity to the Model; species considered to be relatively accomplished Mimics did score a high similarity rating, but so too did some "poor" Mimics. The perceived similarity between a hoverfly and its apparent Model may depend, not upon the degree of actual similarity, but upon some as yet undetermined features or properties of its pattern structure. This immediately leads to the suggestion that "poor" Mimics may in some sense be exploiting the properties of predator perceptual systems to achieve mimetic protection, despite a relatively low degree of actual similarity.

The similarity index has also enabled a novel comparative analysis of mimicry by allowing direct comparison of the degree of Model-Mimic similarity in a wide variety of examples of visual mimicry. Even the single demonstration comparison carried out in Chapter Six was sufficient to indicate that, if there is at least a broad correlation between actual and perceived similarity, either the hoverfly-wasp or the Monarch-Viceroy system is exceptional for its respective class of mimicry. Alternatively, it may suggest that one aspect of mimicry theory, the prediction that Model-Mimic "resemblance" should be lower in Mullerian than in Batesian systems, may no longer be appropriate with the advent of a distinction between actual and perceived similarity.

Undoubtedly the most intriguing determinant of mimetic success is the perceptual and cognitive performance of predators. It is in this context that an objective index of similarity may have the most significant impact. Appendix Five contains a journal reprint reporting work by Dittrich Winand and others on an operant conditioning approach to imperfect mimicry in the hoverflies. In one group of these trials, pigeons trained to peck in response to the presentation of wasp images, were presented with images of various apparently mimetic hoverflies. The rate of pecking at the hoverfly images was used as an index of the perceived similarity between wasp and hoverfly. In themselves, the results of this experiment would have been informative about the possible status of the "poor" Mimics. However, they were given a unique dimension by relating the index of perceived similarity to actual pattern similarity, as measured by a software system developed by F.S. Gilbert. This system is in some sense the descendant of the similarity-indexing software described in this thesis. Consequently, while it would be inappropriate to draw too heavily on the results reported in Appendix Five, this thesis can claim a legitimate interest in how the use of an index of similarity contributed to the operant conditioning approach, and in how the results obtained relate to the ideas put forward in the preceding chapters. Those results provide an astonishingly clear indication of the relationship between actual and perceived similarity in the apparently mimetic hoverflies and their supposed Models. This relationship is certainly not a simple correlation, though it is perhaps not as irregular as that implied by the results in Chapter Five. Nevertheless, the nature of that relationship is such that species with relatively low actual similarities to the Model may enjoy a significant degree of mimetic protection. "Poor" Mimics, it seems.

may not be unsuccessful.

The second major theme of this thesis, the need for mathematical models of mimicry which relate the action of predators to the structure and dynamics of mimetic systems, requires further development. However, the operant conditioning results reported in Appendix Five provide precisely the type of information required if the most significant impediment to the development of such models, i.e. modelling predator behaviour, is to be removed.

At the beginning of the project reported in this thesis, the need for, and potential benefits of, an index of objective similarity were entirely apparent. How such an index might be devised, and how it might behave, were not. The single most significant achievement of this thesis has been to demonstrate that an objective index of similarity can enable a variety of new approaches to some of the most intractable problems in mimicry, including the apparent paradox of mimicry in the hoverflies.

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Appendix One

Simpack User Guide.

A.1.1 The Purpose of *Simpack* .

Simpack has been developed for the purpose of assigning, independently of human subjective judgement, a value to the similarity of two or more visual patterns.

A.1.2 Principle.

The principle adopted to assign such values is based upon a simple assumption about "similarity". The assumption is that if two patterns are dissimilar, relatively coarse grained information will be sufficient to discriminate between them. Conversely, discriminating between two similar patterns will require detailed, fine grained information. The quality of information required to discriminate two patterns, acts as an index of similarity for those patterns.

A.1.3 Method.

The package produces a series of files to describe each pattern in the comparison. Each file in each file series represents a different degree of quality of information about the original pattern. In principle, assigning a value to the similarity of the two patterns is then simple. The files representing the two patterns at the lowest level of quality are tested for statistical difference. If they are not statistically seperable, the analysis proceeds to the next highest level of information quality (i.e. the next most detailed file) and tested again. The level of the file series (scale of information quality) at which the respective data sets become seperable is taken as the index of similarity for the two patterns represented by those files. (This remains a good way of visualizing the purpose and behaviour of *Simpack* , but, in practice, various limitations on the system restrict the value of this method of analysis; Chapter Four describes the analysis of *Simpack* data in greater detail).

A.1.4 Image Information Quality.

Details of the generation of the required data sets will be discussed later, but it is important to appreciate what is meant by "information quality" before detailed operating instructions are presented. The package deals with video images of patterns digitized onto a 320x256 pixel format, each pixel taking one of four colours. To produce a low quality representation of an image on this format, the picture is divided up into a set of "blocks", each block being a sort of "super-pixel" covering many of the original pixels. The colour value taken by this block is the colour most common among the original pixels covered by the block. Thus, if a block covers 100 pixels, 90 of which are yellow, the block is designated yellow. In the event that two colours are equally common, the block is randomly assigned as one of the colours. A low quality representation of an image consists of a few large blocks, and a high quality one, many small blocks. The different levels of information quality needed for the analysis are actually different sizes of "blocking" of the original image. Note, though, that no new "blocked" image is produced, it is the data which would represent such an image that is dealt with.

A.1.5 Overview of the System.

The process which the package is designed to follow is very simple. Images of the patterns to be compared are input into the computer and stored on disc. Any image capture faults in this image are corrected manually, and the revised version saved. Each image is then broken down into a file which lists the colour value of every point (pixel) on the image. It is this "Primary" file which provides the raw data set for the generation of all "blocked" files (i.e. for all levels of "quality of information"). The Primary file also constitutes a level of quality, the highest, in its own right. The User then constructs a list of the block sizes to be used in the image blocking process. The package examines this list and works out various details necessary for the running of the rest of the system, such as the length, name, size and destination of the files to be generated. The next task is to "run" this list on a specified Primary file and this automatically generates some or all of the blocked files specified in the series. When the list has been run on all the Primary files which the User wishes to deal with, files or groups of files are compared and the degree of correspondence between them is reported. The package does not provide a means for analysing this data; performing the appropriate statistical analysis is the responsibility of the User.

A.1.6 Required Equipment.

To operate the *Simpack* similarity system, the following are required;

A BBC "B" micro-computer installed with a Watford Electronics Video Beeb micro-processor, the LVL disc operating system and two floppy disc drives.

The Simpack Systems Disc containing the software described below.

A Watford Electronics VideoBeeb Digitising Unit

A Monochrome Video Camera.

A BBC compatible printer.

A.1.7. Operating the *Simpack* Package.

Programs to perform the various stages of the image analysis described above are integrated by a simple menu system. The following sections describe how to call up this menu and how to access the various programs from it. Specific key presses appear enclosed in "<" and ">" symbols.

To load the *Simpack* Menu, place the Systems disc in the top drive and type;

CHAIN "MENU" <return>

The result of this command will be the appearence of a simple menu with a series of options corresponding to *Simpack* program modules. Each module has a unique three letter mnemonic shown at the right hand side of the screen and modules are selected by entering these mnemonics at the keyboard. The appropriate module is loaded from the Systems Disc, so this should be left in place unless there are instructions to remove it. Some modules will request a confirmation from the User before performing operations which might result in data loss. When asked to confirm an operation simply type;

CON <return>

Another common request is for the location of a file or group of files and here "location" means "which disc drive". Reply by typing the number of the drive 0,1,2,3 (0 being the top side of the top disc, 2 its under side, 1 the top side of the bottom disc and 3 its underside). In some cases it will be essential that the Sytems disc be present in the top drive ("locations" 0 and 2). The bottom drive should be used for data discs when possible. Only in the two options that deal with the comparison of files (SFC and

GFC) will it be useful to remove the Systems disc, and here prompts are provided for its removal and re-insertion.

A.1.8. Error Handling.

Each module affords only the most basic error trapping facilities. If a module fails, for instance as a result of entering the incorrect kind of data, typing;

RUN <return>

will restart it. The User should assume that any work produced before the failure is lost and will need to be repeated. Some modules will re-start themselves under instruction from the User. A failure during one of these re-runs does not mean that data from previous run has been lost. If RUN fails to restart the module, the most likely explanation is that some files are still "open" for alteration. They should be closed with the command;

CLOSE#0 <return>

followed by;

RUN <return>

A.1.9. Module Operating Instructions.

A.1.9.1 Image Capture (ICP).

Purpose: Capturing and storing images digitized from a video source.

Entry into this module elicits a prompt to connect the camera and digitizer. Ensure that the camera is switched on and its "video out" port connected to the digitizser, which should itself be connected to the BBC's User Port. The digitizer controls should be set to Mode 1 and "Manual Level" control. Press any key to continue. If any connections are at fault the program returns to the original prompt. Check for faults and press a key again. Note that the <escape> key is disabled and the only way of halting the program is to press <break>. A digitized image from the camera will now be displayed on the screen. Two cross-hair lines are temporarily superimposed on the image to help with alignment. The top (command) line presents two options which are explained below. The image will now remain static until a key is pressed, whereupon the display will be updated from the video camera. Pressing and holding down the <space> bar will cause several successive updates, but long key holds can overload the system. Adjustments should be made to the digitizer controls in accordance with the instructions given in the Watford Electronics Digitizer User Guide, to achieve a good representation of the image. If necessary, one or both of the centre-lines can be used to align the image, ensuring that it is completely contained within the screen boundary (i.e. below the command line and to the right of the left hand margin). Once the image has been satisfactorily represented on the screen, it can be saved as a disc file. Press <S> (not followed by <return>) and a request for a file name will appear, give the image a two letter name and press <return>. Specify which drive the image should be stored on, preferably one of the two bottom drives. The package then waits for a synch signal from the camera and updates the image on the screen, but it does not overlay the centrelines or command line. The digitized image has now been stored on disc. The program will return to the normal mode of operation in preparation for a new image. Pressing "Q" (no <return>) will quit this module and return to the menu.

A.1.9.2. Image Editor (FSE).

Purpose: To retrieve image files, allow alterations to them and to save the new files.

On entering, the module requests the name and location of an image file created under the Image Capture option. Insert the disc holding the file to be dealt with, and enter these details, then press a key to continue. The module opens the requested Image file and displays it on the screen. The command line offers the User a set of options and, at the far right of the screen, a "Pen" which can be used to alter the picture. The Pen is moved around the screen with the four arrow keys on the top right of the keyboard. The rate at which the Pen moves can be increased by a factor of four by simultaneously holding down the <TAB> key and one of the arrow keys. The Pen can be moved out of the normal range of the screen without causing error and will plot new points here, but be careful not to lose the Pen. Any area of the screen can be altered using the Pen, but changes to the command line will be erased when the line is re-printed. The Pen should used to create a polygon around the area to be changed and this polygon can then be filled with any of the four colours which the screen can display in its digitizing mode. To construct the polygon, move the Pen to a point at the edge of the area to be changed; pressing the <return> key will store this point in the computer's memory. Moving the pen again will reveal that a "rubber banded" line will be drawn from the last point stored to the current position of the Pen. Use the cursor control keys to lay this line along the edge of the area to be changed and press the <return> key again. The new point is also stored and the previously "rubber banded" line now becomes permanent. Repeat this process until the area to be changed is encircled with permanent lines. Note that the maximum number of points that can be stored is 50 (a 49 sided polygon) and that if this limit is exceeded, the program will fail. Once the polygon has been constructed around the area to be changed, place the pen within its boundary and press the <Q> key (shown on the command line as the prompt for "fill"). When the key is pressed the command line is changed and will offer the choice of four colours to fill the area with. Select the appropriate colour by typing in its number followed by <return>. (Sometimes a "Q" will appear on the command line, make sure this is deleted before entering a colour choice, otherwise the area will be filled with black regardless of the colour number input). The area will be filled with this colour and the command line returned to its original status. The program will treat each side of the polygon as the outer edge of triangle and the final Pen position as its apex, and will fill each such triangle with the requested colour. This means that care must be taken to place the Pen in such a position that the computer can draw lines from the ends of each of the polygon sides to the final pen position without cutting through any of the other edges. This becomes readily apparent after some practice on the editor and the results of such mistakes are fairly easy to correct.

Repeating this procedure, make appropriate alterations to the image and then press the <@> key. The command line will request a file name under which to store the edited file and will show the original name of the Image File. If this original file name is re-used, the un-edited image will be lost, so it is recommended that a new name be derived from the previous name, for instance by suffixing another letter. This will mean that both old and new versions of the image will be saved. It is further recommended that the new filename should not exceed three characters. It is necessary to specify which disc the file should be sent to. Entering this and pressing <return> will save the image, so if discs are to be changed, do so before pressing <return>.

After the file had been saved, the program offers the option of continuing; any reply other than <Y> <return> will return control to the menu.

A.1.9.3. Primary File Generation (PFG).

Purpose: To recall an edited Image file from disc and generate from it a named Primary file that lists the colour value of every point on the image.

The module requests the name and location (disc number) of an edited Image file. Load the disc with the Image file and press a key to call the image onto the screen. The command line at the top of the screen requests a four character name for the Primary File to be generated and a location to send the file to. Supply these details and, when prompted, insert a disc to receive the new Primary file, making sure there is sufficient space to hold it (one side of a disc will hold only two Primary files). Press a key to begin the generation. The process will take about five minutes. After file generation is complete the module gives the option of processing further Image files. Typing <Y> re-starts the unit, <N> returns to the main menu.

A.1.9.4. Master List Options (MLO).

Purpose: To load, edit or construct a list of block sizes which the user wishes to use in generating the blocked file series for each Primary file.

Entering this module automatically loads the most recently used Master List from the Systems disc. The first column of the display shows the "level" number of each entry in the Master List; each level contains information about a file which will be generated when the Master List is "Run" on a Primary file. There are 80 levels to the Master List, but they need not all be filled. For each level an "NPVB" and an "NPHB" value is required. These values specifiy the block size to be used for that level in terms of the number of pixels on each axis of the block. Thus an NPVB of

4 and an NPHB of 6 will generate a block 4 pixels high and 6 pixels wide, it therefore would cover 4x6 of the original pixels. When values for NPVB and NPHB are entered the editor divides the height of the screen (256 pixels) by NPVB and the width of the screen (320 pixels) by NPHB to give two new values, NVB and NHB, the number of blocks on the vertical and horizontal axes of the picture. Thus if NPVB is 4 and NPHB is 4, NVB will be 64 (256/4) and NHB will be 80 (320/4). This means that the orignal image (more accurately the data for that image) will be divided into 64 rows by 80 columns and hence a total of 5120 (80x64) blocks will be generated. This latter figure is represented in the TOTAL column of the dipslay. The values of NPVB and NPHB chosen above produce a whole number of blocks. It is possible to choose block sizes which would generate fractions of blocks, for instance a NPVB of 12 would give an NVB of 21.333 blocks. In fact, the fraction of a block is never generated, it is simply missed off. Hence in this instance 0.333 of a block which is 21 pixels high will not be processed, so about 7 pixels (0.333 x 21) at the very top of the screen will be ignored. A similar argument will apply for the horizontal axis of the image. If NHVB and NPHB values which generate fractions of blocks are chosen, it is always the fractions of blocks at the right hand margin of the screen and the top of the screen which are "chopped off". It is in the interests of the User to minimize this chop-off effect, but as long as the chop-off is small, it will have a negligible effect on the final result. For instance, seven pixels above each block at the top of the image will fall within the command line space so nothing of value will be lost. The User is free to create a Master List from scratch . Enter <C>, as indicated by the options list at the bottom of the screen, and a new command line will appear requesting

the value of NPVB for the first level of the new list. After entering this value, a request for the corresponding value of NPHB will appear. Repeat this until a new Master List has been created. In response to the next request for an NPVB value, enter -1. The display will then be updated. Any errors made in the construction of a new list can be corrected, or alterations made to the list loaded from the Systems disc, using the editing facilities. Enter <E> to request an edit, then enter the value of the level to be altered. The prompts will request new NPVB and NPHB values. After entering this new data there are two options for dealing with it. "Inserting" (<I>) will cause all other entries in the list to be moved down and the new values to be slotted in at the requested level. "Replacing" (<R>) will simply over-write the old values at that level with the newly entered values. The Master List is held on the systems disc so that it can be stored between sessions. Consequently, if any changes are made to the Master List, they must be saved onto the Systems disc. The options line at the bottom of the editor offers a Save facility and when this is called a confirmation will be required. Enter CON <return> to save. Alternatively, if an attempt is made to exit back to the main Menu having made, but not saved, an alteration to the list, the system will advise that no save has been made and will give the option of saving. If this option is taken, the Master List is saved and control is passed back to the editor. An attempt to exit will not now be obstructed. If the option to save is not taken, any changes made to the Master List will be lost. Any Master List created or altered, and then saved, will now become the new Master List and will be automatically loaded from the Systems disc when *Simpack* requires it.

A.1.9.5. Compile Master List (CML).

Purpose: To examine the Master List produced by the User to determine the number, name, length and location of all the files to be generated when the Master List is "Run" on a Primary File.

This module is self-running and requires no input other than to confirm the compilation (type "CON"<return>), a precaution against mistakenly erasing the previous Master List before it is finished with. The module works out information needed by the rest of the system to run itself, and to guide the User. The module offers the option of producing a hard copy of the compiled Master List and Users should obtain a copy (reply <Y> to the request) before beginning to Run the Master List on any Primary files. The compiled Master List is the guide through the rest of the system, do not change it by recompiling unless a new Master List is created.

A.1.9.6. Running the Master List (RML).

Purpose: To generate a series of blocked files, according to the compiled Master List, representing a given Primary file .

Before running this module, ensure that the desired Master List has been compiled, since this will contain information necessary to run the module. If the module has been used before, and has not finished processing the entire Master List for the specified Primary file, it will report which Primary file was being used and the next level of the Master List to be generated. The User should therefore continue to process this Primary file. If the module has not been used, or if it has completely finished with the Primary file it was previously processing, it will request the name of a new Primary File. Enter this name and the location of the file (this must be either 1 or 3 since only the bottom drive can be used). Insert the disc and press a key. The system will request a confirmation that any previously held Primary can be erased, reply <Y> but do not press <return>. The system will delete this file and copy the new Primary onto the underside of the Systems Disc. Unfortunately, copying such a large file destroys anything currently held in the computer's memory, so the program will need to be reloaded after the copying process is complete. A short hand method is provided for doing this by pressing the f0 key when instructed. The system will now be satisfied that a new Primary file is present and will next request how it should be dealt with. The User has three options when generating the new files. Files can be generated singly (i.e. the next blocked file specified by the Master List), in small groups, or in groups large enough to fill one disc. Selecting NXT will generate the next file on the Master List. Selecting GRP will request a Master List level to begin and end file generation. When using this option, make sure that the first and last file in the group will fit onto the same disc (check on the compiled Master List printout that all the files in the specified group have the same Disc name, though they do not have to have the same Disc side value). Selecting DSC will generate all files on the Master List sufficient to fill up the current data disc. This can take a considerable amount of time, although it requires no attention once started. Whatever option is used, the computer will instruct the User to insert a particular, named disc into the lower of the two drives. If a disc of that name is already in use, re-insert it and press a key to begin processing. If no such disc is in use then take an empty, formatted disc, label it as instructed on the screen, insert it and press a key. The screen will change colour and display information about which file it is processing. Until the files have been generated there is no way of stopping the program except by pressing "break", and this is to be avoided. "Break"ing the program will upset the flow of the system and it may mean that the Master List will have to be re-run from the begining for the current Primary file. When the program has finished, the screen returns to original colour and gives the option of continuing to generate more files or returning to the main menu.

A.1.9.7. Group File Comparison (GFC).

Purpose: Comparing two sequential sets of blocked files.

The Group File Comparison module is designed to automatically compare the series of files produced by the Run Master List module for two different Primary files. For instance, if a User is comparing pattern A with pattern B, it will be necessary to generate Primary A and Primary B, and then to run the Master List on both of these. This will produce two series of files: A1, A2, A3 etc and B1, B2, B3 etc. At the end of the process it will be necessary to compare A1 with B1, A2 with B2 and so on. The Group File Comparison allows the User to do this more or less automatically. The module requests the names of the Primary files used to originate the two series to be compared, the locations of the two series and the levels to start and end the analysis. "Level" here corresponds to the level of the Master List, thus to compare the series A6, A7, A8 with the series B6, B7, B8 the start level would be 6 and the end level 8. The series A6 to A8 must be on the same disc, as must the series B6 to B8. The User must consult a hard copy of the compiled Master List to be sure of the locations of the files which are to be compared. This module is written to give a hard copy output of the results automatically, so the User should ensure that a printer is connected and switched on before the comparison is started. Output is given in terms of "matches" and "mismatches" between each pair of files. A match is scored when the same block colour value occurs at corresponding points in the two files under comparison, unless that colour represents the background. Mismatches are scored when corresponding points in the files are not the same.

A.1.9.8. Single File Comparison (SFC).

Purpose: Comparing specific named files, usually Primary files.

The Group File Comparison module (A.1.9.7. above) is designed to cope with the sequential series of files produced by the Run Master List option. The Single File Comparison module allows a list of non-sequential files to be compared. It is designed to allow the construction of a list of pairs of Primary files which need to be compared, and to perform these comparisons without need for further input. Comparing two Primary files takes about thirty minutes so this module is simply a time saving device which allows a set of jobs to be queued so that the User can leave the computer unattended. On entry to the module, four column headings are set up. Type in the name of the first file for comparison and press <return>. Notice that the cursor jumps to the next column and here, under "Loc", enter the location of the first file. This module does allow the Systems disc to be removed, so any of the four drives can be specified. Pressing the <return> key advances the cursor to the next column and the second file name should be entered. Press <return> and enter its location. Pressing <return> again will now send the cursor to the next row in the table, and the process should be repeated for the next pair of files to be compared. The program allows for twenty such entries but bear in mind that specifying 20 pairs of Primary file comparisons will mean that the disc drive will have to run continuously for about 10 hours. When a list of the files to be compared has been constructed, enter at the begining of the next row a <*> to end the list. The program unit assumes that the list can be run without the need to change any discs. If any of the files are not present as specified on the list, the program will fail. Make sure that all the files in the list will be found on the discs being inserted. Ending the list will elicit a prompt to remove the Systems disc if required. Insert the discs bearing the files in the list and press any key to continue processing. The module provides a hard copy output, so ensure that a printer is connected and turned on before the unit is run. Output is given in terms of match/mismatch between files. Although the module is designed primarily for use with Primary files, any files can be specified. When the program has finished it offers the option of setting up a new list, typing <Y> <return> will restart the unit, any other response will return to the menu.

Appendix Two

Simpack Programming Guide.

A.2.1 Foreword.

This Programming Guide provides no information about the operation of the *Simpack* similarity package additional to that in the User Guide presented in Appendix 1. None of the information provided here will be of any value unless the reader has a thorough understanding of the principles of *Simpack* , as outlined in that Guide.

The Programming Guide exists for three reasons. The first is one of principle, no software package is complete until sufficient documentation exists to ensure that it can be understood in detail, and perhaps modified, by someone other than its creator. Secondly, it provides a resource for those who agree with the underlying principles of *Simpack* operations, but who wish to extend or implement them using different hardware or software. Finally, it is intended to be of some benefit to those users who require more information about how the package operates, so that they might improve their understanding of its limits.

It is hoped that enough information is provided to permit a reasonably competent programmer make alterations to the programs that make up *Simpack* . It should be understood, however, that *Simpack* is a means to an end, not an end in itself. It is not an object lesson in programming. The purpose was to create a package that fulfiled the research aim of determining the similarity of patterns, and to make it useable by others, such that its useful life could extend beyond that of the current research project. As a consequence, experienced programmers would find the code a little odd or inefficient in some places. For each of the problems encountered during development, the solution adopted was usually the first or the simplest feasible one, not necessarily the most efficient.

Given the available hardware, any reasonably detailed image analysis will be inherently time consuming. Much emphasis has therefore been placed on making *Simpack* run many of its operations unattended, so programmers should not be surprised if they encounter code which goes to some length to automate what may appear to be infrequent and undemanding operations.

A.2.2 Format.

In the following document, each program in the *Simpack* package is described in turn. Each description consists of a short prose explanation of the overall purpose of the program and a breakdown of how that purpose is achieved, followed by a listing of the program code. Using these descriptions, programmers should be able to work out all that they need to know in order to replicate or modify the programs.

A.2.3 Menu Management.

A.2.3.1 Program MENU.

MENU sets up a menu showing the available *Simpack* options and, on some occaisions, details of the previous sessions' usage of the package. The User inputs a three letter code specifying the desired *Simpack* option. MENU then loads the appropriate program from the system disc, over-writing itself. MENU refers to a central information file, CNTRL, for the details of the previous usage of the package.

Code Lines	**Function**
10 - 20	Prepares menu screen.
30 - 50	Opens, reads from and closes the CNTRL file on the system disc. CNTRL contains the name of the Primary file upon which the Master List was last run, and what level of the List was achieved, unless the List was completed.
60	Flushes all internal buffers.
80 - 142	Outputs the available options and their three letter mnemonic.
150	If filename variable is null ("*"), the Master List has been fully executed on a Primary File and the next module is skipped.
160 - 170	Highlights that Master List has been partially run on a Primary File and reports the name of the latter.
180 - 270	Requests the input of the mnemonic, checks input against a list of valid options and if request is valid, CHAINs in the appropriate program from the Systems disc.

A.2.3.2 MENU Code

```
 10 MODE 6
 20 VDU 19,0,4,0,0,0
 30 IN=OPENIN "CNTRL"
 40 INPUT# IN,START%,F$
 50 CLOSE# IN
 60 *FX21,0
 70 CLS
 80 PRINT TAB(12,2);"**OPTIONS**"
 90 PRINT TAB(5,4);" 1. Image Capture         (ICP) "
100 PRINT TAB(5,6);" 2. Fast Edit            (FSE)"
110 PRINT TAB(5,8);" 3. Primary File Generation (PFG) "
120 PRINT TAB(5,10);" 4. Master List Options    (MLO) "
130 PRINT TAB(5,12);" 5. Compile Master List    (CML) "
140 PRINT TAB(5,14);" 6. Run Master List        (RML) "
141 PRINT TAB(5,16);" 7. Single File Comparison  (SFC) "
142 PRINT TAB(5,18);" 8. Group File Comparison   (GFC) "
150 IF F$="*" THEN GOTO 180
160 PRINT TAB(1,20);"You are running master on file ";F$
170 PRINT TAB(3,12);"*"
180 INPUT TAB(1,22) "INPUT INSTRUCTION CODE " INS$
190 IF INS$="MLO" THEN CHAIN "SCREEN"
200 IF INS$="CML" THEN CHAIN "COMPML"
210 IF INS$="RML" THEN CHAIN "RUNML"
220 IF INS$="PFG" THEN CHAIN "LOOP2"
230 IF INS$="FSE" THEN CHAIN "EDSYS"
240 IF INS$="ICP" THEN CHAIN "IMCAP"
250 IF INS$="SFC" THEN CHAIN "MATCH"
260 IF INS$="GFC" THEN CHAIN "GMATCH"
```

A.2.4 Image Capture.

A.2.4.1 Program IMCAP.

IMCAP prompts for the connection of the digitzer and camera inputs. Once connection is confirmed, it repeatedly digitizes current camera input and makes it possible to store the data in a user named file on floppy disc.

Code Lines	**Function**
10	Simple error trap to restart program if the input from digitizer is either not present or faulty.
20 - 30	Allocation of space for the routine which calls the Command Line Interpreter and the string which is passed to it.
40 + 370 - 450	Installs machine code subroutine to call the Command Line Interpreter.
60 - 100	Sets up prompt screen and awaits a key press.
120 - 190	Repeatedly digitizes images, super-imposes centrelines over image and awaits user instructions. If the instruction is to Quit, MENU is CHAINed back from the System Disc. If the request is to save then the procedure PROCsave is initiated.
230 - 360	The save procedure. A file name and location are requested. The image is digitized without centrelines. The instruction string including the save instruction, the file name and the disc location is constructed and passed to the Command Line Interpreter. Oddly, the use of some machine code routines appear to make the development machine "forget" that it is in disc rather than Tape Mode, so line 240 serves as a reminder.
450 - 540	A procedure to catch Disc Errors encountered when attempting to save images. This module is currently redundant because problems arose when trying to call it.

A.2.4.2 IMCAP Code.

```
 10 ON ERROR GOTO 60
 20 DIM COM% 100
 30 DIM SPACE% 100
 40 PROCcli
 50 :
 60 MODE6:VDU 19,0,4,0,0,0
 70 :
 80 PRINT TAB(2,4);"Connect Digitizer and Camera "
 90 PRINT TAB(2,6);"Press any key when ready"
100 A=GET
110 :
120 MODE1
130 REPEAT
140 *WIMAGE
141 MOVE 668,0
```

```
142 PLOT 6,668,1269
143 MOVE 40,504
144 PLOT 6,1279,504
150 PRINT TAB(0,0);"    S for Save    Q for Quit          "
160 G$=GET$
170 IF G$="S" THEN PROCsave
180 IF G$="Q" THEN CHAIN "MENU"
190 UNTIL FALSE
200 :
210 :
220 :
230 DEF PROCsave
240 *DISC
250 PRINT TAB(0,0);"                              "
260 INPUT TAB(0,0);"Give the file name " FILE$
270 PRINT TAB(0,0);"                          "
280 INPUT TAB(0,0);"Which Drive ?" DR%
290 *WIMAGE
300 PRINT TAB(0,0);"                              "
310 D$="*WIMSAVE :"+STR$(DR%)+"."+FILE$
320 $COM%=D$
330 LE%=COM%+LEN(D$)+1
340 ?LE%=&0D
350 CALL SPACE%
360 ENDPROC
370 DEF PROCcli
380 P%=SPACE%
390 [ OPT 0
400 LDX# COM% MOD 256
410 LDY# COM% DIV 256
420 JSR &FFF7
430 RTS
440 ]
450 ENDPROC
460 DEF PROCerror
470 MODE 6
480 VDU 19,0,4,0,0,0
490 CLS
500 PRINT TAB(5,4)"Need new data disc"
510 PRINT TAB(5,6)" Or fresh data disc"
520 A=GET
530 GOTO 120
540 ENDPROC
```

A.2.5 Image Editing.

A.2.5.1 Program EDSYS.

EDSYS allows the User to recall an image file from disc and edit it manually. The program displays the stored image on screen and provides a pen with which the user can demarcate any area of the image. That defined area is then filled with a specified colour. Edited images can be stored under a new name. Using this program, minor digitizing errors can be edited out of an image.

The polygon defined by the pen movements can have up to 49 sides before running out of array space, though in practice much simpler shapes are defined. For the filling of this area with a defined colour to be successful, the final location of the pen must be in the approximate centre of the shape created. The routine which performs the fill treats each side if the polygon in turn as the side of a triangle, the apex of which is defined at the final pen position. The routine then makes a call to a standard function of BASIC which actually performs the fill. It is this method which imposes the limitation on polygon shape and pen position. The fill routine fills any area within the defined triangle and so cannot take into account a poorly chosen final pen position or the fact that one of the sides of the triangle may pass through another face of the polygon.

Code Lines	Function
10 - 20	Space allocation for the routine which calls the Command Line Interpreter and the string which is passed to it.
30 + 940 - 1020	Installation of routine which calls the CLI.
40 - 50	Dimensions array to hold the defined points.
60	DFL% is a flag which acts as a subscript value for the arrays defined above. It is incremented each time a new point is defined.
65 - 69	Sets up a screen requesting the name and location of the image file to be input.
71	Constructs a string containing the input name and location details.
73	Locates the string to be picked up by the CLI.
74 - 110 + 880 - 860	Sets up the screen mode and executes the load instruction via the CLI and sets up top line for prompts to user.
130 - 160	Infinite loop to await inputs and replot the pen in the same or the revised location.
180 - 240	Draws a temporary (rubber banded) line from the last stored point to the current cursor position. It also draws a diagonal pen at this position.
260 - 380	Awaits keyboard input and replots pen or takes other actions. The possible actions are as follows;
280	Increasing the speed of the pen movement increases A%, the amount added or subtracted to the current pen position.
290 - 320	Vertical or horizontal pen movement.
330	Stores the current pen position (see PROCstore).
340	Fills a pen defined area (see PROCdraw).
350	Saves an edited picture (see PROCsave).
360	Quits program by CHAINing MENU back in.
400 - 480	Stores the current pen position then draws a permanent line between this and the previously saved point, if any.
500 - 630	Fills pen defined area with a user specified colour.

	Filling is achieved by sorting through the stored points and selecting consecutive pairs (i.e. stored points 1 and 2, then 2 and 3, then 3 + 4, etc.) and treating them as points of a triangle, the third point being defined by the final pen position. BASIC's standard fill instruction is then called to fill the triangle. When all points have been used, the subscript value is set to zero ready to begin a new shape.
650 - 690	Prompts the user for a fill colour.
710 - 840	Procedure to save the edited file. The name of the orginal image file is presented as a prompt so that a derivative name can be specified. A disc location is also requested. A string is constructed from this information and then passed to the CLI to execute the save. The program then re - run or the MENU CHAINed back in.
900 - 920	Prints a blank line to act as a prompt line.

Note that response to the keyboard is a little imperfect, key presses get stored in the input buffer and can subsequently appear in unexpected places. Issuing the command "*fx 21, 0" at line 720 alleviates the problem but doesn't solve it so the User still has to take care in keyboard use.

A.2.5.2 EDSYS Code

```
 10 DIM COM% 100
 20 DIM L1% 100
 30 PROCcli
 40 DIM XC%(50)
 50 DIM YC%(50)
 60 DFL%=0
 65 MODE6:VDU 19,0,4,0,0,0
 67 INPUT TAB(2,4);"Which Image File to Load ? " INFL$
 69 INPUT TAB(2,6);"Which Disc ? " SD%
 71 D$="*WIMLOAD :"+STR$(SD%)+"."+INFL$
 73 PROCstring
 74 MODE1
 75 CALL L1%
 90 X%=1260:Y%=1000
100 PRINT TAB(34,0);"Pen : "
110 PROChead
120 :
```

```
130 REPEAT
140 PROCcursor
150 PROCinput
160 UNTIL FALSE
170 :
180 DEF PROCcursor
190 IF DFL%>=1 THEN MOVE XC%(DFL%),YC%(DFL%)
200 IF DFL%>=1 THEN PLOT 6,X%,Y%
210  FOR L%=0 TO 16 STEP 4
220 PLOT 70,X%+L%,Y%+L%
230 NEXT
240 ENDPROC
250 :
260 DEF PROCinput
270 A%=4
280 IF INKEY(-97) THEN A%=16
290 IF INKEY(-58) THEN Y%=Y%+A%
300 IF INKEY(-42) THEN Y%=Y%-A%
310 IF INKEY(-26) THEN X%=X%-A%
320 IF INKEY(-122) THEN X%=X%+A%
330 IF INKEY(-74) THEN PROCstore
340 IF INKEY(-17) THEN PROCdraw
350 IF INKEY(-72) THEN PROCsave
360 IF INKEY(-56) THEN CHAIN "MENU"
370 PROCcursor
380 ENDPROC
390 :
400 DEF PROCstore
410 DFL%=DFL%+1
420 XC%(DFL%)=X%
430 YC%(DFL%)=Y%
440 IF DFL%<2 THEN GOTO 480
450 MOVE XC%(DFL%-1),YC%(DFL%-1)
460 PLOT 6,XC%(DFL%),YC%(DFL%)
470 PROChead
480 ENDPROC
490 :
500 DEF PROCdraw
510 PROCcolour
520 FX%=X%:FY%=Y%
530 FOR D%=1 TO DFL%-1
540 MOVE XC%(D%),YC%(D%)
550 MOVE XC%(D%+1),YC%(D%+1)
560 PLOT 85,FX%,FY%
570 NEXT D%
580 MOVE XC%(1),YC%(1)
590 MOVE XC%(DFL%),YC%(DFL%)
600 PLOT 85,FX%,FY%
610 DFL%=0
620 PROChead
630 ENDPROC
640 :
650 DEF PROCcolour
660 *FX21,0
661 PROCblank
670 INPUT TAB(0,0);"Colour ? 0=Bl,1=Rd,2=yllw,3=wht" C%
680 GCOL0,C%
```

```
 690 ENDPROC
 700 :
 710 DEF PROCsave
 720 *FX21,0
 730 PROCblank
 731 PRINT TAB(25,0);"Old "INFL$
 740 INPUT TAB(0,0);"Name Edited File " EDFIL$
 750 PROCblank
 760 INPUT TAB(0,0);"To Disc ?" SD%
 770 PROCblank
 780 D$="*WIMSAVE :"+STR$(SD%)+"."+EDFIL$
 790 PROCstring
 820 CALL L1%
 830 PROChead
 840 ENDPROC
 850 :
 860 DEF PROChead
 870 PRINT TAB(0,0);"'Ret'=mark  Q=fill  @=Save  P=Quit Pen: "
 880 ENDPROC
 890 :
 900 DEF PROCblank
 910 PRINT TAB(0,0);"                      "
 920 ENDPROC
 930 :
 940 DEF PROCcli
 950 P%=L1%
 960 [ OPT 3
 970 LDX# COM% MOD 256
 980 LDY# COM% DIV 256
 990 JSR&FFF7
1000 RTS
1010 ]
1020 ENDPROC
1028 :
1029 DEF PROCstring
1030 $COM%=D$
1040 LE%=COM%+LEN(D$)+1
1050 ?LE%=&0D
1060 ENDPROC
```

A.2.6 Master List Operations.

A.2.6.1 Program SCREEN.

SCREEN provides a fairly simple screen editor to permit the User to create, store and subsequently modify the Master List of files to be created during the analysis of the Primary File. The program creates or makes reference to MLIST, a datafile which is stored on disc and which guides the operation of much of the rest of the package. The program creates a number of levels in this file, each entry specifying the block size to be used in the generation of a single child file from the Primary File. Block sizes are specified in terms of the number of pixels in their vertical and horizontal axes.

Code Lines	**Function**
10 - 90	Screen and variable initialization.
100 - 140	Opens, reads from and closes the MLIST file on the disc. The number of pixels in the vertical and horizontal axes of the block size at each level in the list are read into arrays.
180 - 250	Prints out the first ten entries from the data in the arrays, the level they represent and the total number of blocks which would be generated using the block size thus specified. Although only ten entries are shown at any one time the screen can be scrolled so that up to a maximum of eighty entries in the Master List can be created.
270 + 920-990	Prints out a header which explains the output of the above listing.
280	Prints out a list of editing options.
290 - 400	Awaits input from the keyboard and takes appropriate action. The following options are available;
310 - 340	Alters the starting point for the 10 entries of the Master List that are displayed at any one time.
350 - 380	Sends program control to the routines handling the editing, saving and creation of Master Lists, and the option to exit from this program.
410 - 500	Handles the editing of the Master List currently held in the arrays in memory. The module requests which level of the currently loaded list is to be altered and what the new values will be. These values are then either written over the existing values at that level (REPLACEMENT) or all the entries above it are shifted "up" one level and the new values placed in the free slot in the list thus created (INSERTION).

520 - 540	Handles the replacement as described above.
550 - 660	Handles the insertion of new data.
670 - 800	Handles the creation of a new Master List from scratch. All previously specified entries are blanked out and a loop running from 1 - 80 levels requesting new data, unless the termination value of -1 is entered thus ending the loop.
810 - 910	Saves the List currently held in the memory to the disc, over writing the previously stored copy of MLIST. The module requests confirmation and if this is not provided it returns control to an earlier part of the program, so avoiding the erasure of the previous list.
1010 - 1030	Creates a blank prompt line.
1040 - 1100	The FLAG% variable is tested to check whether any changes that were made to a list previously loaded from the disc have been saved. If they have not, then attempts to exit the program are blocked and the option to save is provided. If it is not taken, the MENU program is CHAINed back in.

A.2.6.2 SCREEN Code.

```
 10 FLAG%=0
 20 MODE6
 30  VDU 19,0,4,0,0,0
 40 :
 50 DIM RAY%(2,80)
 60 H$="U=Pg up, D=Pg down, E=edit, C=Create   S=Save, M=Return to menu"
 70 B$="                                  "
 80 COUN=0
 90 PT%=0
100 CHAN=OPENIN"MLIST"
110 FOR L1%=0 TO 79
120 INPUT# CHAN,RAY%(1,L1%),RAY%(2,L1%)
130 NEXT
140 CLOSE#CHAN
150 CLS
160 :
170 :
180 CLS:FOR G=1 TO 10
190 X=G+2
200 PRINT TAB(1,X);PT%+G;" ";TAB(8,X);RAY%(1,PT%+G);" ";TAB(14,X);RAY%(2,PT%+G);" "
210 IF RAY%(1,PT%+G)=0 THEN GOTO 250
220 PRINT TAB(20,X);INT(256/RAY%(1,PT%+G));" "
230 PRINT TAB(25,X);INT(320/RAY%(2,PT%+G));" "
240 PRINT TAB(30,X);INT(320/RAY%(2,PT%+G))*INT(256/RAY%(1,PT%+G))
250 NEXT
260 :
270 PROChead
280 PRINT TAB(1,22);H$
```

```
290 REPEAT
300 A=GET
310 IF A=85 THEN PT%=PT%+10
320 IF PT%=80 THEN PT%=70
330 IF A=68 THEN PT%=PT%-10
340 IF PT%=-10 THEN PT%=0
350 IF A=69 THEN GOTO 410
360 IF A=67 THEN GOTO 670
370 IF A=83 THEN GOTO 810
380 IF A=77 THEN PROCexit
390 GOTO 180
400 UNTIL FALSE
410 FLAG%=1:PRINT TAB(1,22);B$
420 INPUT TAB(1,22);"Input level     ";I%
430 INPUT TAB(1,22);"Input new NPVB value ";NX%
440 PROCblank
450 INPUT TAB(1,22);"Input new NPHB value ";NY%
460 PROCblank
470 INPUT TAB(1,22);"Insert or Replace";IV$
480 IF IV$="I" THEN GOTO 550
490 IF IV$="R" THEN GOTO 520
500 GOTO 180
510 :
520 RAY%(1,I%)=NX%:RAY%(2,I%)=NY%
530 PRINT TAB(1,22);H$
540 GOTO 180
550 FOR L1%=1 TO 80
560 IF RAY%(1,L1%)=0 THEN GOTO 580
570 NEXT
580 EOA%=L1%
590 FOR L2%=EOA% TO I% STEP-1
600 RAY%(1,L2%+1)=RAY%(1,L2%)
610 RAY%(2,L2%+1)=RAY%(2,L2%)
620 NEXT
630 RAY%(1,I%)=NX%
640 RAY%(2,I%)=NY%
650 PRINT TAB(1,22);"                              "
660 GOTO 180
670 FOR X=1 TO 80
671 RAY%(1,X)=0:RAY%(2,X)=0
672 NEXT
680  FLAG%=1:PRINT TAB(1,22);B$
690 REPEAT
700 COUN=COUN+1
710 PRINT TAB(1,22);"For level ";COUN
720 INPUT TAB(15,22);"Input NPVB ";XV%
730 PROCblank
740 IF XV%=-1 THEN COUN=0
750 IF XV%=-1 THEN GOTO 180
760 PRINT TAB(1,22);"For level ";COUN
770 INPUT TAB(15,22);"Input NPHB ";YV%
780 PROCblank
790 RAY%(1,COUN)=XV%:RAY%(2,COUN)=YV%
800 UNTIL COUN=79
810 FLAG%=0
820 CLS
830 INPUT  TAB(8,12);"Please confirm save ";ANS$
```

```
 840 IF ANS$="CON" THEN GOTO 860
 850 GOTO 150
 860 CHAN=OPENOUT "MLIST"
 870 FOR L1%=0 TO 79
 880 PRINT #CHAN, RAY%(1,L1%),RAY%(2,L1%)
 890 NEXT
 900 CLOSE#CHAN
 910 GOTO 150
 920 DEF PROChead
 930  PRINT TAB(0,1);"LEVEL"
 940 PRINT TAB(7,1);"NPVB"
 950 PRINT TAB(13,1);"NPHB"
 960 PRINT TAB(20,1);"NVB"
 970 PRINT TAB(25,1);"NHB"
 980 PRINT TAB(30,1);"TOTAL"
 990 ENDPROC
1000 :
1010 DEF PROCblank
1020 PRINT TAB(1,22);"                              "
1030 ENDPROC
1040 DEF PROCexit
1050 IF FLAG%=0 THEN CHAIN "MENU"
1060 CLS:PRINT TAB(2,4)"You have not saved the modification "
1070 INPUT TAB(2,6);"Do you want to SAVE (YES OR NO) ? " INS$
1080 IF INS$="NO" THEN CHAIN "MENU"
1090 GOTO 810
1100 ENDPROC
```

A.2.7 Compiling Master List.

A.2.7.1 Program COMPML

Much effort has gone into making the generation of a series of blocked file a largely automatic process, subject to time and disc capacity. File generation cannot be automatic unless the file names, block size parameters and disc file destinations are provided in advance. COMPML generates the information required both for this and for the purpose of guiding Users in the organisation of their discs.

This program accesses the MLIST file and from the block size specifications therein, calculates the length of each of the files to be generated. It calculates how many discs will be required to hold the entire file set and on which side of the discs particular files will reside. Once all the calculations have been made and each file to be generated has been allocated a disc and disc side, this and other information is written to a file which is consulted during the process of file generation.

The program also sets up the CNTRL control file to its null state, a state which indicates that file generation is to start at level one of the Master List and that there is no default Primary File (i.e. the Primary File name field is set to "*"). Obviously, the running of COMPML will destroy the information relating to the generation and analysis of previous file series.

Code Lines	**Function**
10 - 20	Screen set up.
40 - 50	Variable initialization.
70 - 100	Dimension Array space.
120 - 160	Reads the MLIST file from the System disc into the internal arrays.
80 - 210	Calculates the number of blocks created by the number of pixels per block data held in the MLIST file and inserts them into the arrays. These data will be the number of entries in each of the files in the file series to be generated.
240 - 260	Requests confirmation to continue with the rest of the program. Currently there is an error which such that the failure to confirm simply restarts the program.
270	Requests a three character name for the discs which will be used to hold the new file series. If, for instance, the name provided was DAT, then the discs will subsequently be named DAT1, DAT2 etc.
290 - 370	Sorts through the block size array and groups together two sequential

	sets of file, one set to go on one side of a disc, the other to go on the other side. The two sets are numbered 1 and 2 respectively. The upper limit on the capacity of a disc is either 30 files or 368,000 bytes.
380 - 440	Sorts through the array containing disc side values and allocates each pair to the same disc name, which is stored in another array.
460 - 510	Opens a file COMP and writes to it the contents of the internal arrays, information which will be made available to the program which generates the files.
520 - 610	Prints out the "compiled" list for the benefit of the User, with a option of a hard copy of the output.
630 - 670	Resets the CNTRL file and exists the program.

A.2.7.2 COMPML Code.

```
 10 MODE6
 20 VDU 19,0,4,0,0,0
 30 :
 40 PT%=0:START%=1:FLAG%=0:EXTRA%=1
 50 NUM%=0
 60 :
 70 DIM BLOCKS%(80)
 80 DIM TITLE$(80)
 90 DIM SIDE%(80)
100 DIM RAY%(2,80)
110 :
120 CHAN=OPENIN"MLIST"
130 FOR L1%=0 TO 79
140 INPUT# CHAN,RAY%(1,L1%),RAY%(2,L1%)
150 NEXT L1%
160 CLOSE#CHAN
170 :
180 FOR L1%=1 TO 79
190 IFRAY%(1,L1%)=0 THEN GOTO 240
200 BLOCKS%(L1%)=INT(321/RAY%(1,L1%))*INT(256/RAY%(2,L1%))
210 NEXT L1%
220 :
230 :
240 CLS
250 INPUT TAB(4,4) "Confirm Compilation (CON) " INS$
260 IF INS$<>"CON" THEN GOTO 60
270 INPUT TAB(4,6) "Input disc name (3 charac.) " DISC$
280 :
290 SUM%=0:FLAG%=1:LMT%=0
300 FOR L1%=1 TO 80
310 IF BLOCKS%(L1%)=0 THEN GOTO 380
311 LMT%=LMT%+1
```

```
320 SUM%=SUM%+BLOCKS%(L1%)
330 IF SUM%>368000 AND FLAG%=1 THEN FLAG%=3:GOTO 350
331 IF LMT%=30 AND FLAG%=1 THEN FLAG%=3:GOTO 350
340 IF SUM%>368000 AND FLAG%=3 THEN FLAG%=1
341 IF LMT%=30 AND FLAG%=3 THEN FLAG%=1
350 SIDE%(L1%)=FLAG%
360 IF SUM%>368000 THEN SUM%=BLOCKS%(L1%)
361 IF LMT%=30 THEN LMT%=0
370 NEXT
380 MARK=1
390 TITLE$(1)=DISC$+"/1"
400 FOR L2%=2 TO 79
410 IF SIDE%(L2%)=0 THEN GOTO 450
420 IF SIDE%(L2%)=1 AND SIDE%(L2%-1)=3 THEN MARK=MARK+1
430 TITLE$(L2%)=DISC$+"/"+STR$(MARK)
440 NEXT
450 :
460 OCHAN=OPENOUT "COMP"
470 FOR L3%=1 TO 80
480 IF SIDE%(L3%)=0 THEN GOTO 510
490 PRINT# OCHAN, RAY%(1,L3%),RAY%(2,L3%),TITLE$(L3%),SIDE%(L3%),BLOCKS%(L3%)
500 NEXT
510 CLOSE#OCHAN
520 ICHAN=OPENIN "COMP"
530 INPUT TAB(4,8) "Hard copy (y/n) " ANS$
531 CLS
540 IF ANS$="Y" THEN VDU2
549 PRINT
550 PRINT TAB(2);"NPVB";TAB(8);"NPHB";TAB(15);"DISC";TAB(24);"SIDE";TAB(30);"BLOCKS":PRINT
559 NUM%=0
560 REPEAT
561 NUM%=NUM%+1
570 INPUT# ICHAN, NPVB%,NPHB%,F$,SI%,BL%
580 PRINT TAB(2);NPVB%;TAB(8);NPHB%;TAB(15);F$;TAB(25);SI%;TAB(30);BL%;TAB(37);NUM%
590 UNTIL EOF#ICHAN
600 CLOSE#ICHAN
610 VDU3
620 :
630 OCHAN=OPENOUT ":0.CNTRL"
640 PRINT# OCHAN, 1,"*"
650 CLOSE#OCHAN
651 PRINT
659 PRINT TAB(2);"Press any key"
660 A=GET
670 CHAIN "MENU"
```

A.2.8 Running the Master List.

A.2.8.1 Program RUNML.

This program represents the core of the package since it performs the central task of transforming the data which describes the original image into the file series which describes that image with initially coarse, and then progressively finer degrees of detail. This is a fairly prolonged and involved task, a fact that is reflected by the extent and complexity of the program. The first part of the program is written in BASIC and this is a straightforward section dealing with opening appropriate files and the calling of routines which perform the blocking process. The most important and laborious section is written in assembler for speed but, since assembler is rather cryptic, it is necessary to provide a reasonably detailed explanation.

The program consists of two nested loops, one running from 1 to the number of blocks on the vertical axis of the image, and one running from 1 to the number of blocks on the horizontal axis. In the centre of the middle loop, routines are called which calculate the location of each block and undertake the counting of the pixels within that block. Recall that the program is dealing with the Primary file representation of an image, not the image itself. The Primary file data can be thought of as being laid down in 256 sections, each section 321 entries long and each describing the a complete horizontal row of colour values from the original image. The analysis effectively runs from the bottom left hand corner of the image to the top right hand corner. The values within the Primary file are accessible by the use of the random access file pointer, much of the program is tasked with calculating where the pointer should be placed in order to read the data pertaining to a particular block. This is done by taking the current values of each of the loops to calculate which is the current block. A calculation is then done to find the file pointer location for the data relating to the pixel in the bottom left hand corner of the block. The program then reads in as many entries (colour values) as there are pixels in the horizontal axis of the block, effectively reading in the bottom row of the block. The next row up in the block is then calculated by adding 321 to the file pointer value at the start of the first row, when the file pointer has been placed at this location, the next row of entries is read in. This is repeated as many times as there are pixels in the vertical axis of the block.

Consider, then, the "construction" of the first block, corresponding to the bottom left hand corner of the image, where the User has specified a block size of 4 x 4 pixels. The value of the loops will generate a value of 1, the number of the first block. The file pointer value is calculated as zero, because the first entry in the Primary file is the one that is required. Four sequential entries are then read in and processed (see later), this corresponds to the data in the bottom row of the first block. The file pointer is then set to the data which represents the next row up in the block, this is done by adding 321 to the original file pointer value (0). Again four entries are read in and processed. This is repeated two further times so that 4 x 4 entries have been read in. Once the data thus acquired is dealt with, the process moves on to handle the second block in the same way.

The data that is read in is of course the colour value of the pixel that that data point represents in the original image. The program counts which is the most common colour value within the current block and it writes out that data to the file which represents the blocked image. In the event that two colours are equally common, the block colour is assigned one of them at random.

Interpreting the precise details of the assembler code is impractical. The most daunting task was that of updating the position of the disc file pointer. The Primary file is in excess of 80,000 entries long. The capacity of the eight bit register is 256 and linking two such registers yields values only up to around 65,000, so four eight bit registers are linked together to handle the large numbers. The problem is made worse by the fact that two large integers need to be multiplied. Birnbaum (1982) gives a multiplication algorithm to deal with a corresponding multiplication problem with four bit registers and then expands is to eight bits. These basic principles were copied to achieve simulated 16 bit multiplication for the purpose of calculating disc pointer values.

Code Lines	**Function**
10 - 110	Space allocation for machine code subroutines and variable locations.
130 - 140	Screen set up.
160 - 170 + 1110 - 1190	Installation of routines to call the Command Line Interpreter

190 - 210	Opening, reading and closing the CNTRL file.
230	If the Primary file name variable is in its null state ("*", ie no Primary file is currently being dealt with) the program SWAP is loaded from the system disc. This program prompts the User for the name and location of the next Primary file to be dealt with, it then copies that file to the system disc.
250 - 300	Reports the name of the current Primary file and the level of the Master List and the level that has been reached in working on it. It requests whether generation of new files should proceed to fill a disc (ie. the file generation to run freely until it reaches the disc limit) or generate a specified group of files or a single file.
310 - 330	Tests which of the three options the User selected and passes control to the relevant procedure.
340 - 370	Changes screen colour back to the normal state, closes input file and drive number back to its default value following changes made in the processing procedures.
410 - 460	Updates the CNTRL file to take account of processing done during the current session.
490	Returns program control to menu.

All three procedures which handle the file generation options are simply concerned with the correct calling of a single shared procedure which performs the actual file generation.

510 - 550	PROCnext generates the next file on the Master List as specified in the START LEVEL report on the screen. It performs a single call to PROCmerge, the procedure for file generation.
570 - 700	PROCnameGRP requests the number of levels of the Master List to process during the current session, starting from the level shown on the screen. It then calls PROCmerge the appropriate number of times.
720 - 850	PROCnameDISC calls PROCmerge until the current data disc, receiving the blocked files, is full (the program can't go beyond this level because the data cannot be changed until the user is present). It does this by comparing the current data disc name with the next name on the MLIST. If the two are the same, the processing of the file at that level continues. If they are different, indicating the disc boundary, processing stops.

The three procedures which control calls to the file generation procedure also call on two other procedures, PROCsetup and PROCdrive.

870 - 970	PROCsetup opens the compiled Master List file, COMP and reads through as many entries as is necessary until it reaches the start level as indicated in the CNTRL file. At this point it requests the insertion of the appropriate data disc and awaits a key press to confirm this action has been taken.

990 - 1050	PROCdrive simply constructs an instruction to change the drive to the appropriate value and then executes the instruction via the Command Line Interpreter.
1020 - 1090	Inputs entries from the COMP file. If it can read entries beyond the current level of processing, the Master List is not yet finished. If it cannot, preparations are made so that the CNTRL file can be set to show completion of the Master List for the current Primary File.
1350 - 1380	Printout of file processing information.
1410 - 1470	Allocation of locations for the assembler variables.
1490 - 1500	Calculation of number of vertical and horizontal blocks produced by the current pixel per block values.
1520 - 1570	Opening of input (Primary) and output files.
1590	Preparation for two pass assembly.
1600 - 1750	This subroutine is an assembler loop that runs from 1 to the number of blocks on the vertical axis of the original image, the value of this loop is stored at &83. Within this loop the following code is called.
1770 - 1920	This is an identical loop to the above except that it runs from 1 to the number of blocks on the horizontal axis. The product of the two nested loop values therefore run from 1 to the total number of blocks to be used in the generation of this file.
1940 - 2310	The next two subroutines again form a nested loop and jointly they perform the counting of pixel colours within the block. This first loop runs from 1 to the number of pixels in the vertical axis of the block. Within it, the file pointer is first set using the values calculated. Having moved to this point in the disc file, the module described immediately below is called and this reads in a number of sequential entries from the file. Having returned from this module, the pointer value is increased by 321, using another module, in preparation for the next cycle of the loop. When the loop is complete a series of routines is called to decide the most common colour in the block, on return from these routines, that value is written to the output file.
2330 - 2460	This is the final one of the total of four nested loops. It runs from 1 to the number of pixels in the horizontal axis of each block. For each cycle of the loop it reads in the next value from the Primary file and calls a routine which test the value of this input and increments the corresponding counter variable.
2470 - 2830	This module, INCTOT, simply tests the input colour value and tests it against the four legal values. It then increments the two byte register which holds the running totals of the colour frequency.
2860 - 3040	A four byte register holds the file pointer value. As explained in the preface, this value must be increased by 321 several times for progress through each block. Note that in the two highest bytes, zero

	is added to the current values; this is done to add any previous carry from the previous additions.
3060 - 3570	The routines described so far results in additions to the four two byte locations which hold the number of pixels of each of the four logical colours for the current block. The most common colour among the four must be found and this value written out to the output (blocked) file. Two routines are used in this decision making. The second of the two, described immediately below, decides which of a pair of two byte values is the highest. The current routine, SORT, controls access to this second routines such that it eventually determines the highest of the four colour totals. It simply installs two of the four totals and calls the WIN routine and stores the result of this call in temporary register. It then arranges the test of the other pair of totals and again stores the highest. Finally it takes the two "winners" and tests which is the highest. The final outcome is then stored in preparation for output.
3590 - 4150	This routine finds the greater of two two byte values, or if the values are equal it arbitrarily assigns one of then the winner of the competition. The process is complicated by the fact that the totals are held in two byte form. The high bytes are compared first and only if these are equal are the lower bytes compared.
4180 - 4570	This module is the simulated 16 bit multiplier and is somewhat out of sequence since the calls to it are actually controlled by a routine situated much earlier in the program. Although MULTI is the technically most sophisticated of the routines no detailed description is presented here, readers are directed to Birnbaum (1982), which explains the same principles with a less complicated example.
4580 - 5110	The PREMULT module employs the MULTI multiplier to calculate the first value of the file pointer on the Primary file needed to read in the first value of the current block. This value is calculated from the current values of the first two nested loops and the horizontal and vertical pixel dimensions of each block.
5120	End of the two pass assembly.
5130	Starts the machine code routines.
5140 - 5150	Closes the input and output files.

A.2.8.2 RUNML Code.

```
10 DIM ROOM1% 200
20 DIM ROOM2% 200
30 DIM ROOM3% 200
40 DIM ROOM4% 200
50 DIM INCTOT% 200
60 DIM SP320% 200
70 DIM SORT% 200
```

```
 80 DIM WIN% 500
 90 DIM MULT1% 1000
100 DIM PREMULT% 500
110 DIM WINRES% 15
120 :
130 MODE6
140 VDU 19,0,4,0,0,0
150 :
160 DIM DR% 100
170 PROCcli
180 :
190 ICNTRL=OPENIN"CNTRL"
200 INPUT# ICNTRL, START%,FILE$
210 CLOSE#ICNTRL
220 :
230 IF FILE$="*" THEN CHAIN "SWAP"
240 :
250 PRINT TAB(5,5);"PRIMARY FILE ";FILE$;" IS PRESENT"
260 PRINT TAB(5,7);"PROCESSING BEGINS AT LEVEL ";START%
270 PRINT TAB(5,11);"BY DISC   (DSC) ?"
280 PRINT TAB(5,13);"BY GROUP  (GRP) ?"
290 PRINT TAB(5,15);"OR NEXT   (NXT) ?"
300 INPUT TAB(5,19);"INPUT THREE LETTER CODE " INS$
310 IF INS$="NXT" THEN PROCnext
320 IF INS$="DSC" THEN PROCdisc
330 IF INS$="GRP" THEN PROCgroup
340  VDU 19,0,4,0,0,0
350 CLOSE#IN
360 *DRIVE 0
370 CLS
400 :
410 PROCcheck
420 REM ********UPDATE CNTRL*********
430 OUT=OPENOUT "CNTRL"
440 PRINT #OUT, C%,FILE$
450 CLOSE#0
460 CLS
480 :
490 CHAIN "MENU"
500 :
510 DEF PROCnext
520 PROCsetup
530 PROCdrive
540 PROCmerge
541 C%=C%+1
550 ENDPROC
560 :
570  DEF PROCgroup
580 CLS
590  INPUT TAB(4,4);"How many levels to process ? " LVL%
600  PROCsetup
609 PROCdrive
610 PROCmerge
615 C%=C%+1
620 C2%=0
630 REPEAT
```

```
 640 PROCinput
 650 C2%=C2%+1
 660 PROCdrive
 670 PROCmerge
 675 C%=C%+1
 680 UNTIL C2%=LVL%-1
 700 ENDPROC
 710 :
 720 DEF PROCdisc
 730 PROCsetup
 732 PROCdrive
 734 PROCmerge
 736 CDISC$=DISC$
 738 C%=C%+1
 760 REPEAT
 770 PROCinput
 771 PRINT TAB(0,0);DISC$;" ";CDISC$
 772 IF DISC$<>CDISC$ THEN GOTO 840
 780 PROCdrive
 790 PROCmerge
 800 C%=C%+1
 830 UNTIL EOF#IN
 840 CLOSE# IN
 850 ENDPROC
 860 :
 870 DEF PROCsetup
 880 IN=OPENIN ":0.COMP"
 890 C%=0
 900 REPEAT
 910 PROCinput
 920 C%=C%+1
 930 UNTIL C%=START%
 950 CLS:PRINT TAB(3,9);"Input disc labelled ";FILE$;".";DISC$
 960 A=GET
 970 ENDPROC
 980 :
 990 DEF PROCdrive
1000 COM$="*DRIVE "+STR$(SIDE%)
1010 $&0C00=COM$
1020 LE%=&0C00+LEN(COM$)+1
1030 ?LE%=&0D
1040 CALL DR%
1050 ENDPROC
1060 :
1070 DEF PROCinput
1080 INPUT# IN, NPVB%,NPHB%,DISC$,SIDE%,BLKS%
1090 ENDPROC
1100 :
1110 DEF PROCcli
1120P%=DR%
1130[ OPT 0
1140LDX# &00
1150LDY# &0C
1160JSR &FFF7
1170RTS
1180]
1190ENDPROC
```

```
1200 :
1210 DEF PROCcheck
1220 REM *******PROC TO CHECK FOR END OF COMP FILE *****
1230 IN=OPENIN ":0.COMP"
1240 C1%=0
1250 REPEAT
1260 C1%=C1%+1
1270 PROCinput
1280 IF C1%=C%+1 THEN GOTO 1310
1290 UNTIL EOF# IN
1300 C%=0:FILE$="*"
1310 CLOSE# IN
1320 ENDPROC
1330 :
1340 DEF PROCmerge
1350 PRINT TAB(3,11);"Currently Processing Primary ";FILE$
1360 PRINT TAB(3,13);"At level ";C%
1370 PRINT TAB(3,15);"Writing to Disc ";SIDE%
1380 VDU 19,0,1,0,0,0
1390 REM ROOM FOR THE MACHINE CODE SUBS
1400 :
1410 RESLL=&84:RESLH=&85:RESHL=&86:RESHH=&87
1420 LIERH=&88:LIERL=&89:LIEDH=&8A:LIEDL=&8B
1430 TEMPL=&8C:TEMPH=&8D:BCOUNTH=&8E:BCOUNTL=&8F
1440 WINNER=WINRES%:TEMP1=WINRES%+1:TEMP2=WINRES%+2
1450 TEMP1L=WINRES%+3:TEMP1H=WINRES%+4:TEMP2L=WINRES%+5:TEMP2H=WINRES%+6
1460 WINL=WINRES%+7:WINH=WINRES%+8
1470 SEMI=&7C:SEMIL=&7D:SEMIH=&7E
1480 REM INPUT TTHE VALUES FROM THE USER
1490 NVB=INT(256/NPVB%)
1500 NHB=INT(320/NPHB%)
1510 :
1520 REM OPEN CHANNEL FOR INPUT
1530 FLUP$=":2."+FILE$
1540 CHAN=OPENUP FLUP$
1550 :
1560 REM OPEN CHANNEL FOR OUTPUT
1565 FLOP$=":"+STR$(SIDE%)+"."+FILE$+STR$(C%)
1570 OCHAN=OPENOUT FLOP$
1580 :
1590 FOR PASS%=0 TO 2 STEP 2
1600 P%=ROOM1%
1610 [ OPT PASS%
1620      LDX#0
1630 STX BCOUNTH
1640 STX BCOUNTL
1650      STX&83   \STORE VAULE OF THE X REGISTER
1660 .LOOPA JSR ROOM2%
1670      LDX &83  \ AFTER RETURN FROM SUB RECOVER VALUE OF THE X REG
1680      INX
1690      BEQ OUTA
1700      STX &83
1710      CPX #NVB-1
1720      BCC LOOPA
1730      BEQ LOOPA
1740 .OUTA  RTS
```

```
1750 ]
1760 :
1770 P%=ROOM2%
1780 [ OPT PASS%
1790     LDX#0
1800      STX &82  \THE TEMP STORE FOR THE X REG VALUE IN THE B LOOP
1810 .LOOPB NOP
1820    JSR PREMULT%
1830     JSR ROOM3%
1840     LDX &82 \RECOVER THE VALUE OF THE X VALUE
1850     INX
1860     BEQ OUTB
1870     STX &82
1880     CPX #NHB-1
1890     BCC LOOPB
1900     BEQ LOOPB
1910 .OUTB  RTS
1920 ]
1930 :
1940 P%=ROOM3%
1950 [ OPT PASS%
1960    LDX #0
1970    STX &81
1980 .LOOPC NOP
1990    LDX#&70
2000    LDY#CHAN
2010    LDA #1
2020    JSR &FFDA
2030     JSR ROOM4%
2040     JSR SP320%
2050     LDX &81
2060     INX
2070     BEQ OUTC
2080     STX &81
2090     CPX#NPVB%-1
2100     BCC LOOPC
2110     BEQ LOOPC
2120 .OUTC JSR SORT%
2130    LDA WINNER
2140    LDY #OCHAN
2150    JSR &FFD4
2170 INC BCOUNTL
2180 BEQ INCHB  \INCREMENT HIGH BYTE
2190 JMP SKIP
2200 .INCHB INC BCOUNTH
2210 .SKIP LDA #0
2220STA&74
2230STA&75
2240STA&76
2250STA&77
2260STA&78
2270 STA&79
2280 STA&7A
2290 STA&7B
2300 RTS
2310 ]
2320 :
```

```
2330 P%=ROOM4%
2340 [ OPT PASS%
2350      LDY#CHAN
2360      LDX#0
2370 .LOOPD  JSR &FFD7
2380      STA &80  \ STORE FOR THE INPUT BYTE
2390      JSR INCTOT%
2400      INX
2410      BEQ OUTD
2420      CPX#NPHB%-1
2430      BCC LOOPD
2440      BEQ LOOPD
2450 .OUTD   RTS
2460 ]
2470 REM ******INCTOT*************
2480P%=INCTOT%
2490[OPT PASS%
2500LDA &80
2510CMP #49
2520BEQ T1
2530 LDA&80
2540CMP #50
2550BEQ T2
2560 LDA&80
2570CMP #51
2580BEQ T3
2590 LDA&80
2600CMP #52
2610BEQ T4
2620 JMP FINISH
2630.T1 INC &74
2640   BEQ T1J
2650   JMP FINISH
2660.T1J INC &75
2670    JMP FINISH
2680.T2  INC &76
2690    BEQ T2J
2700    JMP FINISH
2710.T2J INC &77
2720    JMP FINISH
2730.T3  INC &78
2740    BEQ T3J
2750    JMP FINISH
2760.T3J INC &79
2770    JMP FINISH
2780.T4  INC &7A
2790    BEQ T4J
2800    JMP FINISH
2810.T4J INC &7B
2820.FINISH RTS
2830]
2840:
2850:
2860 REM *******SP320*********
2870P%=SP320%
2880:
```

```
2890[ OPT PASS%
2900CLC
2910LDA &70
2920ADC#&41
2930STA &70
2940LDA&71
2950ADC#&01
2960STA&71
2970LDA&72
2980ADC#&00
2990STA&72
3000LDA&73
3010ADC#&00
3020STA&73
3030RTS
3040]
3050 :
3060 REM ********SORT*********
3070 P%=SORT%
3080 [ OPT PASS%
3090LDA #49
3100STA TEMP1
3110LDA #50
3120STA TEMP2
3130LDA&74
3140STA TEMP1L
3150LDA&75
3160STA TEMP1H
3170LDA &76
3180STA TEMP2L
3190LDA&77
3200STA TEMP2H
3210JSR WIN%
3220LDA WINNER
3230STA SEMI
3240LDA WINL
3250STA SEMIL
3260LDA WINH
3270STA SEMIH
3280NOP
3290LDA #51
3300STA TEMP1
3310LDA #52
3320STA TEMP2
3330LDA&78
3340STA TEMP1L
3350LDA&79
3360STA TEMP1H
3370LDA &7A
3380STA TEMP2L
3390LDA&7B
3400STA TEMP2H
3410JSR WIN%
3420NOP
3430LDA WINNER
3440STA TEMP1
3450LDA SEMI
```

```
3460STA TEMP2
3470LDA WINL
3480STATEMP1L
3490LDA WINH
3500STA TEMP1H
3510LDA SEMIL
3520STA TEMP2L
3530LDA SEMIH
3540STA TEMP2H
3550JSR WIN%
3560 RTS
3570 ]
3580 :
3590 REM *********WINNER*********
3600 :
3610 P%=WIN%
3620 [ OPT PASS%
3630LDA TEMP1H
3640CMP TEMP2H
3650BEQ SAME1
3660CMP TEMP2H
3670BMI NEG1
3680CMP TEMP2H
3690BPL POS1
3700.SAME1 LDA TEMP1L
3710     CMP TEMP2L
3720     BEQ SAME2
3730     CMP TEMP2L
3740     BMI NEG2
3750      CMP TEMP2L
3760    BPL POS2
3770.SAME2 LDA#RND(2)
3780     CMP #2
3790     BEQ RD1
3800     LDA TEMP1
3810      STA WINNER
3820      JSR SUB1
3830     JMP FIN
3840.RD1  LDA TEMP2
3850      STA WINNER
3860    JSR SUB2
3870     JMP FIN
3880.POS1  LDA TEMP1
3890      STA WINNER
3900      JSR SUB1
3910     JMP FIN
3920.NEG1  LDA TEMP2
3930      STA WINNER
3940      JSR SUB2
3950     JMP FIN
3960.POS2  LDA TEMP1
3970      STA WINNER
3980      JSR SUB1
3990     JMP FIN
4000.NEG2  LDA TEMP2
4010      STA WINNER
```

```
4020     JSR SUB2
4030    JMP FIN
4040.SUB1 LDA TEMP1L
4050   STA WINL
4060   LDA TEMP1H
4070   STA WINH
4080   RTS
4090.SUB2 LDA TEMP2L
4100    STA WINL
4110    LDA TEMP2H
4120    STA WINH
4130    RTS
4140.FIN RTS
4150]
4160:
4170:
4180 REM ************MULT1************
4190 :
4200 :
4210 P%=MULT1%
4220 :
4230 [ OPT PASS%
4240LDA#0
4250STARESLL
4260STARESLH
4270STARESHL
4280STARESHH
4290 STA TEMPL
4300 STA TEMPH
4310     LDX #&10
4320 .LOOP
4330     LSR LIERH
4340     ROR LIERL
4350     BCC ZERO
4360     CLC
4370     LDA LIEDL
4380     ADC RESLL
4390     STA RESLL
4400     LDA LIEDH
4410     ADC RESLH
4420     STA RESLH
4430     LDA TEMPL
4440     ADC RESHL
4450     STA RESHL
4460     LDA TEMPH
4470     ADC RESHH
4480     STA RESHH
4490 .ZERO NOP
4500     ASL LIEDL
4510     ROL LIEDH
4520     ROL TEMPL
4530     ROL TEMPH
4540     DEX
4550     BNE LOOP
4560     RTS
4570     ]
4580 REM *******PREMULT**********
```

```
4590P%=PREMULT%
4600:
4610 [OPT PASS%
4620LDA #NPVB% MOD 256
4630STA LIERL
4640LDA #NPVB% DIV 256
4650STA LIERH
4660LDA #321 MOD 256
4670STA LIEDL
4680LDA #321 DIV 256
4690STA LIEDH
4700JSR MULT1%
4710LDA RESLL
4720STA LIERL
4730LDA RESLH
4740STA LIERH
4750LDA &83
4760STA LIEDL
4770LDA #0
4780STA LIEDH
4790JSR MULT1%
4800LDA RESLL
4810STA &70
4820LDA RESLH
4830STA &71
4840LDA RESHL
4850STA &72
4860LDA RESHH
4870STA &73
4880LDA &82
4890STA LIEDL
4900LDA#0
4910STA LIEDH
4920LDA #NPHB% MOD 256
4930STA LIERL
4940LDA #NPHB% DIV 256
4950STA LIERH
4960JSR MULT1%
4970CLC
4980LDA &70
4990ADC RESLL
5000STA&70
5010LDA &71
5020ADC RESLH
5030STA &71
5040LDA &72
5050ADC RESHL
5060STA &72
5070LDA &73
5080ADC RESHH
5090STA &73
5100 RTS
5110 ]
5120 NEXT PASS%
5130 CALL ROOM1%
5140 CLOSE# CHAN
```

```
5150 CLOSE# OCHAN
5160 ENDPROC
```

A.2.9. Matching Groups of Files.

A.2.9.1 Program GMATCH.

The RUNML program generates a file series, within which, each file is named according to the four letter name of the Primary File from which it is derived, plus a suffix indicating which level of the Master List was used to generate it. For instance, suppose a User constructs a Master List, the ninth level of which specifies a block size of 4 x 4 pixels, and that this list is run on a Primary file called PRIM. The file generated from the 4 x 4 dimension will be named PRIM9. This program, GMATCH uses this ordered naming of files to make comparisons between two similar file series a simple process.It takes a specified Primary File root name for each file series to be compared, and repeatedly increments a suffix to derive the name each pair of files which require comparison. Again the aim is to make the program run with the minimum of user intervention. The program tests the opened file pair for equivalence, in accordance with the principles outlined in the User Guide in Appendix One.

Code Lines	Function
20 - 31	Requests the names of the Primary files from which the files series to be compared are derived and the location of each of the series.
40 - 50	Requests a level corresponding to the level of the Master List at which to begin and end the comparisons. Hence if the start level was 10 and the end level was 20, and the names of the Primary files

	which derived the series were A and B, the program would compare A10 with B10, A11 with B11, through to A20 with B20.
51 - 52	Offers the option of removing the systems disc and halts until a key press is given to confirm continuation of processing.
60	Initiates a loop from start level to end level.
70 - 80	Constructs file names from the input values and the value of the loop initiated at line 60.
100	Calls a procedure which performs the comparison.
130 - 134	Either restarts the program or reloads the menu.
160 - 170	Opens the files for comparison.
190 - 200	Setting counters to zero.
220 - 250	Output the number of bytes checked.
270 - 280	Input of bytes from respective files.
300 - 330	Tests for equality in input bytes. If both bytes are 52 (the background colour) then the next byte is input and no change is made to the counters. Note that in MODE 1 of the BBC, four logical colours are supported, but in the current application only three are required. To cope with this, any byte values of 50 are converted to 51, in this case making red have the same value of yellow. If the bytes are then equal the match total is incremented and if not the mismatch counter is incremented.
370 - 380	Input channels closed.
400 - 441	Output of match and mismatch data.

A.2.9.2 GMATCH Code.

```
10 CLS
20 INPUT TAB(2,2) "Name First Primary " P1$
21 INPUT TAB(2,4) "Location of data ? "D1%
30 INPUT TAB(2,6) "Name Second Primary " P2$
31 INPUT TAB(2,8)"Location of data ? " D2%
40 INPUT TAB(2,10)"Start Level ? "SL%
50 INPUT TAB(2,12) "End Level  ? " EL%
51 PRINT TAB(2,14)"Remove Systems Disc if necessary"
52 PRINT TAB(2,16)"Insert Data Discs then press key "
53 WAIT=GET
60 FOR LP%=SL% TO EL%
70 FILE1$=":"+STR$(D1%)+"."+P1$+STR$(LP%)
80 FILE2$=":"+STR$(D2%)+"."+P2$+STR$(LP%)
```

```
90 :
100 PROCcount
110 :
120 NEXT
130 CLS
131 INPUT TAB(2,4) "More Files to process ? " INS$
132 IF INS$="Y" THEN GOTO 10
134 CHAIN "MENU"
140 :
159 DEF PROCcount
160 CHAN1=OPENIN FILE1$
170 CHAN2=OPENIN FILE2$
180 :
190 T%=0:T2%=0
200 C%=0
210 :
220 PRINT TAB(10,20)"BYTE"
230 REPEAT
240 C%=C%+1
250 PRINT TAB(20,20);C%
260 :
270 B1%=BGET#CHAN1
280 B2%=BGET#CHAN2
290 :
300 IF B1%=52 AND B2%=52 THEN GOTO 240
310 IF B1%=50 THEN B1%=51
320 IF B2%=50 THEN B2%=51
330 IF B1%=B2% THEN T%=T%+1 ELSE T2%=T2%+1
340 :
350 UNTIL EOF#CHAN1
360 :
370 CLOSE#CHAN1
380 CLOSE#CHAN2
390 :
400 CLS
401 VDU2
410 PRINT TAB(2,4)"FOR ";P1$;" vs. ";P2$;"  at level ";LP%
420 PRINT TAB(2,6)"Matches = ";T%
430 PRINT TAB(2,8)"Mismatches = ";T2%
431 PRINT:PRINT:PRINT
440 :
441 VDU3
450 ENDPROC
```

A.2.10. Matching Single Files.

A.2.10.1 Program MATCH1.

MATCH1 performs the same match / mismatch count as GMATCH. This program, however, is designed to work through a series of specifically named files rather than the systematic series generated by the RUNML program. The match counting protocol is identical to that in GMATCH, it is simply the front end of the program that differs, and for this reason there is only a partial description of the code below. The early part of the program provides facilities for the User to construct a list of individually named files. These names are loaded into an internal array. Each pair of files is opened in turn by the program and compared. The main practical purpose of the program is to compare a series of Primary files.

Code Lines	Function
10 - 20	Sets up the array space.
50 - 60	Sets up list headings.
80 - 120	Controls the input of file names and locations until the "*" delimeter is entered. Up to 20 file pairs are catered for.
170 - 220	This loop works through the list until the "*" delimeter is encountered. It uses the information in the list to run a procedure which is essentially the same as the matching procedure in GMATCH.

A.2.10.2 MATCH1 Code

```
40 CLS
50 :
60 INPUT TAB(2,4)"Input name of first File " P1$
70 INPUT TAB(2,6)"Location ? " L1%
80 INPUT TAB(2,8)"Second File ? " P2$
90 INPUT TAB(2,10)"Location ? " L2%
100 :
110 FILE1$=":"+STR$(L1%)+"."+P1$
120 FILE2$=":"+STR$(L2%)+"."+P2$
130 :
140  PRINT TAB(4,1);"Remove systems Disc if necessary"
141 PRINT TAB(8,2)"and insert data discs"
150 WAIT=GET
160 CHAN1=OPENIN FILE1$
170 CHAN2=OPENIN FILE2$
180 :
190 T%=0:T2%=0
200 C%=0
210 :
220 PRINT TAB(10,20)"BYTE"
230 REPEAT
240 C%=C%+1
250 PRINT TAB(20,20);C%
260 :
270 B1%=BGET#CHAN1
280 B2%=BGET#CHAN2
290 :
300 IF B1%=52 AND B2%=52 THEN GOTO 240
310 IF B1%=50 THEN B1%=51
320 IF B2%=50 THEN B2%=51
330 IF B1%=B2% THEN T%=T%+1 ELSE T2%=T2%+1
340 :
350 UNTIL EOF#CHAN1
360 :
370 CLOSE#CHAN1
380 CLOSE#CHAN2
390 :
400 CLS
410 PRINT TAB(2,4)"FOR ";P1$;" vs. ";P2$
420 PRINT TAB(2,6)"Matches = ";T%
430 PRINT TAB(2,8)"Mismatches = ";T2%
440 :
450 INPUT TAB(2,12)" More files ? " INS$
460 IF INS$="Y" THEN GOTO 40
470 CHAIN "MENU"
```

A.2.11 SWAP Utility.

A.2.11.1 Program SWAP.

The package as whole is designed to use a twin floppy drive BBC machine and whilst running the RUNML program, the lower one of the two (the lower on the development machine) is reserved to hold the generated file series. This means that the Primary file (the input file for RUNML) that is currently being worked upon must be transferred to the underside of the Systems disc. The disc operating system holds a procedure for copying files but this has the unfortunate effect of wiping the RAM when transferring large files such as the Primary File. The current program is concerned with a simple way of restoring the package to its proper state after such a copy has been done.

Code Lines	**Function**
10 - 40	Screen set up and prompt that the package requires a new Primary file to work upon. It requests the name of the Primary file that is to be processed next.
45 - 47	The control file CNTRL is updated to include the new file name and a default start level of 1.
50 - 51	Requests location of the new Primary file named and prints a message that the previous Primary file is to be overwritten. Note that no User input is taken here, but it is required by the operating system when the *DESTROY command in the program is executed.
60	This is the somewhat crude means of recovering from the failure caused by the copying of a large file. The Special Function Keys are not disrupted by the copy command, so this line installs a command line into the memory used by these keys. The command simply instructs the system to reload the RUNML program upon a single,

	prompted key press.
61 - 65	The copy of a new Primary File to the underside of the disc will fail if the disc already has a file on it. All previous files on this side of the disc must be erased. These lines do this.
70 - 100	The command to perform the copy must be passed to the Command Line Interpreter. This module installs the command in memory to be picked up by the CLI later.
110 - 130	Prepares the prompt for the User to recover after the copying of a new Primary file.
150 - 180	Installation of the CLI.
188 - 260	A further simple message to instruct the user on how to recover by writing a simple "Hit f0" message.
270	Initiates the CLI thus executing the copy command.

A.2.11.2 SWAP Code.

```
 10 MODE6
 20 VDU 19,0,4,0,0,0
 30 CLS
 35 PRINT TAB(2,5);"The systems disc requires new primary"
 40 INPUT TAB(2,8) " Input name of next primary " F$
 45 OCHAN=OPENOUT"CNTRL"
 46 PRINT# OCHAN, 1,F$
 47 CLOSE# OCHAN
 50 INPUT TAB(2,11) " Which side of disc ? (1 or 3)" SD%
 51 PRINT TAB(2,14);"Confirm delete of previous primary"
 60 *KEY 0 CHAIN "RUNML" ||M
 61 *DR.2
 62 *ENABLE
 64 *DESTROY *.*
 65 *DR.0
 70 COM$="*COPY "+STR$(SD%)+" 2 "+F$
 80 $&0C00=COM$
 90 LE%=&0C00+LEN(COM$)+1
100 ?LE%=&0D
110 CLS
120 PRINT TAB(2,8) "WARNING : IGNORE any error messages "
121 PRINT TAB(2,10) "Hit f0 when copy complete"
130 PRINT:PRINT:PRINT
140 P%=&0070
150 [ OPT 0
160 LDX# &00
170 LDY# &0C
180 JSR&FFF7
188 LDA#12:JSR&FFEE
190 LDA#72:JSR &FFEE
200 LDA#105:JSR &FFEE
210 LDA#116:JSR &FFEE
220 LDA#32:JSR &FFEE
```

```
230 LDA#102:JSR &FFEE
240 LDA#48:JSR &FFEE
250 RTS
260 ]
270 CALL &0070
```

Appendix Three

Complex Source Code.

A.3.1. Complex.

Chapter Eight describes the design and development of two mathematical models of mimicry, *Complex* and *MacComplex* . Of these, the former was the most sophisticated and the least successful, exhibiting little reproducibility between replicates of a given simulation. It does, however, represent a more comprehensive description of mimicry systems than the later, simpler *MacComplex* , and is therefore presented here for the interest of other modellers. Almost certainly, the evident instability is due to the complexity of the predator sub-model adopted, and this in itself is interesting as it suggests that modelling predator behaviour is likely to be the most intractable aspect of a comprehensive, realistic mathematical model of mimicry.

The program presented in section A.3.2 below is written in Fortran for IBM PC compatible machines. The source code listing includes some subroutines which were included in test versions but which are not called in the implementation presented below.

A.3.2. Complex Source Code.

```
c. Complex - A stochastic model of Mimicry Complexes
c. Written in Fortran for the IBM PC Compatible Environment.
c. Dave Grewcock. Dept Zoology 1990.



c. Parameter List.

c ispnum= number of species in the prey community.
c ivalue= the number of individuals in each species.
c ipreyarr = the prey array, 1000 entries long, 2 entries wide
c itotal= temporary running total used in set up routines
c imark = marker used to set up ipreyarr
c itype = code for prey types, numbered 1 to however many species
c R = seed for the random number generator
c sim = mean similarity value for each species
c temp = store for random number to decide whether spreading factor
c is added or subtracted to the mean similarity
c ipredsp = the number of predator species
c discrim = the discriminatory capacity of each predator species
c inum = the number of individuals in each species
c will = the base willingness of each species to attack
c itp = the number of time periods per season
c inseas = number of seasons to simulate
c itotpred = total number of predator individuals
c itotprey = total number of prey individuals
c iselect = the subscript value of the predator chosen
c select = the random number generated times the no of entries in array
c phit= the probability that a visible prey item will be taken
c tsim= temp store for the similarity of the chosen prey item
c pdet= the probability that the chosen prey item will be detected


c ================= initialization==========================

real ipreyarr, predarr
real base(100),recrut(100),prednos(100),basewill(100)
real p,means(100,5)
```

```
integer num
dimension ipreyarr(1000,2), predarr(100,5)
dimension ispacealloc(100), inosurv(100)
dimension itemplist(1000)

itotal=0
imark=1
itype=1

c Randomize the random number generator using DOS clock

call clock_seed (ix,iy,iz)

c Open the ASCII file for output

open(34,file='result',status='old')

c Input initial population variation and variation added at the  time of
c reproduction

print*, 'intial population variation ? '
read*, startvar

print*, ' reproduction variation ? '
read*, reprovar

c Input the interval at which results are written to the results file

print*, ' How many generations before reporting  ? '
read*, ireport
iseascount=ireport-1

c Set up prey community

print*, 'How many prey species ? '
read*, ispnum

do 10 i=1,ispnum

call insub (i,ivalue,sim)

do 50 i3=imark,imark+ivalue
```

```
ipreyarr(i3,1)=itype
call norng(r,p,ix,iy,iz)
ipreyarr(i3,2)=sim+(p/startvar)
print*,ipreyarr(i3,2)

50          continue

imark=imark+ivalue
itype=itype+1
itotal=itotal+ivalue
means(i,3)=sim

10     continue

itotprey=itotal

c How many individuals of the Model species ?

print*,'how many models ? '
read*,nmod

c Set up the Predator array

c imark is reset to 1 to set up the pred. array

imark=1
itype=1
itotal=0

print*, 'How many predator species ? '
read*, ipredsp

do 30 i5=1,ipredsp

call predsub (i5,inum,discrim,will,crut)

c The elements of the array are now assigned, 1st is prey type,
c 2nd is capacity to discriminate, 3rd the estimate of model
c freqeuncy, 4th the willingness to attack, 5th is the number
c of encounters that the predator has been involved in.
```

```
do 60 i6=imark,imark+inum


predarr(i6,1)=itype
predarr(i6,2)=discrim
predarr(i6,3)=0
predarr(i6,4)=will

60          continue

imark=imark+inum
base(itype)=discrim
recrut(i5)=crut
prednos(i5)=inum
basewill(i5)=will
itype=itype+1
itotal=itotal+inum

30     continue

itotpred=itotal

c Request number of Time Periods per Season and number of Seasons
c to simulate

print*,' '
print*,'How many time periods per season ? '
read*, itp
print*, 'How many seasons to simulate ?'
read*, inseas

do 100 i9=1,inseas

c Call DOS clock again for a random number for the following
c random  number series

398    call time (ihours,mins,isecs,ihuns)

r=float(ihuns)
huns=(float(ihuns))/10000
r=(r/100)+huns
```

```
if(r.eq.0.0) goto 398

do 110 i10=1,itp

c Select predator and prey individuals at random and play them off

c Random selection of predator

call random (r,ix,iy,iz)
select=r*itotpred
iselect=int(select)+1

c Random selection of prey. The prey may have been killed in a
c previous encounter so test that array entry isn't empty.

call random (r,ix,iy,iz)
select=r*(itotprey+nmod)
ipselect=int(select)+1

if(ipselect.le.itotprey) then
call submim(model,tsim,ipreyarr,itotprey,r,ix,iy,iz)
else
call submod(model,tsim,r,ix,iy,iz)
end if

c Does the selected prey item become visible to the predator ? If
c so, the program continues to the predators' decision, if not then
c it goes to the next time period.

call subvis(tsim,visible,r,ix,iy,iz)

if (visible.eq.0) go to 110

c The predator selects whether to hit or leave the visible prey

call subsurv(isurv,iselect,predarr,tsim,r,ix,iy,iz)

c If prey item does not survive then isurv is 0 and that entry in
c prey array is blanked out

if (isurv.eq.0) then
ipreyarr(ipselect,1)=0.0
ipreyarr(ipselect,2)=0.0
```

```
endif

c Update the predator array thresholds according to the resluts

if(model.eq.1.and.isurv.eq.1) call corrmod1(predarr,iselect)
if(model.eq.0.and.isurv.eq.0) call corrmod0(predarr,iselect)
if(model.eq.1.and.isurv.eq.0) call icorrmod1(predarr,iselect)
if(model.eq.0.and.isurv.eq.1) call icorrmod0(predarr,iselect)

c Increment the predators' number of encounters recorded

predarr(iselect,5)=predarr(iselect,5)+1

c Degrade the entries of all other predators by 2%

do 140 i11=1,itotpred

if(i11.eq.iselect) goto 140
num=int(predarr(i11,1))
p=base(num)
predarr(i11,2)=((predarr(i11,2)-p)*.980)+p

140   continue

110   continue


c This point represents the end of one season so the arrays are
c updated for the next season. Prey population is replenished.
c Naive predators are recruited.

91      format(' ',5(\f9.5))

c recruit some new predators

ilowbound=0

do 150 i12=1,ipredsp

inoreplen=int(recrut(i12)*prednos(i12))+1

do 160 i13=1,inoreplen
```

```
call random (r,ix,iy,iz)
select=r*prednos(i12)
irselect=int(select)+1
irselect=irselect+ilowbound
predarr(irselect,2)=base(i12)
predarr(irselect,3)=0
predarr(irselect,4)=basewill(i12)
predarr(irselect,5)=0

160        continue

ilowbound=ilowbound+prednos(i12)

150     continue

c Replenish the prey array with new values
c Call subroutine to count the number of free spaces in the
c whole prey population

call freecount(ipreyarr,itotprey,inofree)

c Call subroutine to count the number of survivors in each species

call survivecount(ipreyarr,ispnum,inosurv,itotprey,intotsurv)

c Call subroutine to allocate the number of free spaces to each
c species in proportion to their survivorship in the preceding
c Season

call allocation (intotsurv,inosurv,ispacealloc,ispnum,inofree)

c Start competition for the empty slots

do 210 i18=1,ispnum

if(ispacealloc(i18).eq.0) goto 210

c This makes up a list of surviving competitors of species i18

call pryslct(ipreyarr,itemplist,itotprey,ilist,i18)
```

```
do 220 i19=1,ispacealloc(i18)

c. call the new improved speed routine

230     call choose (r,ix,iy,iz,ilist,icompete,itemplist)

c. call subroutine to check whether the selected competitor gets the place or
c. not.

simdiff=(means(i18,3)-ipreyarr(icompete,2))
call winner(iwin,simdiff,r,ix,iy,iz)

if(iwin.eq.0) goto 230

c find any vacant slot in the prey array

do 240 i20=1,itotprey
if(ipreyarr(i20,1).eq.0.0) then
goto 250
else
goto 240
endif

240          continue

250          ivacant=i20

c. fill the slot with a copy of the parent plus or minus some variation
c. Bound checks are included to stop similarity value going above 1 or
c. below 0.0001.

ipreyarr(ivacant,1)=ipreyarr(icompete,1)
call random (r,ix,iy,iz)
call norng(r,p,ix,iy,iz)

ipreyarr(ivacant,2)=ipreyarr(icompete,2)+(p/reprovar)

if(ipreyarr(ivacant,2).gt.1.0) then
ipreyarr(ivacant,2)=1.0
endif

if (ipreyarr(ivacant,2).lt.0.0001) then
ipreyarr(ivacant,2)=0.0001
```

```
endif

220    continue

210    continue

c here call a subroutine which calculates the means for the replenished
c array of prey

call submeans(means,itotprey,ipreyarr,ispnum)

c print out the means to the open ascii file and to screen
c if it is time to report

iseascount=iseascount+1

if (iseascount.eq.ireport) then
print*, ' '
print*, ' SEASON ',i9
print*, ' '
write(6,96)((means(i,j),j=1,5), i=1,ispnum)

96     format(5(' ',f9.3,6x))
write(34,36) (means(i,3),means(i,5),means(i,2),i=1,ispnum)
36     format (20(f9.3,3x))

iseascount=0
endif


c 100 is the end of the seasons loop

100    continue

c Close files and end the program

print*,'finished'
close(34, status='keep')
close(92)
end
```

```
c ============= BEGINNING OF SUBROUTINES ============


c SUBROUTINE PREDSUB to input data for the predator community

subroutine predsub (i5,inum,discrim,will,crut)

print*, 'How many individuals in predator species ',i5,'  '
read*, inum

print*, 'Discriminatory capacity ?'
read*, discrim

print*, 'Willingness to attack'
read*, will

print*,' Recruitment rate ? '
read*, crut

return
end


c SUBROUTINE INSUB to request the numbers of each prey species,
c. and the mean similarity value for each species.


subroutine insub (i,ivalue,sim)

print*, 'How many individuals in prey species',i,'  '
read*, ivalue

print*, 'Mean similarity value ? '
read*, sim

return
```

```
end


c SUBROUTINE RANDOM taken from Wichmann and Hill, Applied
c. Statistics 1982.

subroutine random (r,ix,iy,iz)

ix=mod (171*ix,30269)
iy=mod (172*iy,30307)
iz=mod (170*iz,30323)
r=amod(float(ix) / 30269.0 + float(iy) / 30307.0 + float(iz) / 30323.0, 1.0)

return
end


c SUBROUTINE SUBMOD This sets the model flag and calculates the
c. similarity value for the model.

subroutine submod(model,tsim,r,ix,iy,iz)

model=1
call random (r,ix,iy,iz)
tsim=1-(r/10)

return
end


c SUBROUTINE SUBMIM  This selects a living mimic individual and
c recalls its similarity value.


subroutine submim (model,tsim,ipreyarr,itotprey,r,ix,iy,iz)

real ipreyarr(1000,2)

model=0

130    call random (r,ix,iy,iz)
```

```
select=r*itotprey
ipselect=int(select)+1

if(ipreyarr(ipselect,1).eq.0.0) then
goto 130
else
tsim=ipreyarr(ipselect,2)
endif

return
end


c SUBROUTINE SUBVIS This routine calculates whether the selected
c.prey item becomes visible to the predator

subroutine subvis (tsim,visible,r,ix,iy,iz)

c Similarity versus probability of detection routine used in the
c working version of the model


if(tsim.lt.0.5) then
pdet=0.01
else
pdet=(tsim-0.5)*2.0
endif

c Relationship as originally designed

c pdet=800/(1+(149*(exp(-0.1*(tsim*100)))))
c pdet=pdet/1000

call random (r,ix,iy,iz)
if (r.ge.pdet) then
visible=0
else
visible=1
end if

return
end
```

```
c SUBROUTINE SUBSURV The routine holds the decision making
c process to see whether the predator chooses to hit the visible prey.
cThe code shown is the simple version which produced the reported
c results.
c In this version the probability of attack is set by a single
c threshold value held by each predator

subroutine subsurv(isurv,iselect,predarr,tsim,r,ix,iy,iz)

real predarr(100,5)

phit2=predarr(iselect,4)
call random (r,ix,iy,iz)

if(r.gt.phit2) then
isurv=1
else
isurv=0
endif

return
end


c Beginning of the subroutines to update the predators' thresholds

subroutine corrmod1(predarr,iselect)

real predarr(100,5)

predarr(iselect,2)=predarr(iselect,2)+(1-predarr(iselect,2))*.7

if (predarr(iselect,2).gt.1.0) then
predarr(iselect,2)=.99
endif

predarr(iselect,3)=predarr(iselect,3)+1

return
end
```

```
subroutine corrmod0(predarr,iselect)

real predarr(100,5)

predarr(iselect,2)=predarr(iselect,2)+(1-predarr(iselect,2))*.15

if (predarr(iselect,2).gt.1.0) then
predarr(iselect,2)=0.99
endif

predarr(iselect,4)=predarr(iselect,4)+(1-predarr(iselect,4))*.1

if (predarr(iselect,4).gt.1.0) then
predarr(iselect,4)=0.99
endif

return
end


subroutine icorrmod1(predarr,iselect)

real predarr(100,5)

predarr(iselect,2)=predarr(iselect,2)+(1-
predarr(iselect,2))*.15

if (predarr(iselect,2).gt.1.0) then
predarr(iselect,2)=.99
endif

predarr(iselect,4)=predarr(iselect,4)-(1-predarr(iselect,4))*.3

if (predarr(iselect,4).lt.0.0) then
predarr(iselect,4)=.01
endif

predarr(iselect,3)=predarr(iselect,3)+1

return
end
```

```
subroutine icorrmod0(predarr,iselect)

real predarr(100,5)

predarr(iselect,2)=predarr(iselect,2)+(1-predarr(iselect,2))*.7

if(predarr(iselect,2).gt.1.0) then
predarr(iselect,2)=.99
endif

predarr(iselect,3)=predarr(iselect,3)+1

return
end


c Start of subroutines which handle the competition for vacant
c spaces by the surviving prey individuals

c SUBROUTINE FREECOUNT which counts up the number of free
c. spaces available at the end of the season

subroutine freecount(ipreyarr,itotprey,inofree)

real ipreyarr(1000,2)

inofree=0

do 170 i14=1,itotprey

if(ipreyarr(i14,1).eq.0) then
inofree=inofree+1
endif

170     continue

return
end
```

```
c SUBROUTINE SURVIVECOUNT counts the number of survivors of
c each species


subroutine survivecount(ipreyarr,ispnum,inosurv,itotprey,intotsurv)

real ipreyarr(1000,2)
integer inosurv(100)

intotsurv=0

do 180 i15=1,ispnum

inosurv(i15)=0

do 190 i16=1,itotprey

        if(ipreyarr(i16,1).eq.i15) then

        inosurv(i15)=inosurv(i15)+1

        intotsurv=intotsurv+1

        endif

  190       continue



  180   continue

return
end


c SUBROUTINE ALLOCATION works out the number of spaces that will
c be awarded to the species, in proportion to their survivorship
c in the previous generation


subroutine allocation(intotsurv,inosurv,ispacealloc,ispnum,inofree)

integer ispacealloc (100),inosurv(100)
```

```
real newspace

do 200 i17=1,ispnum

if(inosurv(i17).eq.0) goto 200
newspace=(float(inosurv(i17))/float(intotsurv))*inofree
ispacealloc(i17)=int(newspace)

200         continue

return
end


c SUBROUTINE WINNER tests whether the selected competitor does
c.get the current vacant space

subroutine winner(iwin,simdiff,r,ix,iy,iz)

x1=simdiff

call normal(x1,y1)
call random (r,ix,iy,iz)

if(y1.le.r) then
iwin=0
else
iwin=1
endif

return
end


c SUBROUTINE SUBMEANS to work out the means for the prey array

subroutine submeans(means,itotprey,ipreyarr,ispnum)

real means(100,5),ipreyarr(1000,2)

c blank out the previous entries in the means array
```

```
do 270 i22=1,ispnum

means(i22,1)=0
means(i22,2)=0
means(i22,3)=0
means(i22,4)=0
means(i22,5)=0

270     continue

c go to each level of the prey array and update the running total for the
c prey type indicated in the first column

do 260 i21=1,itotprey

if(ipreyarr(i21,1).eq.0) goto 260
ilevel=ipreyarr(i21,1)
means(ilevel,1)=means(ilevel,1)+ipreyarr(i21,2)
means(ilevel,2)=means(ilevel,2)+1
means(ilevel,4)=means(ilevel,4)+(ipreyarr(i21,2)*ipreyarr(i21,2))

260     continue

c into the third column of the means array insert the means as
c calculated from the entries in the first two columns

do 280 i23=1,ispnum

if(means(i23,2).eq.0.0) then
means(i23,3)=0.0
else
means(i23,3)=means(i23,1)/means(i23,2)
term1=(means(i23,1)*means(i23,1))/means(i23,2)
term2=(means(i23,4)-term1)/means(i23,2)
means(i23,5)=sqrt(term2)

end if

280     continue

return
end
```

```
c SUBROUTINE NORMAL which gives the probability of reproduction
c according to a normal distribution, x1 will be the difference
c between the competing individuals' similarity value and the
c species' mean. y1 will be the corresponding probability of
c reproduction, given that difference.


subroutine normal(x1,y1)

y=1/(.3*(sqrt(2*3.14159)))
b=(x1*x1)/(2*(0.3*0.3))
y1=y*exp(-b)

return
end


SUBROUTINE NORNG(R,P,ix,iy,iz)

c. THIS SUBROUTINE GENERATES A SEQUENCE OF NUMBERS
c  NORMALLY AND RANDOMLY DISTRIBUTED OVER THE INTERVAL -3
c TO 3 FROM UNIFORMLY DISTRIBUTED RANDOM NUMBERS BY THE
c METHOD OF LINEAR APPROXIMATION TO THE INVERSE OF THE
c ACCUMULATIVE NORMAL DISTRIBUTION FUNCTION.

DIMENSION Y(6), X(6), S(5)

DATA Y/0.,.0228,.0668,.1357,.2743,.5/,

&X/-3.01,-2.0,-1.5,-1.0,-.6,0./,
&S/43.8596,11.3636,7.25689,2.891352,2.65887/

CALL RANDOM(R,IX,IY,IZ)

P = R
I = 1

   IF (P.GT.0.5) P = 1.0-R
2  IF (P.LT.Y(I + 1)) GOTO 8

I = I + 1
```

```
 GO TO 2

 8   P = ((P-Y(I))*S(I) + X(I))

 IF (R.GE.0.5) P = -P

 RETURN

 end


 c SUBROUTINE PRYSLCT to search for competing prey items

 SUBROUTINE pryslct(ipreyarr,itemplist,itotprey,ilist,i18)

 real ipreyarr(1000,2)
 integer itemplist(1000)
 integer ilist

 c ilist is the number of entries in the list of competitor candidates
 c loop through the ipreyarr and select out those cases where they are
 c empty slots or the wrong prey type. Note that the entry in ipreyarr
 c is NINted so that a true comparison for equality can be done

 ilist=0

 do 400 i30=1,itotprey

 icompare=nint(ipreyarr(i30,1))
 if(icompare.eq.0) goto 400
 if(icompare.ne.i18) goto 400

 ilist=ilist+1
 itemplist(ilist)=i30

 400    continue

 return
 end
```

```
subroutine choose (r,ix,iy,iz,ilist,icompete,itemplist)

integer itemplist(1000)

c Having created a list of the locations of suitable candidates in
c ipreyarr, select a random one of them.

call random(r,ix,iy,iz)
select=r*ilist
iselect=nint(select)+1
icompete=itemplist(iselect)

return
end


c subroutine to set up seed values from the dos clock

SUBROUTINE clock_seed (ix,iy,iz)

call time(ihours,mins,isecs,ihuns)

c to produce ix

imins=mins*1000
rmins=(float(imins))/2.0
imins=(int(rmins))+(isecs*10)+ihours

ix=imins

 c to produce iy

iisecs=isecs*1000
secs=(float(iisecs))/2.0
iisecs=(int(secs))+(mins*10)-ihours

iy=iisecs

c to produce iz

huns=(float(ihuns))
huns=huns/3.0
```

```
ihuns=((int(huns))*1000)+(isecs*10)+ihuns
iz=ihuns

return
end


c SUBROUTINE MATE  A routine which provides for assortative mating
c which was used during the testing of the program. It allows
c prey items which win places in the next generation to find the
c individual of the same species with the similarity value
c  closest to it. This then allows the "offspring" to have an
c  intermediate  similarity value.

SUBROUTINE mate (ipreyarr,icompete,r_mate_similarity,itotprey)

real ipreyarr(1000,2)

r_mate_similarity = 1.0

 do 321 imate=1,itotprey

if (ipreyarr(imate,2).eq.0.0) goto 321
if (ipreyarr(imate,1).ne.ipreyarr(icompete,1)) goto 321
if (imate.eq.icompete) goto 321

r_mate_diff=ipreyarr(imate,2)-ipreyarr(icompete,2)
r_mate_diff=sqrt(r_mate_diff*r_mate_diff)

if(r_mate_diff.lt.r_mate_similarity) then
r_mate_similarity=r_mate_diff
i_chose_mate=imate
endif

321     continue

r_mate_similarity=ipreyarr(i_chose_mate,2)

return
end
```

Appendix Four

MacComplex Source Code

A.4.1. MacComplex.

Chapter Eight contains a detailed discussion of the results produced by a mathematical model of mimicry, *MacComplex* , which follows some of the "Monte Carlo" principles adopted by Turner *et al* (1984). The most significant extension of the basic Turnerian framework is that *MacComplex* sustains simulated prey populations which are capable of "evolving" a new mimetic character as a result of the "selection pressure" from simulated predators. In a basic sense, *MacComplex* therefore has one of the attributes argued for in Chapter Eight, in that the outcome of a long series of encounters between predators, Models and Mimics, is capable of shaping one aspect of the structure of the simluated mimicry complex. A mathematical model with such attributes, it is argued, might represent an almost unique opportunity to test our theoretical understanding of mimicry against field observations.

As with other software elements presented in this thesis, *MacComplex* is intended to be functional rather than elegant. The program presented below, for example, contains no provision for keyboard input of parameter values; for each type of simulation the parameter values must be edited in the source code and the program re-compiled.

A.4.2. MacComplex Source Code.

```
' MacComplex - A stochastic model of Mimicry Complexes
' Created with MicroSoft QuickBasic 1.0 for Macintosh.
' Dave Grewcock 1992.

DEFINT A-Z

DEF FNPickRandomInteger(UpperLimit)=INT(UpperLimit*RND)+1
DEF FNVisibility!(Similarity!,Power!)=(Similarity!^Power!)

OPTION BASE 1

DIM SHARED PredatorSpecies! (3,4)  '1 is pop, 2 is seed p. attack, 3 is seed tolerence
DIM SHARED PreySpecies! (4,4)      '1 is pop, 2 is sim, 3 is mean, 4 is sd
DIM SHARED Prey! (2,200)
DIM SHARED Predators! (5,100)    '1 is type, 2 is p attack, 3 is memory
                                   '4 is memory flag, 5 is individual tolerence

RANDOMIZE TIMER

' Initialisation

InitialisePlotWindow
OpenResultFile
GetPreyAttributes
GetPredatorAttributes

InitialisePreyArray
InitialisePredatorArray

GetSimulationAttributes
```

```
' Main Program Loop

FOR Season = 1 TO NumberOfSeasons

LOCATE 1,1
PRINT Season

    FOR Encounter = 1 TO NumberOfEncounters

     'Select Random Prey item and check it is alive

    PreyAlive!=0!
     WHILE PreyAlive!=0!
     PreyItem=FNPickRandomInteger (TotalPrey)
     PreyAlive!=Prey!(2,PreyItem)
    WEND

     ' Check whether Prey becomes visible

     pAppear!=FNVisibility!(Prey!(2,PreyItem),Power!)

    IF pAppear! > RND THEN Available=1 ELSE Available = 0

            SELECT CASE Available

                CASE 1

                 'Select random predator

                   PredatorItem=FNPickRandomInteger (TotalPredators)

                  'Predator decides whether prey is model or mimic

                   phit!=Predators!(3,PredatorItem)-Predators!(5,PredatorItem)
                  Difference!=phit!-Prey!(2,PreyItem)

      IF Predators!(4,PredatorItem) > 0! AND Difference! < RND
      THEN
```

```
                  Model = 1
               ELSE
                  Model = 0
              END IF


     'Predator decides whether to hit or leave prey

     IF Model = 0 THEN 'AND RND < Predators!(2,PredatorItem) THEN

     RevisePredator            ' revises predator parameters (experience)
     KillPrey                  ' sets prey to dead status

     ELSE

     END IF

     CASE 0


     END SELECT

   NEXT Encounter

 RevisePreyArray
 RecruitPredators

 CalculateMeans
 FileResults

 NEXT Season

 CLOSE

 WHILE MOUSE(0)<>1 : WEND


 END


 '  Sub Programs
```

```
SUB GetPreyAttributes STATIC

SHARED ModelType
SHARED Power!


  'PreySpecies!(1,1)=
  'PreySpecies!(2,1)=
  PreySpecies!(1,2)=10
  PreySpecies!(2,2)=.5
  PreySpecies!(1,4)=10    ' This is the model pop
  PreySpecies!(2,4)=.97   ' This is the model similarity

ModelType=4
Power!=.3

END SUB


SUB GetPredatorAttributes STATIC

PredatorSpecies! (1,1)=5      'Population  was five
PredatorSpecies! (2,1)=.9     'p attack
PredatorSpecies! (3,1)=.2      'tolerence

END SUB


SUB InitialisePreyArray STATIC

SHARED TotalPrey

PreyCounter=1  ' Sequential Counter of the number of prey individuals

FOR PreyType=1 TO 4

     FOR PreyIndividual = 1 TO PreySpecies!(1,PreyType)

     Prey!(1,PreyCounter)=PreyType

     UpperLimit!=(PreySpecies!(2,PreyType)+.1)
     LowerLimit!=(PreySpecies!(2,PreyType)-.1)
```

```
        CALL RandomFloater (UpperLimit!,LowerLimit!,Float!)

        IF Float!>1! THEN Float!=1!
        IF Float!<0! THEN Float!=.0001

        Prey!(2,PreyCounter)=Float!
        PreyCounter=PreyCounter+1

  NEXT PreyIndividual

  NEXT PreyType

  TotalPrey = PreyCounter-1
```

END SUB

SUB InitialisePredatorArray STATIC

```
 SHARED TotalPredators

 PredatorCounter = 1  ' Sequential Counter for the number of Predators

 FOR PredatorType=1 TO 4

      FOR PredatorIndividual = 1 TO PredatorSpecies!(1,PredatorType)

      Predators!(1,PredatorCounter)=PredatorType
      Predators!(2,PredatorCounter)=PredatorSpecies!(2,PredatorType)
      Predators!(3,PredatorCounter)=0!
      Predators!(5,PredatorCounter)=PredatorSpecies!(3,PredatorType)

      PredatorCounter=PredatorCounter+1

     NEXT PredatorIndividual

NEXT PredatorType

TotalPredators = PredatorCounter-1
```

END SUB

```
SUB  GetSimulationAttributes  STATIC

SHARED NumberOfEncounters
SHARED NumberOfSeasons

NumberOfEncounters =10
NumberOfSeasons = 1000

END  SUB


SUB  SelectPrey  STATIC

SHARED PreyItem
SHARED TotalPrey

PreyItem = INT(TotalPrey*RND)

END  SUB


SUB  KillPrey  STATIC

SHARED PreyItem
SHARED ModelType

  IF INT(Prey!(1,PreyItem))<>ModelType THEN
  Prey!(2,PreyItem)=0!
 END IF

END  SUB


SUB  RevisePredator  STATIC

SHARED PreyItem
SHARED PredatorItem
SHARED ModelType

IF INT(Prey!(1,PreyItem))=ModelType THEN
```

```
   Predators!(2,PredatorItem)=(Predators!(2,PredatorItem))*.8
   Predators!(3,PredatorItem)=Prey!(2,PreyItem)                ' Memory of model
   Predators!(4,PredatorItem)=1!                               ' Flag model encountered
   Predators!(5,PredatorItem)=Predators!(5,PredatorItem)*1.2   ' make more cautious
ELSE

   Predators!(2,PredatorItem)=(Predators!(2,PredatorItem))*1.05
   IF Predators!(2,PredatorItem) > 1 THEN Predators!(2,PredatorItem)=.99
   Predators!(5,PredatorItem)=Predators!(5,PredatorItem)*.8   ' make less cautious

END IF

END SUB


SUB RevisePreyArray STATIC

FOR LocatePreyType= 1 TO 4          ' Loop through all the Prey Species

   CALL CountSurvivors(LocatePreyType,Survivors)
   CALL AllocateSpaces(LocatePreyType,Survivors,FreeSpaces)

   FOR SpaceAllocation=1 TO FreeSpaces

      CALL FindParent(LocatePreyType,Survivors,ParentalSimilarity!)
      CALL SetChildSimilarity(LocatePreyType,ParentalSimilarity!)

   NEXT SpaceAllocation

NEXT LocatePreyType

END SUB


SUB CountSurvivors (LocatePreyType,Survivors) STATIC

SHARED TotalPrey

Survivors=0

FOR Counter= 1 TO TotalPrey
```

```
  IF Prey!(1,Counter)=LocatePreyType AND Prey!(2,Counter)<>0! THEN
  Survivors=Survivors+1
  END IF

NEXT Counter

END SUB


SUB AllocateSpaces (LocatePreyType,Survivors,FreeSpaces) STATIC

FreeSpaces=PreySpecies!(1,LocatePreyType)-Survivors

END SUB


SUB FindParent(LocatePreyType,Survivors,ParentalSimilarity!) STATIC

SHARED TotalPrey

PickParent=FNPickRandomInteger(Survivors)

ParentCounter=0
FOR Finder=1 TO TotalPrey

  IF Prey!(1,Finder)=LocatePreyType AND Prey!(2,Finder)<>0 THEN
    ParentCounter=ParentCounter+1
    IF ParentCounter=PickParent THEN ParentalSimilarity!=Prey!(2,Finder)
  END IF

NEXT Finder

END SUB


SUB SetChildSimilarity(LocatePreyType,ParentalSimilarity!) STATIC

SHARED TotalPrey

FOR Finder=1 TO TotalPrey

  IF Prey!(1,Finder)=LocatePreyType AND Prey!(2,Finder)=0! THEN
```

```
    ChildCounter=Finder
   END IF

 NEXT Finder


 UpperLimit!=ParentalSimilarity!+.05:IF UpperLimit! > 1 THEN UpperLimit!=1!
 LowerLimit!=ParentalSimilarity!-.05:IF LowerLimit! < 0 THEN LowerLimit!= .001

 CALL RandomFloater(UpperLimit!,LowerLimit!,ChildSimilarity!)

 Prey!(2,ChildCounter)=ChildSimilarity!

 END  SUB


 SUB  RandomFloater  (UpperLimit!,LowerLimit!,Float!)  STATIC

 Float!=((UpperLimit!-LowerLimit!)*RND)+LowerLimit!

 END  SUB


 SUB  ReportArrays  STATIC

 SHARED TotalPrey
 SHARED TotalPredators
 SHARED Season
 PRINT Season


 FOR Pred=1 TO TotalPredators
 FOR Index=1 TO 5

 PRINT USING "#.#####     ";Predators!(Index,Pred);

 NEXT Index
 PRINT ""

 NEXT Pred

 END  SUB
```

```
SUB CalculateMeans STATIC

SHARED TotalPrey
SHARED Season

FOR Species=1 TO 4

Sum!=0!
Count=0
Mean!=0!
SumSquared!=0!
SumofSquares!=0!
StandardDeviation!=0!

  FOR Individual=1 TO TotalPrey

  IF INT(Prey!(1,Individual))=Species THEN
  Count=Count+1
  Sum!=Sum!+Prey!(2,Individual)
  SumofSquares!=SumofSquares!+(Prey!(2,Individual)*Prey!(2,Individual))
  END IF

  NEXT Individual


  IF Count > 0 THEN   ' dont plot species that arent there!

  Mean!=Sum!/Count
  SumxSquared!=SumofSquares!-((Sum!*Sum!)/Count)
  s2!=SumxSquared!/(Count-1)
  StandardDeviation!=SQR(s2!)

  PreySpecies!(4,Species)=StandardDeviation!
  PreySpecies!(3,Species)=Sum!/Count

  LOCATE 1,(INT(10*Species))
  PRINT Mean!
    Ypixel=10 + INT(250-((Sum!/Count)*250))

   IF Season > 440 THEN
    SCROLL (21,10) - (459,259),-1,0
```

```
      PSET (459,Ypixel)
     ELSE
      PSET (Season+20,Ypixel)
    END IF

  END IF

NEXT Species

END  SUB


SUB  OpenResultFile  STATIC

ResultExtension$=DATE$
FileName$="Qisk:QuickBasic:Model:" + ResultExtension$

OPEN FileName$ FOR OUTPUT AS 1

PRINT#1, "Simulation Time ";TIME$
PRINT#1,"Simulation Date ";DATE$

END  SUB


SUB  FileResults  STATIC

SHARED Season

PRINT #1,USING "####"; Season;

FOR result=1 TO 4

   PRINT #1,PreySpecies!(1,result);
   PRINT#1, USING "   #.#####"; PreySpecies!(3,result);PreySpecies!(4,result);

NEXT result

PRINT#1, " "

END  SUB
```

```
SUB InitialisePlotWindow STATIC

' Opens window

WINDOW 1, "MacComplex",(10,45)-(500,335),1

' Plots Axes

PSET (460,260)
LINE - (20,260)
LINE - (20,10)

'Writes Legends

CALL TEXTFONT(20)  ' Times
CALL TEXTFACE(1)   ' Bold

LOCATE 23,33
PRINT "Season"

END SUB


SUB RecruitPredators STATIC

SHARED TotalPredators
SHARED Season

'KillPredators=FNPickRandomInteger (TotalPredators/3)
KillPredators=INT(TotalPredators/5)

'PRINT "Season "; Season;"killing "; KillPredators

FOR Recruitment=1 TO KillPredators

  'Select random individual

  KillIndividual=FNPickRandomInteger (TotalPredators)
  PredatorType=INT(Predators!(1,KillIndividual))

    Predators!(2,KillIndividual)=PredatorSpecies!(2,PredatorType)
    Predators!(3,KillIndividual)=0!
```

```
    Predators!(4,KillIndividual)=0!
    Predators!(5,KillIndividual)=PredatorSpecies!(3,PredatorType)



NEXT Recruitment

END SUB
```

Appendix Five.

An Operant Conditioning Approach to "Poor Mimicry" in the Hoverflies.

1.5.1 Operant Conditioning.

The following appendix contain a paper reporting the work of Winand Dittrich, who has adopted an operant conditioning approach to poor mimicry in the hoverflies. This work included the use of an objective index of similarity similar to the one developed in this thesis.

Imperfect mimicry: a pigeon's perspective

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[Plate 1]

SUMMARY

Despite the dearth of field-based evidence from natural model–mimic communities, theory suggests that Batesian mimicry should have limits placed upon the model:mimic ratio for mimics to benefit. Paradoxically, hoverflies that are apparently mimics are often superabundant, many times more abundant than their supposed models. One possible solution to this paradox is that perhaps they are not mimics at all. We use discriminative operant conditioning methods to measure the similarity perceived by pigeons between wasps and various species of supposedly mimetic hoverflies, and an image processing technique to measure objective similarity. We demonstrate that pigeons rank mimics according to their similarity to a wasp model, in an orderly broadly similar to our own intuitive rankings. Thus pigeons behave as if many hoverflies are indeed wasp mimics. However, they rank the two commonest hoverflies as very similar to wasps, despite these looking decidedly poor mimics to the human eye. In these species, 'poor' mimicry may have been sustainable because it exploits some constraint in birds' visual or learning mechanisms, or some key feature used in pattern recognition. Furthermore, the relation between similarity and mimicry is nonlinear: small changes in similarity can lead to dramatic increases in the degree of mimicry.

1. INTRODUCTION

Biologists have always been fascinated by the phenomenon of mimicry in all its various forms (see Wickler 1965, 1968; Sheppard 1959, 1975; Turner 1984; Malcolm 1990). Mimicry has even been accorded the status of a paradigm of adaptive evolution by natural selection (Turner 1987; Brower 1988), although surprisingly there is still a dearth of good empirical evidence, particularly for field evidence of the protective effects of mimicry (see the review by Malcolm 1990). In defensive Batesian mimicry, the selective agent is a predator selecting amongst prey, often visually; visual mimics are palatable and gain protection by looking like other organisms that are unpalatable or unprofitable in some other way (models).

Here we are particularly interested in the evolution of imperfect mimics in a visual Batesian mimicry complex. Imperfect mimics constitute an almost completely neglected part of the problem of Batesian mimicry, as their existence is usually discounted (see, for example, Sheppard 1975, p. 182). (Their occurrence amongst Müllerian mimicry complexes is acknowledged: Sheppard 1975; Ackery & Vane-Wright 1984.) They have only rarely been addressed in the theory of mimicry (see, for example, the review by Huheey (1988)), with some notable exceptions (see, for example, Getty 1985). Even rarer are experimental studies, although there are some (see, for example, Hetz & Slobodchikoff 1988). Nearly all theoretical treatments assume that strong selection pressure on mimics in the past has resulted in close resemblance to models (Sheppard 1975; Huheey 1988), and suggest further that there is a limit to the sustainable model:mimic ratio, set by absolute abundance, model noxiousness, prey spatial distribution, and the profitability of alternative prey (Huheey 1964, 1988; Pough *et al.* 1973; Estabrook & Jespersen 1974; Luedemann *et al.* 1981).

However, paradoxically, in nature species which to the human eye appear to be poor mimics (cf. figure 1) often far outnumber both good mimics and models (see Turner 1984). This is certainly true in the mimicry complex of wasp models and hoverfly (Diptera, Syrphidae) mimics we study here (see figure 1; see also Gilbert 1986; Stubbs & Falk 1983; Owen 1981, 1991; Owen & Gilbert 1989). There are various hypotheses that can account for this discrepancy, including (Grewcock 1992): man-made habitat disturbance leading to non-natural relative abundances; potential distastefulness and hence the possibility that they might be Müllerian not Batesian mimics, which are said to show less exact resemblance to one another (Sheppard 1975, p. 182–183; Ackery & Vane-Wright 1984); aposematism through unprofitability because of their flight agility; predators may perceive them as good mimics because they only get a fleeting glimpse; and finally, the possibility that they are not mimics at all, but merely have black and yellow colour patterns for some other reason. This paper addresses the last hypothesis, that perhaps these 'poor mimics' are not in fact mimics at all.

Two contradictory hypotheses suggest themselves: at one extreme, their natural predators may not perceive any similarity between them and models; at the other, they may be perceived as very good mimics, in spite of what to the human eye is a poor match. To decide between these explanations, we need two important parameters: the physical similarity between model and mimic, and the degree of mimicry, the similarity perceived by a predator. In the experiments reported here, we show that pigeons rank mimics according to their similarity to a wasp model in an order broadly similar to our own intuitive rankings (see figure 1); with two interesting exceptions, pigeons behave as if many hoverflies are indeed wasp mimics.

2. MATERIALS AND METHODS

We used pigeons to represent generalized avian predators; although pigeons are not insectivorous, bird visual systems are known to be highly conservative (Hodos 1972). There is also evidence that pigeons are readily able to classify insects in a taxonomically relevant way (W. Dittrich, F. Gilbert, P. McGregor, P. Green & D. Grewcock, unpublished results). Pigeons were trained to discriminate between sets of photographic slides of wasps and non-mimetic flies, and then tested for generalization to slides of supposedly mimetic hoverflies (see figure 1).

We obtained 12 retired racing pigeons, with no previous experimental history: they were maintained at 85% of the *ad libitum* body mass on a 14 h:10 h light:dark cycle with water and grit continuously available other than in the test apparatus. Pigeons were assigned randomly to three categories before the start of the experiment: wasp$^+$, the presence of wasp images was the positive stimulus; fly$^+$, the presence of non-mimetic flies was the positive stimulus (this is analogous to the natural situation); and pseudocategory, 40 randomly chosen slides of wasps and non-mimetic flies (20 of each) were arbitrarily classified as positive stimuli. The last category was included as a control for memorization of individual images (Vaughan & Greene 1984).

We used a one-key operant chamber, with colour slides being back-projected from a Kodak S-RA2000 random access projector onto the response key. A shutter, operated by a rotary solenoid, controlled the presentation of images. In addition to the response key, the panel carried an aperture that gave access to a solenoid-operated food hopper containing the reward, a mixture of food grains. An Apple II microcomputer controlled events and recorded responses.

Pigeons were first trained by standard methods (see Dittrich & Lea 1993) to find food in the hopper, and then to peck at the illuminated centre key. The schedule of reinforcement was a fixed interval of 20 s, with a 10 s delay after each food reinforcement during which the shutter closed and the projector moved to a new random position (no slides present at this stage). (Full details of the methods will be published elsewhere.) Discrimination training then began, using 40 slides of different individual wasps (*Vespula vulgaris* and *V. rufa*: see figure 1*a*) and 40 slides of different individuals of non-mimetic flies (these included 1–3 slides of different individuals of various Dipteran species (*Rhagio*, *Tabanus*, *Tachina*, *Sarcophaga*, *Scathophaga*, etc.), including some hoverflies that are not wasp mimics (*Eristalis tenax* (a honeybee mimic), *Xylota sylvarum*, *Chrysogaster* spp.)). On each slide there was an image of a single insect, always in the same central position, photographed against an identical and homogeneous blue background. All specimens were photographed at the same magnification, so that size as well as pattern cues were available, although size differences were not substantial. In each session all 80 slides were used, each projected once for 20 s. In the case of a positive stimulus, the end of a 20 s period or the next peck caused the shutter to close and the bird to be reinforced. In the case of a negative stimulus, after 20 s of stimulus presentation the shutter closed and the houselight turned off regardless of the bird's behaviour. A new pseudorandom stimulus sequence was generated for every session. Training continued until performance reached a criterion of five successful sessions after learning the discrimination.

Significant discrimination was assessed by the *rho* statistic (Herrnstein *et al.* 1976), and occurred in both wasp$^+$ and fly$^+$ groups after only two sessions, but never occurred in the pseudocategory group. Two conclusions can be drawn: first, that a pigeon's behaviour was not influenced by any preexisting aversion to wasps or wasp-like patterns (cf. discussion in Guilford 1990); and second, that, although pigeons can remember a large number of individual images and respond to them adequately (Vaughan & Greene 1984), the complete lack of discrimination in the pseudocategory group shows that successful discrimination did not depend on memory for individual images.

We then used a new set of 260 colour slides, each of a different individual wasp, non-mimetic fly, mimetic hoverfly (see figure 1*c*, *e*, *g*), or non-insect control (a black polygon), in a series of experiments to test the trained pigeons' generalization to other images. The photographic format of these test slides was the same for all but one experiment: in this last experiment, we tested whether discrimination was maintained with a set of 48 photographs taken in the field. These natural pictures (see figure 1*b*, *d*, *h*) showed the insect as the focal object in the centre, but size and orientation were uncontrolled, against a wide variety of natural backgrounds.

Each test session consisted of 80 trials. In each, a subset of 80 slides was used. Of the slides, 40 (20 positive and 20 negative) were chosen from the training stimuli, 20 slides

---

Description of Plate 1

Figure 1. Examples of standard (*a*, *c*, *e*, *g*) and natural (*b*, *d*, *h*, *i*) slides used in the discrimination experiments using pigeons trained by operant conditioning methods. (*a*, *b*) *Vespula vulgaris*, (*c*) *Temnostoma vespiforme*, (*d*) *Episyrphus balteatus*, (*e*, *f*) *Syrphus ribesii*, (*g*, *h*) *Scaeva pyrastri*, and (*i*) *Temnostoma alternans*. Using the standard slides, most people agree that there is a rank order of mimetic quality, from (*c*) *Temnostoma* to (*e*) *Syrphus* to (*g*) *Scaeva*. (*f*) is a natural slide of *Syrphus ribesii*. Photographs were taken by David Fox (*b*, *h*), John French (*d*) and Francis Gilbert (*f*, *i*).

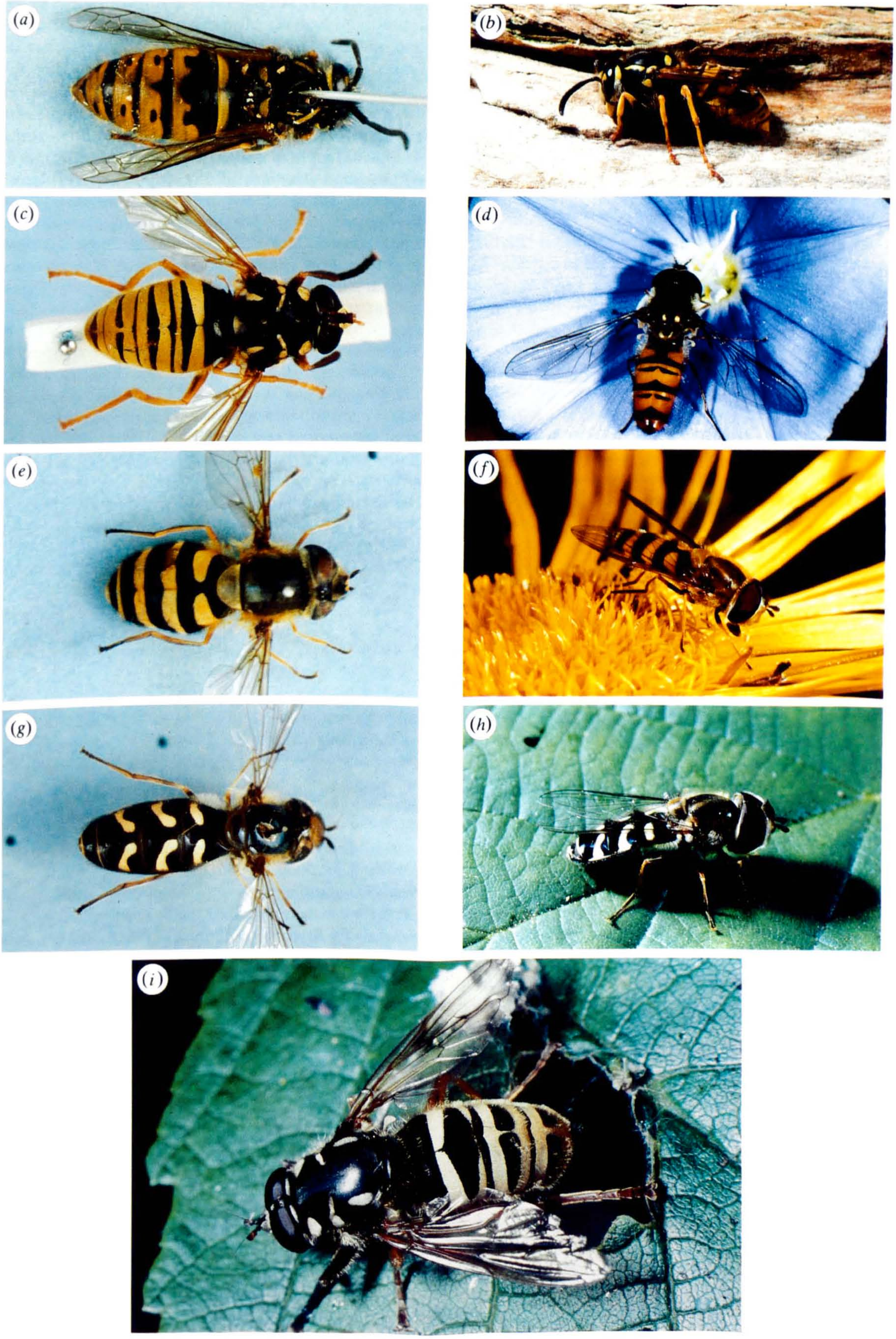

Figure 1. For description see opposite.

were novel exemplars of the original insect species, and the remaining 20 slides were novel exemplars of mimetic hoverflies or non-mimetic flies. Each slide was shown once in a test session. After four test sessions the original set of slides and the initial training contingencies were given for one retraining session. Sessions were normally given one per day, four days per week.

To assess similarity in a relatively objective manner, we have developed and extended an image analysis technique (Grewcock 1992) that compares two-dimensional images to yield a single-value description of the similarity between two patterns. The method has been tested by the successful statistical discrimination between the colour patterns of wasps from different nests (Nevison 1989) and between wasps and various hoverfly patterns (Parker 1990). We used it here to quantify the similarity between model and mimic abdominal colour patterns. By using field-guide illustrations (Stubbs & Falk 1983) as a basis, or in some cases the images actually used in the operant conditioning experiments, tergite patterns were scanned into colour bitmaps. By using BitEdit™ running under Windows 3.1™, we edited and adjusted the images so that the distance between the anterior edge of the scutellum and the tip of the abdomen was represented by a standard number of pixels (100), and the pattern represented by a limited number of colours. All British hoverfly patterns can be represented adequately by a set of eight colours (Red, Green, Blue (RGB) values in parentheses): black (0, 0, 0), dark red (160, 10, 15), red–orange (215, 100, 20), orange (240, 155, 25), yellow (255, 255, 0), pale yellow (240, 240, 130), cream (230, 240, 200), and grey (180, 240, 180): the background is white (255, 255, 255). A single wasp image was randomly chosen as a reference image, and all other images (including several other wasps) were compared with it. The comparison operates by superimposing the two images in software and calculating the proportion of colour-matching pixels, slightly shifting (5–10 %) the images relative to one another in both horizontal and vertical directions to find the maximal match. Although we have used the computer-generated RGB values here for convenience, it would also be possible to use Endler's (1990) four-colour classification.

Colour matches and mismatches are recorded in the following manner. When corresponding pixels are both the background colour (white), nothing is accumulated. Where only one is white, or one is black and the other is not black, a complete mismatch of 1 is added. When both pixels have the identical colour, a complete match of 1 is added. Where colours are not the same but do not include black, their match is calculated by using the RGB values for the two pixel colours (1 and 2) in the following manner:

$$p = \sqrt{[(\mathrm{red}_1-\mathrm{red}_2)^2 + (\mathrm{green}_1-\mathrm{green}_2)^2+(\mathrm{blue}_1-\mathrm{blue}_2)^2]}/(255\sqrt{3});$$

p merely represents the euclidean distance apart of the two pixel colours in RGB-colour space relative to the same distance between black and white (and hence whose distance apart is $255\sqrt{3}$); p varies between 0 and 1, the larger it is, the less alike are the two colours. Hence having calculated this, $(1-p)$ is then added to the match sum, and p to the mismatch sum. Having obtained the match and mismatch sum for the overlapping pictures, the similarity between images is calculated as:

$$\text{similarity} = \text{match}/(\text{match}+\text{mismatch}).$$

This results in a relatively objective estimate of image similarity to a wasp exemplar, either including or excluding size effects (by adjusting image sizes either to the standard width of 100 pixels or to be proportional to their real size). We use only images standardized for size.

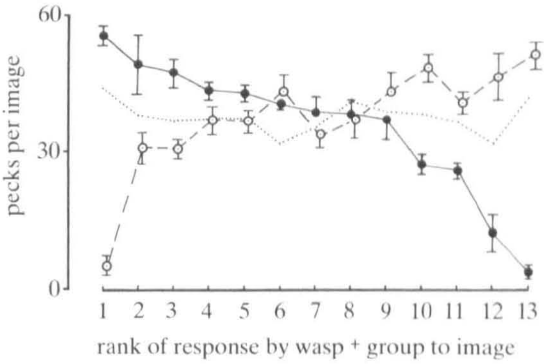

Figure 2. Results of the test for generalization to standardized mimetic images. The graph shows the number of pecks per image (±s.e.) given by pigeons trained to peck at wasp images (wasp$^+$, solid line and filled circles), or to peck at non-mimetic fly and not to wasp images (fly$^+$, broken line and open circles). The dotted line shows the responses of the pseudocategory control group. Species are ranked along the x-axis by the mean response of the wasp$^+$ group, and are, in rank order: 1, wasps (*Vespula* spp.); 2, *Syrphus ribesii*; 3, *Temnostoma vespiforme*; 4, *Chrysotoxum cautum*; 5, *Helophilus pendulus*; 6, *Epistrophe grossulariae*; 7, *Xanthogramma pedissequum*; 8, *Chrysotoxum bicinctum*; 9, *Sphecomyia vespiformis*; 10, *Volucella zonaria*; 11, *Scaeva pyrastri*; 12, *Ischyrosyrphus glaucius*; and 13, non-mimetic hoverflies.

3. RESULTS

When tested with mimetic hoverfly images, pigeons showed highly consistent performances, responding at various intermediate rates between those to wasp and non-mimetic fly images. By using the pecking frequencies of pigeons of the wasp$^+$ group, we can order the images of the mimetic hoverflies in descending order of mean values (figure 2). As expected for this group, the greatest response was to the wasp images, with a pecking frequency of more than 55 pecks per image. The images of seven hoverfly species elicited 40–50 pecks per image: *Syrphus*, *Temnostoma*, *Chrysotoxum*, *Helophilus*, *Epistrophe*, *Xanthogramma* and *Sphecomyia*. The pigeons pecked with substantially lower rates (10–30 pecks per image) at *Volucella*, *Scaeva* and especially *Ischyrosyrphus*. Response frequencies to unfamiliar non-mimetic fly images were less than 5 pecks per image.

Furthermore, pigeons of the fly$^+$ group showed a very similar set of responses (Spearman rank correlation, $r_s = -0.88$, $n = 13$, $p < 0.001$), although as expected in the opposite direction (figure 2). The less-than-exact correspondence might be attributable to slightly different cues upon which each group apparently concentrates (W. Dittrich, F. Gilbert, P. Green, P. McGregor & D. Grewcock, unpublished results). Thus birds from both these groups clearly rank mimetic images along the same continuum from wasp to non-mimetic fly. The pseudocategory group responded to all images almost equally, often pecking 35–40 times per image, and showing the highest pecking rates for the most familiar images of wasps and non-mimetic flies.

Remarkably, in the visually highly complex situation of insects in the field, pigeons were still able to find the relevant features which they had previously acquired

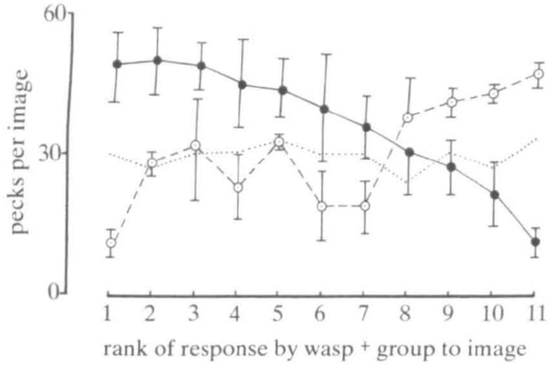

Figure 3. Results of the test for generalization to images of mimetic hoverflies taken in natural surroundings. Symbols and arrangement as in figure 2. Rank order of species along the x-axis is: 1, wasps (*Vespula* spp.); 2, *Episyrphus balteatus*; 3, *Chrysotoxum arcuatum*; 4, *Sericomyia silentis*; 5, *Epistrophe eligans*; 6, *Helophilus trivittatus*; 7, *Myiatropa florea*; 8, *Volucella zonaria*; 9, *Scaeva pyrastri*; 10, *Volucella pellucens*; and 11, various other hoverflies (*Ischyrosyrphus glaucius*, *Leucozona lucorum*, *Eristalis* spp. and *Xylota segnis*).

during discrimination learning; thus they were well able to transfer this ability to unfamiliar stimuli, in this case either the same or novel species in an unknown natural setting. Birds of the wasp$^+$ and fly$^+$ groups significantly discriminated between totally novel wasp and hoverfly images photographed in their natural habitat. Although the equivalence in the results of the two groups was not as high as in the mimicry experiment with a homogeneous background and controlled posture, there remains a highly significant negative correlation between them ($r_s = -0.76$, $n = 12$, $p = 0.011$). It was again possible to order the different images in terms of their response frequencies (figure 3), and for those species in common the order is highly comparable to the order previously achieved (cf. figure 2: $r_s = 0.91$, $n = 14$, $p < 0.001$). Once again the pseudocategory group failed to discriminate between wasps and non-mimetic insects.

What is the relation between a relatively objective measure of pattern similarity and mimicry, as measured by the pigeons' responses? We use the results of the image analysis to relate similarity to the average degree of mimicry as assessed by the pigeons (figure 4). We present only the results for images adjusted to equal sizes because there is less scatter to the fitted curves (W. Dittrich, F. Gilbert, P. Green, P. McGregor & D. Grewcock, unpublished results), consistent with our experimental evidence that pigeons use pattern rather than size cues (figure 3).

4. DISCUSSION

In these experiments, a group of pigeons rapidly acquired successful discrimination between images of wasps and non-mimetic flies. When tested with images of mimetic hoverflies, the pigeons' responses ranked the images along a continuum from wasp-like to fly-like, providing a measure of the degree of mimicry for each hoverfly species, i.e. of the pigeons' perception of the pattern similarity between wasp model and hoverfly mimic. When related to an objective similarity, this now creates a powerful tool with which to investigate the evolution of these patterns, and a vital component of models of the evolution of mimicry. Imperfect mimicry as established by the birds themselves is clearly present in these flies, and requires an explanation.

There may be a similar spectrum of mimicry among sympatric assemblages of Müllerian mimics (danaine butterflies): the suggested explanation here was the 'generalisation series' (Ackery & Van Wright 1984). The idea is that contact with a few species across this series causes predators to generalize to the entire spectrum. This mechanism cannot work, of course, with a series of Batesian mimics.

Alternatively, Duncan & Sheppard (1965) suggested that, if the model is very noxious, there would be little selection pressure to improve mimetic quality beyond a certain degree. In contrast, where the model is only slightly noxious, there is continuing selection until the mimic is indistinguishable from the model. This could have happened in the case of the Syrphidae. Bumblebees are more cautious in stinging attackers, and could therefore be described as less noxious than wasps, which readily sting. There are many bumblebee mimics amongst the syrphids, all of which are extremely good mimics to the human eye (see Stubbs & Falk 1983). The contrast with wasp mimics is striking.

However, the relative abundances of model and mimic in this system are clearly not explicable using normal Batesian mimicry theory. As de Ruiter (1952) demonstrated, birds will switch feeding behaviour to concentrate upon mimics if these are found to be palatable. In nature, palatable hoverfly mimics will be encountered many times more frequently than wasps. Just how noxious do wasps have to be in order that predators never take a chance and sample a black and yellow insect? Various attempts to answer this question suggest that the combination of a really foul model and a predator that learns quickly and remembers for a long time might provide 'significant' protection at only 10% model frequency (Brower 1960; Brower *et al.* 1970; Pough *et al.* 1973), but these all used perfect mimics.

The fact that pigeons are able to generalize their training discrimination to the natural slides (Figure 3) demonstrates two things. First, the mimicry ranking as identified by the pigeons is a very stable one; and secondly, that discrimination does not occur via a single feature, but is a composite of many features forming the polymorphous concept (Lea & Harrison 1978) of a fly or a wasp that is used to classify these insects. In particular, discrimination does not rely on size, orientation or brightness alone, nor does it even use size as an important cue. This is interesting because human subjects learn very quickly to discriminate between wasp or bee models and hoverfly mimics, but rely mainly on size (Grewcock 1992). There are additional data relevant here concerning the visual recognition of insects in non-human primates. There is strong evidence that macaque monkeys primarily use form and contrast cues. Furthermore, their response intensity towards wasp-like patterns directly depends on

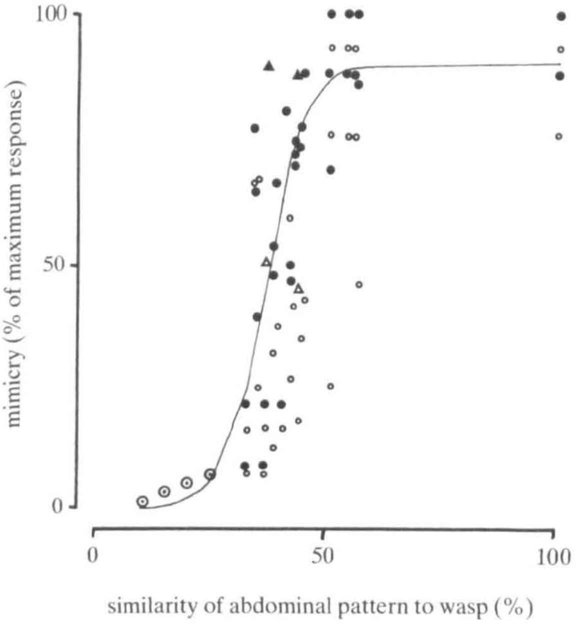

Figure 4. Relation between similarity to one single wasp exemplar (measured by image comparison) and mimicry (assessed by the response of trained pigeons to images). Logistic curves have been fitted, by using nonlinear least squares with the Marquardt method, implemented by the STATGRAPHICS statistical package. R^2 values cited below are the proportion of variance explained by the model. To fit similar curves, mimicry estimates (i.e. pigeon response rates, M) for the wasp$^+$ group were adjusted to range from 0–100% by applying the transformation $M\cdot 100/M_{\max}$. To fit data for the fly$^+$ group onto the same graph, mimicry estimates were inverted and changed to the same range by applying the transformation $(M_{\max}-M)\cdot 100/M_{\max}$. Four extra points were added to form the left-hand tail of the curve to allow the curve fitting (open circles with central dots), making $n = 36$ in all. The logistic curve fitted was of the form: mimicry $= a/[1+b.\exp(-c.\text{similarity})]$. wasp$^+$ group (filled circles), $a = 90$, $b = 7400$, $c = 0.24$ ($R^2 = 0.71$). fly$^+$ group (open circles), $a = 86$, $b = 210$, $c = 0.12$ ($R^2 = 0.59$). Filled triangles (wasp$^+$ group) and open triangles (fly$^+$ group) are the points for the species *Episyrphus balteatus* and *Syrphus ribesii*.

the completeness or similarity of wasp-like insects as well as their previous experiences with wasps (Dittrich 1988).

It is also interesting to note that deviations from a line of best fit in figure 4 are much smaller in the wasp$^+$ group. This is probably because this group was trained to peck at a much more unified set of images (all *Vespula* wasps) than the other group (many different kinds of non-mimetic flies). An important implication of the sigmoidal curve is that hoverflies can improve dramatically their degree of mimicry for a small increase in similarity to a wasp model. This does not agree with our own assessments, and thus human perception of mimicry is an unreliable guide to the function of colour patterns. The use of objective similarity calibrated against birds' mimicry rankings provides an important new solution to this problem. This result should now be incorporated into models of the evolution of mimicry.

The most surprising result of this study is also one of the most interesting for ideas about mimicry. It concerns the response of pigeons of the wasp$^+$ group to two of the commonest species of hoverfly, *Syrphus ribesii* (figure 1*f*) and *Episyrphus balteatus* (figure 1*d*). Neither can be regarded as successful wasp mimics by human standards; most human observers consider much rarer species such as *Temnostoma* (figure 1*i*), *Sphecomyia* or *Chrysotoxum cautum* as much more wasp-like. However, *S. ribesii* and *E. balteatus* can be superabundant in particular years (Owen 1981, 1991; Owen & Gilbert 1989), thus these apparently poor mimics can be much more common (hundreds to thousands of times more common) than both their models and 'much better mimics'. A partial resolution of this apparent paradox is suggested by the pigeons' assessment of their degree of mimicry, which places them as the most wasp-like of all the hoverflies we presented (see figures 3 and 4). To a pigeon, therefore, these hoverflies are not poor mimics at all, but the best. The question of why the visual systems of humans and pigeons reach such different conclusions remains open, but the answer is likely to lie in visual or learning constraints in the way in which birds classify their prey, processes possibly exploited by these patterns. This could be a factor in the undoubted 'success' of these two hoverflies (i.e. their high abundance), but again underlines the problem that the theory of the evolution of mimicry has in accounting for the relative abundances of this model–mimic complex (see discussion in Turner (1984)).

Thus humans may overestimate the ability of predators in making discriminations. It then follows that we may be under-estimating the frequency and significance of mimicry in nature, especially as mimetic effects need not necessarily depend upon obviously noxious or dangerous species: models may simply be unprofitable. Thus mimicry may be a much more pervasive feature of nature than is generally realized. If this is true then the general paucity of good experimental data on mimicry becomes even more unfortunate.

This study has underlined the importance of considering perception from the viewpoint of the potential predator rather than humans: mimicry seems indeed to be in the eye of the beholder.

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