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Aggressive mimicry in the Pirate Spider, *Mimetus notius* (Aranae; Mimetidae)

By

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ABSTRACT

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Aggressive mimicry has long been an ignored aspect of the phenomenon of mimicry. A literature review is carried out which determines that current theory developed to help understand protective mimicry does not apply to aggressive mimcry. A new modeling paradigm, based on a combination of an optimal foraging model (the f/μ criterion) and signal detection models is developed to try to aid our understanding of aggressive mimicry systems. A representative aggressive mimic, the pirate spider *Mimetus notius*, was chosen for developing and testing this paradigm. The natural history of this spider was virtually unknown, so basic natural history data was collected and is presented. This data leads to the identification of *Theridion* sp. as the most common prey and victim of aggressive mimicry. Measurements of the response of *Theridion* sp. to a variety of organisms in the web were conducted, and the signals emitted by each of these organisms were also measured. These measurements lead to the conclusion that *M. notius* does not mimic prey, but mimics small invading spiders. This information is used to develop a species-specific model based on the modeling paradigm developed previously, and this model is tested using a combination field/laboratory experiment. The model accurately predicts the level

of cautiousness displayed by *Theridion* in a variety of sites varying in the abundance of *Theridion* and *Mimetus*. These predictions serve to validate, in part, the new modeling paradigm, and give confidence that the predictions of simpler, more general models developed within this paradigm can be used to increase our understanding of aggressive mimicry and the perceptual interactions between predators and prey in these systems.

This dissertation is dedicated to my wife, Jennifer White-Kloock and my parents, Marilyn and Peter Kloock. Without their unswerving support and confidence in my abilities, this dissertation would never have been completed.

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LIST OF ABBREVIATIONS

Chapter 2.

A = the background rate of harvesting alternative resources.

C = the probability of successfully harvesting resource from the risky opportunity.

D = (1 - S) = the probability that the risky resource is dangerous.

F = the probability of accepting the opportunity, given that it is dangerous (a false alarm).

H = the probability of accepting the opportunity, given that it is safe (a hit).

K = the probability of being killed given an encounter with a risky resource.

m = the background rate of mortality.

P = the probability of being killed, given acceptance of a dangerous resource.

R = the rate of encountering the risky opportunity.

S = the a priori probability that the risky resource is safe.

V = the value of a successfully harvested resource.

Chapter 5.

E_i=Encounter rate with invading *Theridion*.

E_m=Encounter rate with *Mimetus*.

F=Probability of a false alarm.

f_{total}=Overall feeding rate.

f_w=Foraging rate while on web.

H=Probability of a Hit.

H/F, $(H/F)^*$=Cautiousness and optimal cautiousness (*).

K=Probability of being killed given defense against *M. notius*.

m=Background mortality rate.

$P_{o,I}$=Probability of leaving web due to an invader.

$P_{o,m}$=Probability of leaving web due to *M. notius*.

T_n=Time to locate a new web.

$T_{o,i}$=Time off of web due to invaders.

$T_{o,m}$=Time off of web due to *M. notius*.

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T_w=Time spent on web.

W=Probability of successful web defense given defense against *Theridion* invader.

μ=Mortality rate.

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INTRODUCTION

The phenomenon of aggressive mimicry has a long history of study, but most of that study has been anecdotal in nature. There has been no comprehensive study of aggressive mimicry. This dissertation aims to develop some general theory about the patterns and processes that occur within and across aggressive mimicry systems. The approach used is threefold. First, in chapter one, the many anecdotal accounts of aggressive mimics are collected, and general patterns among these diverse organisms are described. Second, in chapter two, a new modeling system is developed that combines life history theory, in the form of the μ/g and f/μ criteria, and signal detection theory. This results in an optimal foraging model that combines the risk of death and perceptual uncertainty, the two most important aspects of foraging under threat of an aggressive mimic. Finally, the last three chapters of the dissertation focus on developing the data needed to use this new theory, including basic natural history (chapter three) and measurement of signal properties and responses (chapter four) of a forager to an aggressive mimic, *Mimetus notius* (Aranae, Mimetidae). All of the information is brought to bear in a comprehensive experiment presented in chapter five, where the new modeling system is used to develop a species-specific model of foraging under threat of predation via aggressive mimicry by *Mimetus notius*. This final chapter draws together information from each of the previous chapters to show that the new modeling system can be used to predict the cautiousness of foragers in a variety of community settings. More importantly, this limited validation allows us to use the model to explore the implications of aggressive mimicry on the behavior of their prey, and look at some potential long-term ramifications of this mode of predation, increasing our understanding of the dynamics of these systems

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Chapter 1

AN OVERVIEW OF AGGRESSIVE MIMICRY SYSTEMS

Introduction

"To many workers, especially theoretical modelists, 'mimicry' means only one phenomenon: Batesian mimicry, the very name of which has obscured the fact that Bates ([1861]) described different kinds of mimicry" – Georges Pasteur (1982: 169).

Eighteen years ago, Georges Pasteur bemoaned the lack of theoretical work on mimicry systems other than Batesian mimicry. Since that time, very little has been done to change the situation. Theoretical work has included Müllerian mimicry, but the many other types of mimicry categorized by Pasteur (1982) have remained unexplored by theoretical biologists, largely due to the paucity of empirical work. Although several good reviews of general mimicry phenomena exist (Wickler 1968, Vane-Wright 1976, Pasteur 1982, Starrett 1993), these have focused on classification rather than the development of theory. Classification is an important first step in understanding any system, but so far no progression beyond this stage has occurred for non-protective mimicry. Here I will refine the current categorizations to better address the important phenomenon of aggressive mimicry. In addition, I will determine whether predictions based on theory derived from study of Batesian and Müllerian mimicry can be used to aid our understanding of aggressive mimicry systems.

To begin, it is necessary to present an operational definition of aggressive mimicry. For the rest of this work the following definition will be used:

> Aggressive mimicry occurs when one organism (the *mimic*), via a resemblance to a *model*, directly reduces the fitness of another organism (the *dupe*) that actively responds to the model.

This definition roughly combines Vane-Wright's (1976) " Class II, synergic aggressive mimicry" and "Class VII, antergic aggressive mimicry", with the minor difference that Vane-Wright did not explicitly include direct fitness effects (though they are implied). The basic difference between antergic and synergic is in the benefit to the model, which I will explore in more detail below. This definition excludes several cases which others may consider to be aggressive mimicry. Cases where dupe fitness is indirectly affected, such as the lacewing larvae system (Eisner et al. 1978), are not considered to be aggressive mimics. In this system the larvae use their mimicry to hide from ants. These ants protect the lacewing's prey, aphids. Although this potentially affects the ants fitness, that effect is indirect – mediated through the aphids. Cases not involving an active response (that is, a change in behavior) by the dupe are not considered aggressive mimicry primarily because of the practical difficulty in discriminating between passive response and no response. For example, if ground squirrels fail to change what they are doing when a zone-tailed hawk approaches (Willis 1963), is it due to a failure to detect them because they are hidden among the turkey vultures they resemble (camouflage), or due to mis-identification as turkey vultures after detection (mimicry)? According to the definition above, such examples are not onsi

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considered aggressive mimicry since the "response" is passive (i.e. they don't do anything) rather than active.

The active response clause in the definition also excludes the many internal parasites that avoid host defenses through resemblance to the host's self-recognition compounds (Goodenough 1990). While this is certainly aggressive, whether it is mimicry or camouflage remains an open question. An analogous situation exists in eusocial insect colonies; some parasites and predators prevent attack from the colony by adopting the colony's cuticular "signature" (Howard, McDaniel and Blomquist 1980; Vander Meer and Wojcik 1982; Bagnères et al. 1996). This exclusion prevents us from getting bogged down in the long-standing debate over where the dividing line between mimicry and camouflage should be (Pasteur 1982; Getty 1987; Starret 1993) and allows us to focus on cases that are unambiguously mimetic.

Pasteur (1982), in his broad treatment of all mimicry systems, used the nature of the model (agreeable vs. forbidding) and the taxonomic relationships between model, mimic and dupe as the backbone for his classificatory scheme. While this was a logical system, it led to a large array of different types of mimicry: eighteen total types of mimicry, five of which can be considered aggressive mimicry. Vane-Wright (1976) also developed a complicated scheme. This scheme was based on taxonomic relationships and fitness effects on the model and dupe. This system produced 5 taxonomic classes and 8 classes based on effects to models and mimics. Combining these two systems produces 40 different classes of mimicry, and 10 different types of aggressive mimicry. These cumbersome classification schemes may serve to obscure rather than clarify broad-scale patterns.

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I propose a simple functional classification based on fitness and following the antergic/synergic dichotomy proposed by Vane-Wright (1976), but removing the taxonomic details. Note that the operational definition of aggressive mimicry above requires that the mimic's fitness is, on average, increased by the mimetic resemblance, and the dupe's fitness is reduced. This is true regardless of taxonomic affiliations. The model, however, can be affected in three different ways. An aggressive mimic might affect the model's fitness positively, neutrally, or negatively. This suggests a simple classification scheme: positive aggressive mimicry occurs when a mimic enhances the fitness of the model, neutral aggressive mimicry occurs when the model's fitness is unaffected, and negative aggressive mimicry occurs when the mimic reduces the model's fitness. (see table 1.1 for examples of each). This scheme holds regardless of the taxonomic affiliations of model, mimic and dupe. The model need not be a living organism, though all such cases must, by default, be classified as neutral since an abiotic model has no fitness. In neutral aggressive mimicry the model does not actively take part in the evolution of the model and mimic, regardless of whether the model is biotic or abiotic. In cases with neutral biotic models, their appearance could change in response to outside factors. While these factors can certainly influence the appearance of the mimics, it would not change the basic concept that the model is not actively involved in the evolution of these systems. This classification also incorporates one of the basic distinctions between Batesian mimicry (model fitness decreased by mimic presence) and "classic" Müllerian mimicry between two equally noxious model/mimics (model fitness enhanced by mimic presence). This classification has two advantages over Pasteur's mimicry classes for aggressive mimicry. First of all, it provides a more manageable num

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number of categories and second, as will be seen below, it reveals an interesting and unexpected pattern across aggressive mimicry systems.

When mimics negatively affect their models, as in Batesian mimicry, the models are expected to "run away" from the resemblance, starting the classical evolutionary chase seen in most Mathematical models of Batesian mimicry (figure 1.1). Recent theory suggests that Batesian systems should evolve to a monomorphic model and polymorphic mimic in most cases. On the other hand, when mimics positively affect their models, as in "classic" Müllerian mimicry, the model and mimic should both become monomorphic (Gavrilets and Hastings 1989). Thus, we would expect closer mimicry in systems where the model and mimic have a mutual interest in similarity than in systems where their interests diverge, an intuitively appealing expectation (see Figure 1.1 for a graphical version of this argument). If there is no effect on the model, then the mimic should eventually converge on the model, but the model should not change its appearance in response to the mimic; resemblance in these cases could vary widely, and would be dependent primarily on the time since mimicry began, selection strength, and the presence or absence of outside selective factors on model appearance. Do these simple and intuitive predictions, based on theory developed for protective mimicry, hold true for aggressive mimicry?

Methods

I have searched the literature on aggressive mimics extensively. Much of this literature is anecdotal in nature, and some is purely speculative. I have followed Pasteur

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(1982) in accepting published reports with a fairly uncritical eye on the theory that what is not reported will not be studied in further detail – and nearly all proposed cases of aggressive mimicry need more study. In order to present the reader with some idea of how well established each example of aggressive mimicry is, I have included a rating with each example, describing the level of work that has been reported supporting it. The ratings I have assigned are based solely on the quality of information for identifying potential aggressive mimics, and do not reflect the overall quality of the papers listed. For example, while many of the cases listed from Wickler (1968) are speculative, I consider this excellent treatment to be required reading for anyone interested in mimicry (aggressive or otherwise). The rating system is given in the legend to table 1.

In order to reduce taxonomic redundancy, taxa where the same type of aggressive mimicry occurs frequently are treated as a single occurence, on the conservative assumption that only one evolutionary origin occurred in these groups. Thus not all species of aggressive mimics receive equal weight: the hundreds of species of Lophiiformes (anglerfish) are treated as a single instance, as is the single species of alligator snapping turtle, which uses a similar tactic but almost certainly acquired it independently.

In most of the cases reviewed, the effect of the mimic on the model has not been demonstrated rigorously. I have inferred an effect for these cases, but these must be considered as potential effects, based on logic, rather than as demonstrated effects based on empirical study. I will detail a few of the more common situations here as examples. Many aggressive mimics mimic prey. In general, prey can potentially benefit from the presence of an aggressive mimic through both reduced numbers (via losses to mimics) and/or increased cautiousness of their predators. Flowers are a food item, but generally benefit (via pollination) from visits by dupes – thus flowers are postulated to be detrimentally affected by mimics through reduced numbers (via losses to mimics) and/or increased cautiousness of pollinators. Similarly, when females are the models of predatory mimics, females are considered as detrimentally affected by mimics through reduced numbers and/or increased cautiousness of males (though indirect fitness may benefit from mating with higher quality males). When the model is inanimate, there are no fitness effects. These cases are therefore considered neutral. Similar deductions, based on the natural history of each individual case, were made for each postulated case of aggressive mimicry.

Cases that can be considered as aggressive mimicry, but where fitness effects on dupes are likely to be negligible have also been excluded so that cases where selection is weak will not obscure any larger patterns. For example, nectar-less flowers (Wiens 1978) can be considered "aggressive" since they rob dupes of time that could be spent in other activities and thus at least potentially reduce dupe fitness; compared to the fitness cost of approaching a predator disguised as a flower this is likely to be negligible, provided abundances are similar. Similarly, mimicry of female bees by some orchids (Wiens 1978) most likely has negligible fitness effects on the dupes unless they are severely sperm-limited. Another borderline case involves the mimicry of females by males, allowing them to approach females defended by a territorial male (e.g. "Sneaker" males). In these cases fitness effects on the female are frequency dependent. Because of this frequency dependence average fitness effects on the model (female) vary over time (when mimics are rare, mating with them is advantageous since mimetic offspring in the

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next generation will likely have high relative fitness; when they are common, however, mimetic offspring will have low relative fitness), This situation is most closely approximated as neutral mimicry. By restricting the cases examined to those in which the dupe is directly and physically harmed (killed, attacked or infected) I keep only those cases where selection strengths on dupes are relatively strong at a given frequency and therefore more likely to have strong effects throughout the aggressive mimicry system.

The main prediction of the arguments presented centers on how similar mimics and models are in appearance. Unfortunately, most of the cases in the literature do not provide measurements of model and mimic signals as presented to dupes. In the absence of this information, the concepts of abstract and concrete mimicry (Pasteur 1982) can be used as a rough, qualitiative guide to similarity. Simply stated, concrete mimicry involves detailed mimicry of a single species (e.g. *Apis mellifera*), while abstract mimicry involves less detailed mimicry of a general group of models (e.g. bees). A concrete mimic, such as the cleaner wrasse mimic, *Aspidontus taeniatus*, mimics the cleaner wrasse *Labroides dimidiatus* in size, appearance and behavior (Wickler 1968). Conversely, an abstract mimic such as the alligator snapping turtle, *Macroclemmys tenmickii*, possesses a wormlike appendage on its tongue – this appendage is easily confused with a worm or insect larvae, but is not identifiable as any particular species of worm. Table 1 identifies each case of aggressive mimicry as either abstract or concrete, based on this dichotomy. This use rests upon the assumption that concrete mimics are, in general, "closer" mimics than abstract mimics.

There are difficulties involved with the abstract/concrete dichotomy. Whether a mimic is considered abstract or concrete will depend to some extent on the level of study it

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it has received.. For example, poor concrete mimics may be improperly identified as abstract mimics if the system is not sufficiently well known. Similarly, it is likely that concrete mimics begin as abstract mimics, and there is no way to identify these "incipient" concrete mimics – that is, mimics that function primarily as concrete mimics but are still abstract enough to fool some organisms (including scientists) that aren't a major target of their mimicry. Another important problem is that of bias – in some systems, for example mimicry of mates, a mimic that is not terribly close in appearance is likely to be defined as abstract if it only captures a single species, while prey mimicry is likely to be defined as abstract, even with a similar level of objective similarity. While these are serious problems with the use of this dichotomy, it is still true that in most examples of concrete mimicry the models are fairly easy to identify to species, while in cases of abstract mimicry models cannot be easily identified. Until measurements are made on models and mimics to quantitatively deal with the question of mimetic "distance", the abstract/concrete dichotomy is the best tool available.

Results

The results of the literature review are presented in table 1, organized by fitness effects on the model (positive, neutral or negative). In one case it is not clear from the papers available whether the mimicry was abstract or concrete – this has been omitted from the following analysis. Only three of the mimics in table 1 were considered to be neutral, and one of these was the case mentioned above, where it was not possible to dete

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determine whether it was abstract or concrete. Although this leaves all of the neutral cases as abstract, it is obviously too small a sample from which to draw conclusions.

The remainder of Table 1 demonstrates a striking pattern: 14 of 19 cases of abstract mimicry involve situations where the model is affected positively, while 13 of 13 cases of concrete mimicry involve cases where the model is affected negatively. A deeper inspection of table 1 reveals that 12 of 13 cases of concrete mimicry involve systems where the dupe and the model are the same species (one variant of conjunct mimicry according to Vane-Wright 1976) and 18 of 19 examples of abstract mimicry involve disjunct (Vane-wright 1976) systems, where model, mimic and dupe belong to three separate species.

These two ways of looking at mimicry systems confound one another. 13 of 18 systems where models are negatively affected involve conjunct systems while 14 of 14 cases where models are positively affected involve disjunct systems. This confounds the affect of "junctivity" of a system with fitness effects. However, even with this confound in place it can easily be seen that the predictions derived from analogy with protective mimicry fail.

Discussion

That predictions from protective mimicry theory should fail for aggressive mimicry is not surprising: after all they are qualitatively different systems. However, this finding also refutes the intuitively reasonable prediction that systems where model and mimic both benefit from the resemblance should tend to resemble each other more than in

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instances where they do not share a common interest in convergent appearance. The failure of both protective mimicry theory and intuition to accurately predict this strong qualitative pattern highlights the need for separate theory to explain the operation of aggressive mimicry.

The data used here are somewhat flawed: the accounts are usually anecdotal, and as can be seen from table 1 much of the "data" is weak or even speculative. The existence of an apparent link between the effect on the model and species composition makes all analysis difficult, since the relative importance of conspecifics vs heterospecifics could have large effects on the magnitude of selective forces. In addition several exclusions have been made in the name of clarity that may influence the results. As far as the data quality, this is the best data available on aggressive mimicry. The overall poor data quality shows more strongly than anything the need for detailed study of this phenomenon.

The link between species composition and effect on the model is a logical consequence of the relationships between model, mimic and dupe in these systems. This makes new studies of those few cases where the link doesn't hold, for example the Cleaner fish system (Wickler 1968), particularly important – these exceptions to the apparent rule may hold the key to developing a firmer understanding of aggressive mimicry. For the moment this problem will be untackled, since the predictions from protective mimicry are silent in regard to this problem – protective mimicry systems with model/dupe conjuctivity appear to be rare (Vane-Wright 1976).

The exclusions present a potentially more serious problem. These were made with the objective of removing difficult to interpret instances so that patterns would not be

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be obscured by mis-interpretations, but it is also possible that these omissions introduced bias. Now that a pattern has been detected we must examine these omissions in an attempt to uncover any potential bias.

First, consider the exclusion of internal parasites and the predators and parasites of social insects. These organisms avoid attack by resembling their hosts, which they damage. Thus, they negatively impact their models. If we consider this as mimicry rather than as camouflage then we must conclude that they are concrete mimics since they appear to mimic species-specific recognition factors (Howard, McDaniel and Blomquist 1980; Vander Meer and Wojcik 1982; Bagnères et al. 1996). As negative, concrete mimics, these examples reinforce the pattern detected if included, so their elimination was conservative with respect to detecting the pattern.

Now consider the exclusion of examples where fitness effects on dupes are expected to be weak. Flowers that rely on pseudocopulation for pollination reduce the availability of mates for their models and appear to be species-specific mimic (Weins 1978). Again, as concrete, negative mimics they reinforce the detected pattern. In other nectar-less flowers, there are two categories: in one category individuals within a species fail to produce nectar, while others produce nectar; in the other category are entire species that have given up nectar production. In the first category, we cannot tell whether the resemblance functions as mimicry, is merely the result of the close phylogenetic link between model and mimic or both. Thus these cases are not appropriate for analysis here. In the second category, mimicry could affect the model species negatively if they compete for pollinators, but could also affect their models positively if they increase the effective size of the flower patch, which can increase visitation rates to the model. Given th

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the contradictory possibilities we cannot predict, in a general sense, whether these cases are more likely to demonstrate positive or negative fitness effects. This situation can add no information to the pattern detected here, since it predicts variation based on the individual details of each example. Wiens (1978) reports cases of both abstract and concrete mimicry among floral mimics. Given the available data, exclusion of cases where selection on the dupe was weak appears not to have introduced bias in detecting patterns in abstract versus concrete mimicry.

The available data are anecdotal and problematical due to large differences in methodologies and interpretation. A strong pattern emerges from them nonetheless. In systems where models suffer from the presence of an aggressive mimic, close resemblance (as measured by concrete mimicry) is common; in systems where models benefit from the presence of an aggressive mimic poor resemblance (as measured by abstract mimicry) predominates. Current mimicry theory is inadequate to deal with this observation; in fact it predicts exactly the opposite pattern.

This situation calls for a two-pronged approach. First, a new theoretical approach to aggressive mimicry that is capable of explaining this pattern must emerge. Then this theory must be tested against new data using a well-documented aggressive mimicry system. This dissertation sets out to accomplish both of these goals. Chapter two develops a new general modeling paradigm based on a combination of two well-developed branches of mathematical ecology: life history theory and signal detection theory. Chapter three presents the natural history of a previously little-known aggressive mimic, *Mimetus notius* (Aranae; Mimetidae) and its most common prey, *Theridion* sp (Aranae; Theridiidae). Chapter four takes an in-depth look at the signal properties in this syst

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system, including the signals received by *Theridion* from six different organisms and *Theridion's* responses to these organisms. Finally, chapter five builds upon all of the previous chapters to develop and test a model specific to the *M. notius* system, extending and testing the general paradigm developed in chapter two. This work thus develops and tests a new theoretical approach to the study of aggressive mimicry.

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Table 1.1 Proposed Aggressive Mimicry Systems

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Proposed Mimic	Scientific name of mimic	Proposed Dupe	Proposed Model	Postulated effect of mimic on model	Concrete or Abstract?	Rating	Reference(s)
Bladderwort	*Utricularia vulgaris*	Crustaceans	Filamentous algae	? Positive or Neutral	? Abstract	Weak	Meyers and Strickler 1979.
Pitcher Plants	*Napenthes* sp. *Cephalotus* sp. *Sarracenia* sp. *Darlingtonia* sp.	Insects	Flowers	Negative	Abstract	Moderate	Wickler 1968, Wiens 1978; Moran 1996; Newell and Nastase 1998.
Siphonophore	*Athorybia rosacea*	Fish Larvae	Fish larvae	Negative	Abstract	Speculative	Purcell 1980.
Praying mantis	*Idolum* sp.	Insects	Flowers	Negative	Abstract	Speculative	Wickler 1968.
Argiope Spiders	*Argiope sp.*	Stingless Bees	Flowers	Negative	Abstract	Weak	Horton 1979; Craig and Bernard 1990; Tso 1998.
Kermadec Petrel	*Pterodroma neglecta*	Procellariids	Skuas (various)	Negative	Abstract	Moderate	Spear and Ainley 1993.
Spiders	*Kaira sp.*	Male moths	Female Pheremones	Negative	Concrete	Moderate	Stowe 1988; Stowe et al. 1995.
Spiders	*Phoroncidia sp.*	Male moths	Female Pheremones	Negative	Concrete	Moderate	Stowe 1988; Stowe et al. 1995.
Paeophagous cichlid	*Cyrtocara orthognathus*	Heterospecific Cichlids	Brood rearing females	Negative	Concrete	Speculative	McKaye and Kocher 1983.
Pirate Spiders	*Ero furcata*	Female spiders	Males	Negative	Concrete	Speculative	Czajka 1963.
Distichodid fish	*Eugnathicthys eetveldii* *E. macroterolepis*	*Synodontus decorus; Mesoborus crocodilus*	*Synodontus decorus* *Mesoborus crocodilus*	Negative	Concrete	Speculative	Roberts 1990.
Robberflies	*Mallophora bombroides*	*Bombus americanorum*	*Bombus americanorum*	Negative	Concrete	Speculative	Brower et al. 1960.
Cleaner mimic	*Aspidontus taeniatus*	Various fish	Cleaner Fish *(Labroides dimidiatus*	Negative	Concrete	Strong	Wickler 1968; Russell et al. 1976.
Cuckoos' chicks and eggs	*Cuculus canorus*	Host chicks and eggs	Host chicks and eggs	Negative	Concrete	Strong	Wickler 1968; Payne 1977; McLean and Waas 1987; Davies 1996.

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Fish	*Erythrinus ereythrinus*	*Rivulus agilae* males	*Rivulus agilae* females	Negative	Concrete	Strong	Brosset 1997.
Bolas Spiders	*Mastophora sp.*	Male Moths	Female Pheremones	Negative	Concrete	Strong	Hutchinson 1903; Gertsch 1947, 1955; Wickler 1968; Eberhard 1977, 1980; Stowe et. al. 1987; Yeargan 1988, 1994.
Fireflies	*Photuris* sp.	*Photinus* males	*Photinus* females	Negative	Concrete	Strong	Lloyd 1975,1984; Copeland 1983; but see Vencl et al. 1994 and references therein.
Widow Birds	*Vidua sp.*	Host Adults	Host Chicks	Negative	Concrete	Strong	Nicolai 1974.
Characoid fish	*Probolodus heterostomus*	*Astyanax fasciatus*	*Astyanax fasciatus*	Negative	Concrete	Weak	Sazima 1977.
Fungus Gnats	*Bolitophila luminosa* *Orfelia fultoni*	Insects	Starlight	Neutral	?	Speculative	Wickler 1968. Sivinski 1982.
Venus Flytrap	*Dionaea muscipula*	Flies and beetles	Carrion	Neutral	Abstract	Speculative	Wickler 1968.
Bird dropping Spider	*Phrynarachne decipiens*	Butterflies	Bird Guano	Neutral	Abstract	Speculative	Poulton 1890; Gray 1990.
Scorpionfish	*Iracundus signifer*	Prey	Fish larva	Positive	Abstract	Moderate	Schallenberger and Madden 1972.
Burtons Pygopodid	*Lialis burtonis*	Skinks	Worms	Positive	Abstract	Moderate	Murray et al. 1991.
Anglerfish	Lophiformes (many species)	Fish	various, usually worm-like or fish-like	Positive	Abstract	Moderate	Pietsch and Grobecker 1978.
Alligator Snapping Turtle	*Macroclemmys temmincki*	Fish	Worms	Positive	Abstract	Moderate	Wickler 1968; Drummond and Gordon 1979; Pritchard 1989.
Pirate Spiders	*Mimetus maculosus*	Various web-weaving spiders	Insect prey	Positive	Abstract	Moderate	Jackson and Whitehouse 1986.
Jumping Spider	*Portia fimbriata*	Various web-weaving spiders	Insect prey	Positive	Abstract	Moderate	Jackson and Blest 1982; Jackson and Hallas 1990
Siphonophores	*Agalma okeni*	Fish	Copepods	Positive	Abstract	Speculative	Purcell 1980

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Proposed Mimic	Scientific name of mimic	Proposed Dupe	Proposed Model	Postulated effect of mimic on model	Concrete or Abstract?	Rating	Reference(s)
Flounder	*Asterorhombus fijiensis*	Fish	Small fish or crustacean	Positive	Abstract	Speculative	Amaoka et al. 1994.
Horned Frog	*Ceratophrys sp.*	frogs, lizards, small mammals	Worms	Positive	Abstract	Weak	Wickler 1968; Murphy 1976.
Trematode (parasitic)	*Leucochloridium macrostomum*	Songbirds (hosts)	Worms	Positive	Abstract	Speculative	Wickler 1968.
Colubrid snake	*Alsophis portoricensis*	Lizards, small mammals	Worms	Positive	Abstract	Weak	Leal and Thomas 1994.
Green Pit Viper	*Bothrops bilineatus*	Lizards, small mammals	Worms	Positive	Abstract	Weak	Greene and Campbell 1972.
Snowy Egret	*Leucophoyx thula*	Surface-feeding fish	Insects	Positive	Abstract	Weak	Kushlan 1973.
Shellfish (Parasitic)	*Lampsilis* sp.	fish (hosts)	Small Animals, Fish or Fish tails	Positive	Abstract	Weak	Wickler 1968; Haag et al. 1995, 1999.

Table 1: Ratings are as follows:

Strong – Comparative data demonstrating that the dupe responds to both the model and mimic in a similar fashion, and that this response towards mimics leads to harm to the dupe.

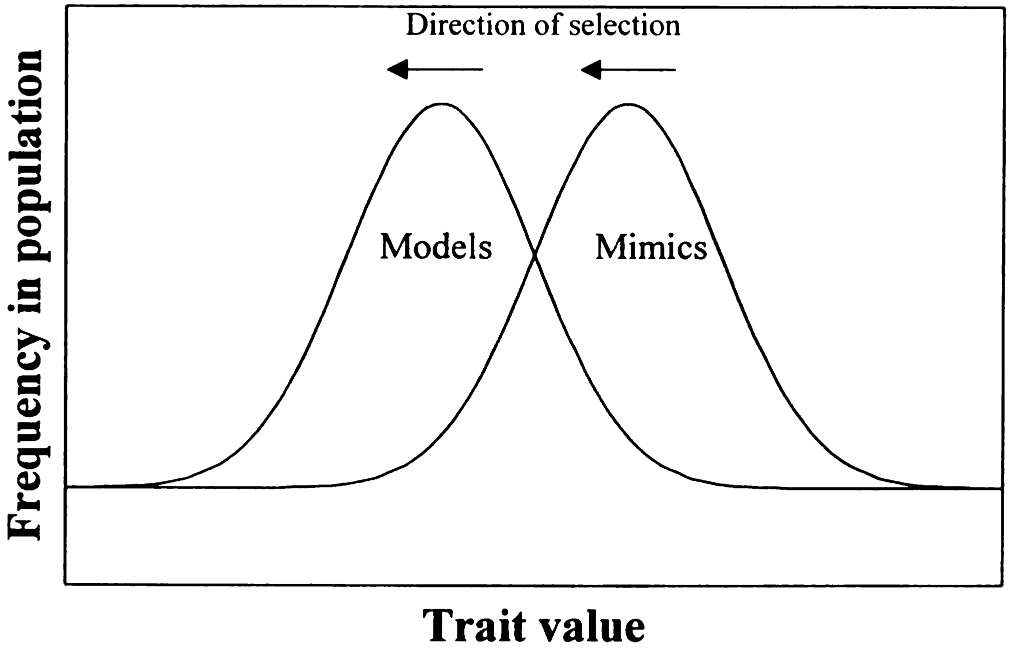
Moderate – Abundant observational data demonstrating that dupes respond in a harmful fashion towards the mimic, but no comparative data show that the dupe's responses to model and mimic are similar.

Weak – Anecdotal observations coupled with data on diet, habitat etc. that support the hypothesis of aggressive mimicry in the organism.

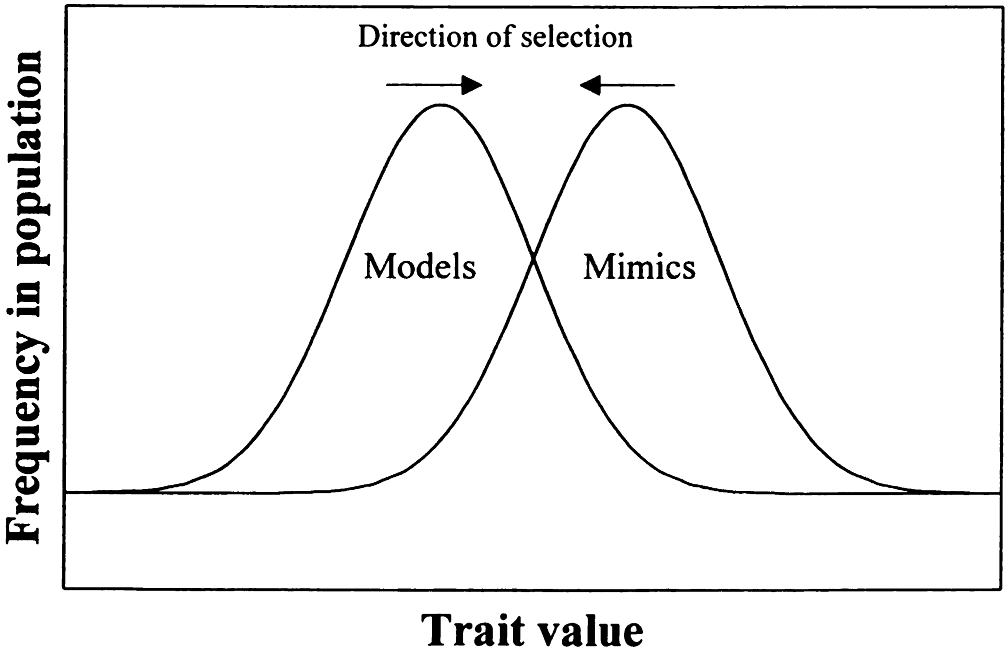
Speculative – Aggressive mimicry inferred from the appearance and/or diet of the organism, but no direct data supporting the hypothesis of aggressive mimicry; may include some indirect supportive evidence.

Figure 1.1. Selection on models and mimics in Batesian and Müllarian mimicry systems. In Batesian systems, a dupe attacks and kills models and mimics based upon their appearance. The dupe must discriminate palatable mimics from unpalatable models, which it avoids. The more similar a mimic is to a model, the more likely it is to be mis-identified as a model and avoided, so it receives more protection from its appearance, and mimics are selected to look more like models. On the other hand, the more a model resembles a mimic, the more likely it will mis-identified as a mimic and consumed. This selects for models whose appearance diverges from that of mimics. In Müllerian systems, a dupe also attacks and kills models and mimics based upon their appearance. In this case, however, both models and mimics (aka co-mimics) are unpalatable. Predators tend to avoid the common mean, so that individual prey at the extremes of the combined distribution are more likely to be killed, selecting for models and mimics that more closely resemble one another.

Figure 1.1



Batesian Mimicry



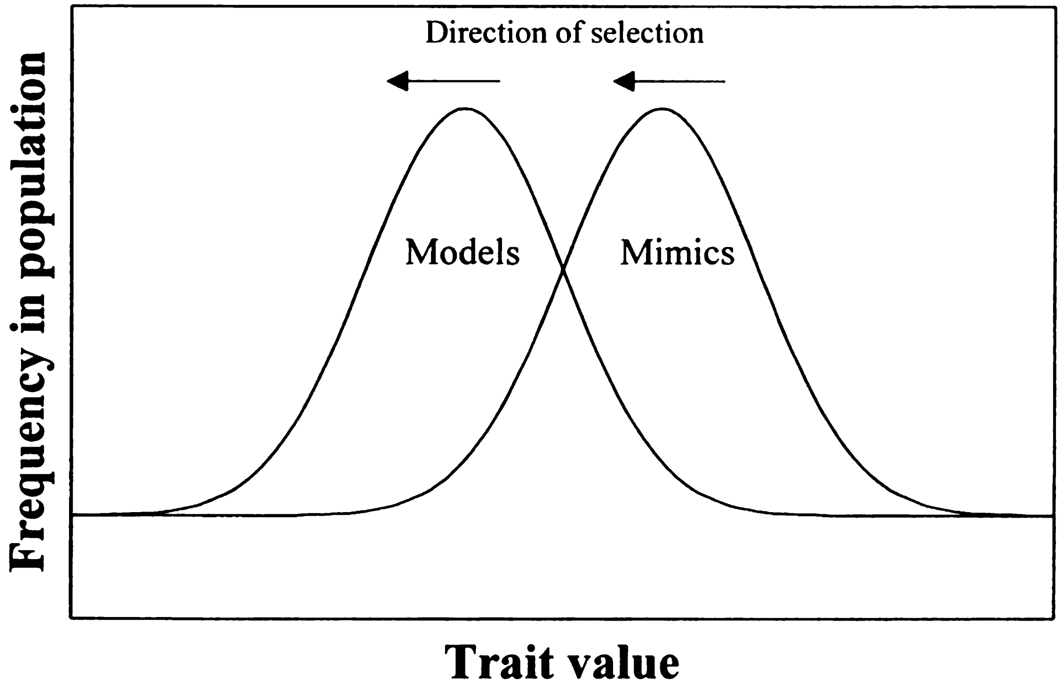
Müllerian Mimicry

Figure 1.2. Selection in aggressive mimicry systems based on analogy with Batesian and Müllerian mimicry systems. In systems in which the model is harmed, dynamics similar to that seen in Batesian mimicry are expected. In these cases, for example when mimics mimic mates, a dupe is attempting to discriminate from a model which benefits when it is found and a mimic which will harm the dupe. Models similar in appearance to the mimic will be avoided by cautious dupes, driving selection of models away from similarity with mimics. In systems where the model benefits, such as when prey are mimicked, the situation is analogous to that seen in Müllerian systems. In this instance the dupe must discriminate between a mimic and a model which is harmed by the dupe. In this case, models whose appearance is similar to the mimics will be more likely to be avoided, thus increasing their fitness.

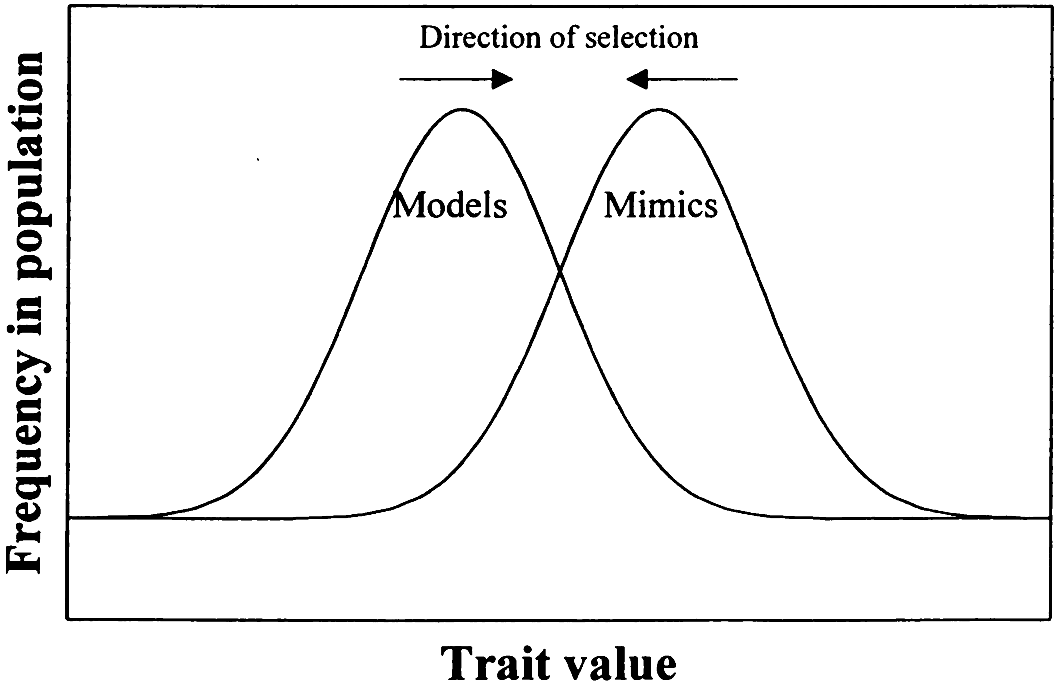
Figure 1.2

Aggressive Mimicry:

Model harmed



Model benefited



Chapter 2: Aggressive mimicry: a new theoretical approach to a long-ignored phenomenon.

INTRODUCTION

All predators must find prey in order to survive. One way for a predator to find its prey is to mimic prey's food and wait for the prey to come to it. This is one type of aggressive mimicry. Familiar examples include the lures of anglerfish and alligator snapping turtles; many other examples exist (see table 1). Other aggressive mimics copy the signals of mates; predatory fireflies (Lloyd 1984) and bolas spiders (Stowe et al. 1987, Yeargan 1994) are stunning examples. As has been shown in chapter one, existing theory dealing with protective mimicry is inadequate for explaining a strong pattern among aggressive mimics. Aggressive mimics that benefit their models tend to display mimicry that is poor relative to mimics that harm their models, counter to expectations based on theory derived for protective mimicry. This paper will use life-history theory and signal detection theory to create a theoretical tool capable of explaining this pattern.

When the risks associated with a particular type of resource are variable and there are correlated cues, there should be selection on prey to discriminate between instances with higher and lower risk. A discriminating fish that selectively avoids some worm-like objects might have higher fitness than one that never eats worms in order to avoid predation by worm-mimicking alligator snapping turtles. Signal detection theory is a powerful mathematical tool that has proven useful in behavioral settings where partial discrimination is important (Getty and Krebs 1985; Getty 1995), including Batesian

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mimicry (Oaten et al. 1975; Getty 1985) and aggressive mimicry (Davies et al. 1996). Thus, signal detection theory is a good place to start. However, due to the risk of death involved, we need to go beyond simple behavioral decisions and approach the problem with a life-history perspective.

Most animals face mortality risks when they seek resource rewards. Ultimately, the risks and rewards combine in the common currency of fitness. In the realm of foraging, it is often useful to analyze these risks and rewards in units of resource returns per unit of investment, for instance, calories/time (Stephens and Krebs 1986). This works when the risks of bad choices or bad luck are lost energy, time or opportunity. However, when the risk is death, the search for a common currency takes us into the realm of life-history theory, with fitness as the currency (Schaffer 1983, Stearns 1992). Gilliam used optimal control theory to show that given certain assumptions, most importantly that reproduction comes later, fitness would be maximized by the criteria: "minimize μ/g" (Gilliam 1982, 1990; Werner and Gilliam 1984; Gilliam and Fraser 1987; Werner 1992), where μ, and g are mortality rate and growth rate. Here I will substitute a more behaviorally oriented criterion using the feeding rate, f, as a stand-in for g. This "maximize f/μ" (Gilliam 1990) criterion has been shown to be an effective predictive instrument (Gilliam and Fraser 1987). This criterion provides the life-history perspective necessary for tackling the problem of aggressive mimicry.

We will tackle the problem of foraging in an aggressive mimicry system by adopting the "maximize-f/μ" criterion and utilizing signal detection theory (Egan 1975; Macmillan and Creelman 1991). The f/μ criterion provides an elegant general framework for understanding the tradeoff between feeding rate and predation risk, while si

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signal detection theory provides a way of integrating variable cues with variable risks. The combination of these frameworks reveals general patterns showing how foragers might adaptively vary their probability of making different kinds of errors, depending on their perceptual abilities and the community context in which they are embedded.

THE MODELING SCENARIO

We will develop this model from the point of view of a forager faced with a predator that mimics a food resource. Whenever the forager encounters cues associated with the resource (and mimicked by the predator) it must decide whether to pursue the opportunity, and risk encountering a predator, or ignore it, and risk missing a profitable reward. (An imperfectly camouflaged predator hiding in or near a resource – for example, a crab spider camouflaged inside a flower – presents its prey with a qualitatively similar dilemma). The decision whether or not to pursue a particular opportunity should depend on the forager's assessment of the likelihood that the cues are from the aggressive mimic. In order to make this assessment, the forager has two potential sources of information. First, it can utilize its individual or phylogenetic experience to estimate the average, prior probability that a predator is present (e.g. alligator snapping turtles are rare here, so it is probably safe). Second, it can use sensory cues to refine this average and estimate the posterior probability for this particular instance (e.g. alligator snapping turtles are rare here but that worm looks wrong in some way; in this particular instance it is probably not safe).

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We will assume that the variable cue used by the forager can be represented along a univariate axis, for example light wavelength or a discriminant function score that incorporates multiple cues. We can then describe the probability density functions for the cue along this axis: one distribution for safe opportunities (i.e. resources) and another for dangerous opportunities (i.e. aggressive mimics). If the predator is not mimetic, there is no overlap in the probability density distributions and resources and predators are perfectly discriminable. The forager can set a threshold criterion cue value (c) that completely separates the two distributions, and consequently reject all dangerous resources and accept all safe resources. If perfect mimicry exists, the probability density distributions are identical. No criterion improves on the prior odds, and the forager must either accept the average risk of the mimic or drop the resource from its diet. Most models of foraging under predation risk assume this situation, which corresponds to a perfectly camouflaged predator (see reviews by Lima and Dill 1990, Brown 1992, and references therein). These models have not yet addressed the situation of an imperfectly mimetic or camouflaged predator. If mimicry is good but imperfect, the probability density distributions overlap partially (fig. 2.1A). In this situation, a forager can use the cue value to update its assessment of the risk of predation at each particular opportunity and selectively pursue only those instances where the cue is below some adaptively variable threshold criterion, c^*. Breipohl (1970) has shown that a threshold criterion is optimal. This results in variable partial preferences for the resource type (Getty 1985; Getty and Krebs 1985).

This scenario can be represented graphically with a useful device known as a receiver operating characteristic (ROC) curve (Egan 1975; Getty 1985, 1995; Macmillan

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and Creelman 1991; Wiley 1994). This curve is drawn in probability space (fig. 2.1B). The X-axis of the ROC curve is the probability of a false alarm (F). A false alarm occurs when the forager misidentifies a predator as the resource being mimicked. (The term "false alarm" is taken from signal detection theory; although its use here may cause some confusion since the forager is seen as "alarming" at food and "false alarming" towards predators, we will keep the terminology so as not to obscure the direct connections with signal detection theory. Think of a false alarm as an error; trying to eat a predator is very intuitively an error in judgment.) The probability of a false alarm equals the cumulative probability of getting a cue greater than the selected criterion c, given that the cue came from a predator. The Y-axis is the probability of a hit (H). A hit occurs when the forager attempts to use the resource when it is in fact a resource. The probability of a hit equals the cumulative probability of getting a cue greater than the selected criterion c, given that the cue came from a resource. For each possible criterion (c) there is a corresponding point (F, H) on the ROC curve.

The ROC curve traces out the tradeoff between hits and false alarms, constrained by the relationship between cue distributions (fig. 2.1 A & B). Although the ROC curve defines an outer edge of possible values of H and F, the particular point on the curve where the forager should operate depends on the probabilities and values of the payoffs for each of the various outcomes. The forager can decide where to operate along the curve by varying the selection criterion c. The ratio H/F decreases along the ROC curve, from the lower left to the upper right, and can be interpreted as the relative cautiousness of the forager. A cautious forager accepts a low level of hits (H) to get a low level of false alarms (F) and consequently operates toward the lower left of the ROC curve, where the ratio H/F is high. A less cautious forager accepts a high level of false alarms (F) to get a high level of hits (H) and consequently operates near the upper right of the ROC curve, where H/F is low (approaching one). ROC curves are constant for a particular relationship between probability density functions -- if that relationship changes, a new ROC curve results. Note that H/F values cannot be used to compare relative cautiousness across different ROC curves.

COMBINING SIGNAL DETECTION THEORY WITH THE f/μ CRITERION

We start with the maximize-f /μ model. The feeding rate, f, depends on the combined encounter rate (R) – which is the encounter rate with both resources and mimics – the probability that any given encounter is with a resource (S), the probability of successfully harvesting an encountered resource (C), the value of the resource if it is successfully harvested (V), and the background rate of harvesting alternative resources (A) (eq. 1). The mortality rate, μ, depends on the combined encounter rate (R), the probability that any given encounter is with a mimic (D=1-S), the probability of being killed as a result of the encounter (K), and the background mortality rate (m) (eq. 2). We make the simplifying assumptions that variation in the probability of accepting or rejecting the resource has a negligible impact on the ambient background mortality rate (m) and resource reward from other sources (A).

$$f = R \cdot S \cdot C \cdot V + A \tag{1}$$

$$\mu = R \cdot D \cdot K + m \tag{2}$$

Next, we use signal detection theory to incorporate the prey's ability to discriminate variable risks. The probability of successfully harvesting an encountered resource (C) depends on the probability that the forager makes a hit by accepting it (H): C = H. The probability of being killed by a mimetic predator (K) depends on the probability that the forager accepts a mimic (F), and the probability that the mimic successfully kills the forager given acceptance (P): K = F •P. Substituting these values in equations 1 and 2 yields equations 3 and 4:

$$f = R \bullet S \bullet H \bullet V + A \qquad (3).$$

$$\mu = R \bullet D \bullet F \bullet P + m \qquad (4).$$

H and F are constrained by a tradeoff given by the ROC curve, so we can represent H as a function of F: H(F). Making this substitution and dividing equation 3 by equation 4 results in equation 5:

$$\frac{f}{\mu} = \frac{R \bullet S \bullet H(F) \bullet V + A}{R \bullet D \bullet F \bullet P + m} \qquad (5)$$

The forager is selected to maximize f /μ subject to the tradeoff constraint between H(F) and F, and the parameters R, S, V, A, D, P, and m. If the ROC constraint H(F) is known, we can solve equation 5 for the value of F (and hence H(F)) that maximizes f /μ. If it is not known, we can still solve for the level of relative cautiousness $(H(F)/F)^*$ that maximizes the criterion along any single ROC, even if we do not know what that ROC looks like (appendix 2.1). At the maximum f /μ:

$$\frac{dH(F)}{dF} = \frac{H + \dfrac{A}{R \bullet S \bullet V}}{F + \dfrac{m}{R \bullet D \bullet P}} \qquad (6)$$

Recall that high values of the ratio H(F)/F (which is just the slope at any point along the ROC) occur at the lower left of the ROC curve, corresponding to high values of the critical threshold c, and vice versa. The optimal operating point, $(H(F)/F)^*$, is just the point on the ROC of interest with slope defined by equation 6. From eq. 6 we can see that this optimal slope (and the optimal threshold c^*) should increase with the prior odds that an encounter is with a mimic (D), the probability that a false alarm results in death (P), and with increasing alternative resources (A). Optimal slope (and the optimal threshold c^*) should decrease with increases in the probability that a risky resource is safe (S), the resource value of a safe resource (V), and with increasing background mortality (m). Hidden in the final form of the equation is the effect of the overlap between signal distributions. The solution uses implicit differentiation, which assumes a simple function describes the relationship between H and F. This is fine for getting a general solution, but does not allow for comparison between specific solutions. When we vary the underlying signal distributions, this effects the relationship between H and F as described earlier, and the general solution cannot analyze these specific differences. Although the general predictions for the "unhidden" variables are straightforward, analysis of the effects of changes in the relationship between the underlying distributions reveals unexpected dynamics in the relationship between optimal error rates (F^*) and discriminability.

In order to vary the overlap between signal distributions, we will retreat from the final form of the model and return to equation 5. This makes it easier to see that varying the overlap between the signal distributions will cause the relation H=H(F) to change, in

turn affecting the optimal behavior. Numerical simulations based on equation 5 show that, under certain conditions, foragers should actually increase their mortality risk in the face of increasing ability to discriminate.

SIMULATIONS

Setting H=H(F) allows for an analytical solution to the model, but obscures important information about how foragers should respond to changes in the overlap between distributions. Remember that H=H(F) depends on the amount of overlap between model and mimic distributions (see figure 2.1). In order to look at the response to variation in the amount of overlap, simple computer simulations have been conducted using Matlab© (see appendix 2 for program). In these simulations the ability of the forager to discriminate between models and mimics was altered by changing the difference between the means of the distributions (for simplicity, both distributions are assumed normal, with identical standard deviations). This simple manipulation changes the amount of overlap between the model and mimic distributions, thus changing the relationship H=H(F) – i.e. changing the ROC curves. All other parameters were held constant and given standard values. A second simulation, where the overlap of the distributions was varied by changing the standard deviation of the distributions with the means held constant (with SD(mimic)=SD(model) in all cases) was also conducted. The qualitative results of these two simulations were identical, so here we will simply report the results of the simulation involving the difference between means.

When the difference between means is varied, we move from one ROC curve to the next; H/F (or H(F)/F) is not a valid indicator of relative cautiousness on different

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ROC curves. For this reason, we will look at changes in optimal H and optimal F (H^* and F^* respectively) separately as the difference between distribution means changes. F^* is a better indicator of cautiousness in these simulations since it can be solved for directly, as opposed to the situation in the general solution. F^* and H^* were found by selecting the values of H and F resulting in maximal f/μ for each ROC curve generated. ROC curves were generated from underlying distributions with identical standard deviation (=0.2), but with their means differing by a variable amount, d (varying between 0 and 1.5 in 0.01 increments). As d increases, discrimination between the distributions becomes easier.

The results of these simulations show two qualitatively different patterns. These patterns show a switch point when $\frac{D \bullet P \bullet A}{S \bullet V \bullet m} = 1$. (See appendix 3 for the derivation of this cutoff point). The results of the simulation when $\frac{D \bullet P \bullet A}{S \bullet V \bullet m} < 1$, are shown in figure 2.2. The difference between distributions (a measure of discriminability) is displayed in increments of standard deviation. Here we see an intuitive pattern; as discriminability increases, the error rate decreases. Since H is tied to F, H shows some initial decrease with F until discrimination becomes easy enough that they are functionally dissociated.

Figure 2.3 displays the results of this simulation when $\frac{D \bullet P \bullet A}{S \bullet V \bullet m} > 1$. The simulation shows, unsurprisingly, that as the difference between distributions increases, H^*, the optimal probability of correctly selecting a model (i.e. resource) increases. However, F^*, the probability of incorrectly selecting a mimic (i.e. a predator), shows counter-intuitive behavior. As discriminabilty increases, F^* first increases, then levels off, and finally decreases, creating two regions with low error rates on either end of the discriminability axis and a region of increased risk at relatively moderate discriminability values (figure 2.3). Thus, when distributions have more than a critical amount of overlap it is actually optimal to increase the error rate (and thus mortality risk) in response to greater ease in discrimination. The energetic gains from increasing H^* outweigh the increased mortality risk associated with increasing F^* when differences between distributions are small and the parameters satisfy the criterion that $\frac{D \bullet P \bullet A}{S \bullet V \bullet m} > 1$. The marginal benefit of increasing H^* decreases as the difference between distributions increases. Eventually, the marginal increase in fitness associated with increasing H^* no longer offsets the marginal decrease in fitness associated with increasing F^*. At this point, F^* begins to decline. This produces the hump-shaped curve in figure 2.3. The exact position of the hump varies with variation in the parameters, but as long as the ratio $\frac{D \bullet P \bullet A}{S \bullet V \bullet m} > 1$, the hump exists. Thus, under certain conditions, as the ability to discriminate increases, individual prey can increase their fitness by increasing their susceptibility to predation via aggressive mimicry. Figure 2.4 redisplays this data in ROC space. The two adaptive basins (the upper curve and left-hand curve) show the same dividing line (at $\frac{D \bullet P \bullet A}{S \bullet V \bullet m} = 1$) as in the above figures, with a better demonstration of why the points (1,1) and (0,0) act as attractors – these can be mapped directly onto figures 2.2 and 2.3 respectively. From this figure it can be seen how the dupes response is constrained by the similarity between model and mimic.

A logical result of this outcome is that aggressive mimics in these circumstances will tend to be more efficient predators when their population consists of imperfect mimics. Feeding rates of the mimic are directly tied to error rates of the prey, so we can also interpret F^* in figure 2.3 as a graph of the relative feeding rates of aggressive mimics in these systems. As a population of mimics approaches perfect mimicry, their average success will actually drop as prey become more cautious. Depending upon the relative frequency of models and mimics, the mimics could eventually cause their prey to stop responding to either model or mimic, reducing mimic success to zero.

This sets up a group/individual conflict that similar to that developed by Stearns (1992). (see figure 2.5 for a graphical representation). The basic conflict is that, regardless of the response rate of dupes, individual mimics that are closer to perfect mimicry should be favored. This will tend to drive the population closer to the left of the graph. However, as the population of mimics moves in this direction, their average success will drop. Thus, although the relative fitness of "better" mimics will select for closer mimicry, the population as a whole will do worse from generation to generation, possibly mimicking itself to extinction, depending on other factors such as alternative prey. This conflict should make aggressive mimicry systems that rely on prey mimicry unstable unless either group selection is an important factor, or some other factor (ability to mimic other prey?) acts to counteract individual selection for enhanced mimicry.

A CORRELATIVE ANALYSIS

In response to changes in the relationship between distributions, the model makes the counter-intuitive prediction that, under certain conditions and when discriminability is below a certain threshold, as the distributions become easier to discriminate dupes should actually increase their probability of making a discrimination error (a false alarm) -- in this case a potentially lethal one.

Lethal mimic populations that are too similar on average to their models should cause their prey to become unresponsive, and we would expect to find food-based aggressive mimicry systems where models and mimics match closely to be relatively rare (Except in cases where alternative foods for dupes are unavailable). Since selection on individual mimics will always favor better mimics when prey are responding (as long as prey respond to the resource, they will respond more to better mimics regardless of the optimal response threshold), we expect that prey-based aggressive mimicry systems where $D \cdot P \cdot A/S \cdot V \cdot m > 1$ should be unstable in the absence of a mechanism preventing model and mimic convergence. If prey response to the model drops to zero, aggressive mimicry becomes useless, regardless of an individual mimic's resemblance; selection for further increases in similarity ends as mimics either starve or switch to an alternative prey. Realistically, this should happen at some point before response drops to zero, when prey response is low enough that mimics relying on this food source can no longer survive. One important caveat is that this model is based upon systems where a food resource is mimicked -- no predictions about the level of matching between model and mimic in other systems (for example, where mates are mimicked) can be supported at this point.

Given this caveat, we can look at the existing literature on aggressive mimics to determine if aggressive mimics tend to be "close" to a particular model – at this point no data exists on the stability of aggressive mimicry systems. Unfortunately, measurements of signal distributions have not been made in aggressive mimicry systems, making quantitative comparisons impossible. In order to provide a qualitative measure of closeness we will use the concept of abstract mimicry as outlined by Pasteur (1982) and Pough (1988). Abstract mimicry involves the mimicry of a class of organisms rather than a specific organism. Thus, the alligator snapping turtle, *Macroclemmys temminckii*, possesses a worm-like organ on its tongue that does not resemble a particular species of worm. Compare this to the concrete mimicry of the cleaner wrasse mimic, *Aspidontus taeniatus* (Wickler 1968), which mimics almost exactly the cleaner wrasse, *Labroides dimidiatus* both physically and behaviorally. Whether a system is considered abstract or concrete will depend to some extent on the level of study it has received, but in most cases concrete mimics very obviously mimic a particular model, while models in abstract mimicry systems are less easily categorized. Thus we can use this dichotomy as a rough index since abstract mimics are generally expected to mimic any specific biological model less "closely" than does a concrete mimic. The model presented here predicts that a general pattern should exist. Mimics that use food as a model should more often display weak mimicry than close mimicry. The abstract/concrete dichotomy can help us to confirm such a pattern.

Table 1 presents twenty-five proposed aggressive mimicry systems (see chapter one for methods of creating this table) involving mimicry of food or mates. Of these twenty-five, eighteen cases involve mimicry of food; in each of these eighteen cases the mimicry is considered abstract. Thus, weak mimicry is more common among lethal aggressive mimics of food (provided alternative foods are available to the dupe) just as we would expect based on arguments resulting from the model.

Table 1 also includes seven cases involving mimicry of mates. Given two major, but realistic, assumptions, the current model can be simply modified to represent the situation of predators mimicking mates. These assumptions are: 1) birth rate/death rate is a valid criterion for maximizing fitness just as feeding rate/death rate has been shown to be and 2) there are no alternatives to mates that result in a fitness benefit in this currency (i.e. A=0). These two assumptions allow a model (equation 7) that is identical to that in equation 5 except that the units of V change to represent offspring/encounter rather than calories/encounter and the variable A drops out.

$$\frac{f}{\mu} = \frac{R \bullet S \bullet H(F) \bullet V}{R \bullet D \bullet F \bullet P + m} \qquad (7)$$

The loss of A yields an equation similar to the previous equations, and once again simulations can be conducted. Figure 2.4 shows the results of this simulation (varying the difference between distribution means). In this case we see that as the difference between means decreases, F* approaches one while H* displays more complex behavior – in this case showing a decrease in hits (i.e. attempting to mate with a potential mate) as discriminability increases, when the means are "close". The shape of this curve allows selection to continue to refine the similarity between model and mimic; dupe response to mimics increases as similarity increases. This leads to the expectation that concrete mimicry should be common among mate mimics. All seven cases of mate mimicry appearing in table 1 are concrete. The data available from the literature thus support the expectations inferred from the models.

DISCUSSION

The models developed here describe a mechanism for adaptive variation in selective risk taking, where one of the risks is death. They are simple and precise, but probably more general than realistic. They make quantitative predictions from measurable variables, and are amenable to experimental and observational tests. Most simply, we expect that in habitats where aggressive mimics are abundant, foragers should be cautious, raising their threshold for accepting a risky opportunity and accepting lower hit rates (many missed opportunities) to lower the false alarm rate. Where aggressive mimics are rare, we expect less cautious foragers with a low threshold for accepting a risky opportunity and accepting high false alarm rates (risking predation) to lower lost opportunity costs (misses). This is analogous to Wiley's (1994) concept of "adaptive gullibility" in mate choice, with the additional oddity that we see in this case dupes being more gullible when the deception is worse (i.e. as discriminability increases).

The models developed here predict logical and intuitive changes in cautiousness in response to changes in other parameter values as well. As parameters positively correlated with mimic associated mortality (D, P) increase, prey should behave more cautiously. Similarly, as alternative resources (A) become more valuable (and/or

available), cautiousness increases. Conversely, as the parameters associated with resource quality (S, V) increase, cautiousness should decrease, and cautiousness also decreases when background mortality rates (m) increase. None of these results are particularly surprising, and they give confidence that the model captures important aspects of the forager's behavior.

Results from simulations varying the level of overlap between the distributions yield counter-intuitive predictions that are supported by the anecdotal data available on aggressive mimicry systems -- aggressive mimicry systems where food is mimicked are abstract in nature while systems where mates are mimicked are concrete. The dichotomy between food and mate mimics also falls closely into the categorization developed in chapter one based on fitness effects of the mimic on the biological model in an aggressive mimicry system. Living food can often (with the exception of flowers) be expected to benefit, at least potentially, from the presence of an aggressive mimic in the community because their own predators will respond to the mimics either by increasing their cautiousness, suffering losses to predation, or both. The fitness of mates will generally suffer from the presence of a mimic because access to their mates (the mimics' prey) will be reduced – either through a reduction in numbers, increased catiousness or both. Thus not only do these models predict the counter-intuitive pattern seen in the above data, but they help to explain at least part of the pattern detected in chapter one – that mimicry systems where the organism being mimicked benefits from the presence of the mimicry tend to be abstract systems whereas concrete mimicry is common in systems where models suffer from the presence of the mimic.

Models and mimics both benefit from similarity in traits in prey-mimicking systems. This would seem to lead to convergence in appearance over time. However, we have seen that these systems are abstract in nature. Some mechanism must prevent convergence of models and mimics for the observed pattern to hold. We will not address here all of the potential mechanisms by which convergence of models and mimics might be prevented. This will require further theoretical development, incorporating evolutionary dynamics between the three actors in the system and, more importantly, empirical observations of additional aggressive mimicry systems. Some potential mechanisms include zero selection for similarity beyond a certain level, prey switching by mimics, or frequency dependent selection. Even group selection, as detailed above, may play a role in resisting the evolutionary forces expected to result in close mimicry.

Similarly, we will not discuss in detail mechanisms preventing mimicked mates from escaping their mimics. The most likely explanation is that large changes in appearance will be prevented by associated difficulties in mate recognition. Other mechanisms are of course also possible in both of these types of systems; detailed experimentation will be necessary to understand which mechanism functions in any given system, and many systems must be studied experimentally to determine if general patterns exist.

The data from the literature search are admittedly flawed – see chapter 1 for a full discussion of the problems with the data set. Another difficulty associated with the way they are used here is that the model was developed in the hopes of finding an analytical means of explaining a pattern seen in the data. The current models do this, but the inherent circularity involved in using old data to check "predictions" makes all of the conclusions of this chapter tentative in nature. What is really needed to test this modelling paradigm is to test it against new data. While it is unlikely that enough new data will arise to allow a test of the general predictions outlined in this chapter, investigation of particular systems can yield valuable insights. For example, selection experiments can be conducted to test for the hump shape in figure 2.3. Selection experiments can also be used to test for the existence of the criterion outlined in appendix 3. On a more short-term basis, the cautiousness of dupes from a variety of sites varying in relative abundances of models and mimics can be measured to see that predictions from these models make realistic ecological predictions.

The models developed here provide insight into the way aggressive mimicry works in a very general way. Further elaboration of this modeling paradigm, development and testing of hypotheses about the dynamics of aggressive mimicry are likely to prove fruitful. The plethora of studies on protective mimicry has made an enormous contribution to the development of ecology and evolution. Mimetic predators, however, have long been ignored; detailed, systematic study of these systems is long overdue and can potentially make a similar contribution to our understanding of predator-prey dynamics, the evolution of discrimination, and the co-evolution of perception and appearance.

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Table 2.1. Proposed aggressive mimicry systems involving food or mates

Mimic	Scientific name of mimic	Proposed model – model type	Concrete or Abstract?	References
Siphonophores	*Agalma okeni*	Copepods – Food	Abstract	Purcell 1980
Scorpionfish	*Iracundus signifer*	Fish – Food	Abstract	Schallenberger and Madden 1973.
Siphonophore	*Athorybia rosacea*	Fish larvae – Food	Abstract	Purcell 1980.
Flounder	*Asterorhombus fijiensis*	Fish or crustacean – Food	Abstract	Amaoka et al. 1994.
Shellfish (Parasitic)	*Lampsilis* sp.	Fish or Fish tails – Food	Abstract	Wickler 1968; Haag et al. 1995, 1999.
Argiope Spiders	*Argiope sp.*	Flowers – Food	Abstract	Horton 1979; Craig and Bernard 1990; Tso 1998.
Pitcher Plants	*Napenthes* sp.. *Cephalotus* sp. *Sarracenia* sp. *Darlingtonia* sp	Flowers – Food	Abstract	Wickler 1968, Wiens 1978; Moran 1996; Newell and Nastase 1998.
Praying mantis	*Idolum* sp.	Flowers – Food	Abstract	Wickler 1968.
Jumping Spider	*Portia fimbriata*	Insects – Food	Abstract	Jackson and Blest 1982; Jackson and Hallas 1990
Pirate Spiders	*Mimetus maculosus*	Insects – Food	Abstract	Jackson and Whitehouse 1986.
Snowy Egret	*Leucophoyx thula*	Insects – Food	Abstract	Kushlan 1973.
Anglerfish	Lophiformes (many species)	worm-like or fish-like – Food	Abstract	Pietsch and Grobecker 1978.
Colubrid snake	*Alsophis portoricensis*	Worms – Food	Abstract	Leal and Thomas 1994.
Green Pit Viper	*Bothrops bilineatus*	Worms – Food	Abstract	Greene and Campbell 1972.
Horned Frog	*Ceratophrys sp.*	Worms – Food	Abstract	Wickler 1968; Murphy 1976.
Burtons Pygopodid	*Lialis burtonis*	Worms –Food	Abstract	Murray et al. 1991.
Trematode (parasitic)	*Leucochloridium macrostomum*	Worms –Food	Abstract	Wickler 1968.
Alligator Snapping Turtle	*Macroclemmys temmincki*	Worms—Food	Abstract	Wickler 1968; Drummond and Gordon 1979; Pritchard 1989.
Characoid fish	*Probolodus heterostomus*	Female *Astyanax fasciatus* – Mates	Concrete	Sazima 1977
Bolas Spiders	*Mastophora sp.*	Female Pheremones – Mates	Concrete	Huthison 1903; Gertsch 1947; Wickler 1968; Eberhard 1977; Stowe et. al. 1987; Yeargan 1988, 1994; Yeargan and Quate 1996.
Spiders	*Kaira sp.*	Female Pheremones – Mates	Concrete	Stowe 1988; Stowe et al. 1995.
Spiders	*Phoroncidia sp.*	Female Pheremones – Mates	Concrete	Stowe 1988; Stowe et al. 1995.
Fireflies	*Photuris* sp.	Female *Photinus* – Mates	Concrete	Lloyd 1975, 1984; Copeland 1983; but see Vencl et al. 1994 and references therein.

Table 2.1. Proposed aggressive mimicry systems involving food or mates

Mimic	Scientific name of mimic	Proposed model – model type	Concrete or Abstract?	References
Fish	*Erythrinus ereythrinus*	Female *Rivuls agilae* – Mates	Concrete	Brosset 1997.
Pirate Spiders	*Ero furcata*	Male *Meta segmentata* – Mates	Concrete	Czajka 1963.

Figure 2.1. Relationship of an ROC curve to the underlying distributions. Panel A illustrates hypothetical overlapping distributions of cues from safe and dangerous resource populations. A threshold criterion (c) divides the safe distribution into misses below c and hits above c. The probability of a hit given a response to cues $\geq$ c is H, given by the area under the curve to the right of c (shaded with horizontal lines). The same criterion divides the dangerous distribution into correct rejections and false alarms with corresponding probability F (vertical lines). The resulting values of H and F are plotted as the point c on the corresponding receiver operating characteristic (ROC) curve in panel B. Two alternative criterion points, d and e, are also shown with corresponding points in ROC space. The ROC curve traces out, from upper right to bottom left, the possible combinations of H and F that would result from moving the criterion from the minimum (left) to the maximum (right) in pane A. The ratio H/F decreases from the lower left to the upper right along the ROC curve. Lower values of H/F, at the upper right of the ROC curve, correspond to a low criterion and indicate a bold forager (point d). Higher values of H/F, at the lower left of the ROC curve, correspond to a high criterion and indicate a cautious forager (point e).

Figure 2.1

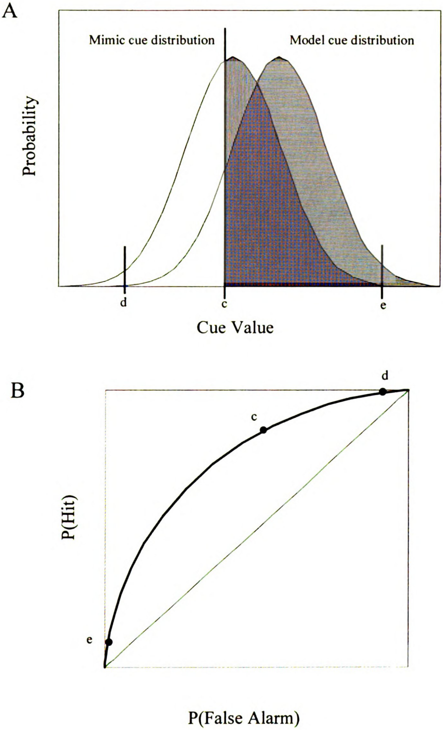

A
Mimic cue distribution
Model cue distribution
Probability
d
c
e
Cue Value
B
d
c
e
P(Hit)
P(False Alarm)

Figure 2.2. Hit (dashed) and False alarm (solid)probabilities with respect to the difference between distribution means, in units of standard deviation when $\frac{D \bullet P \bullet A}{S \bullet V \bullet m} < 1$, based on simulations for prey mimicry.

Figure 2.2

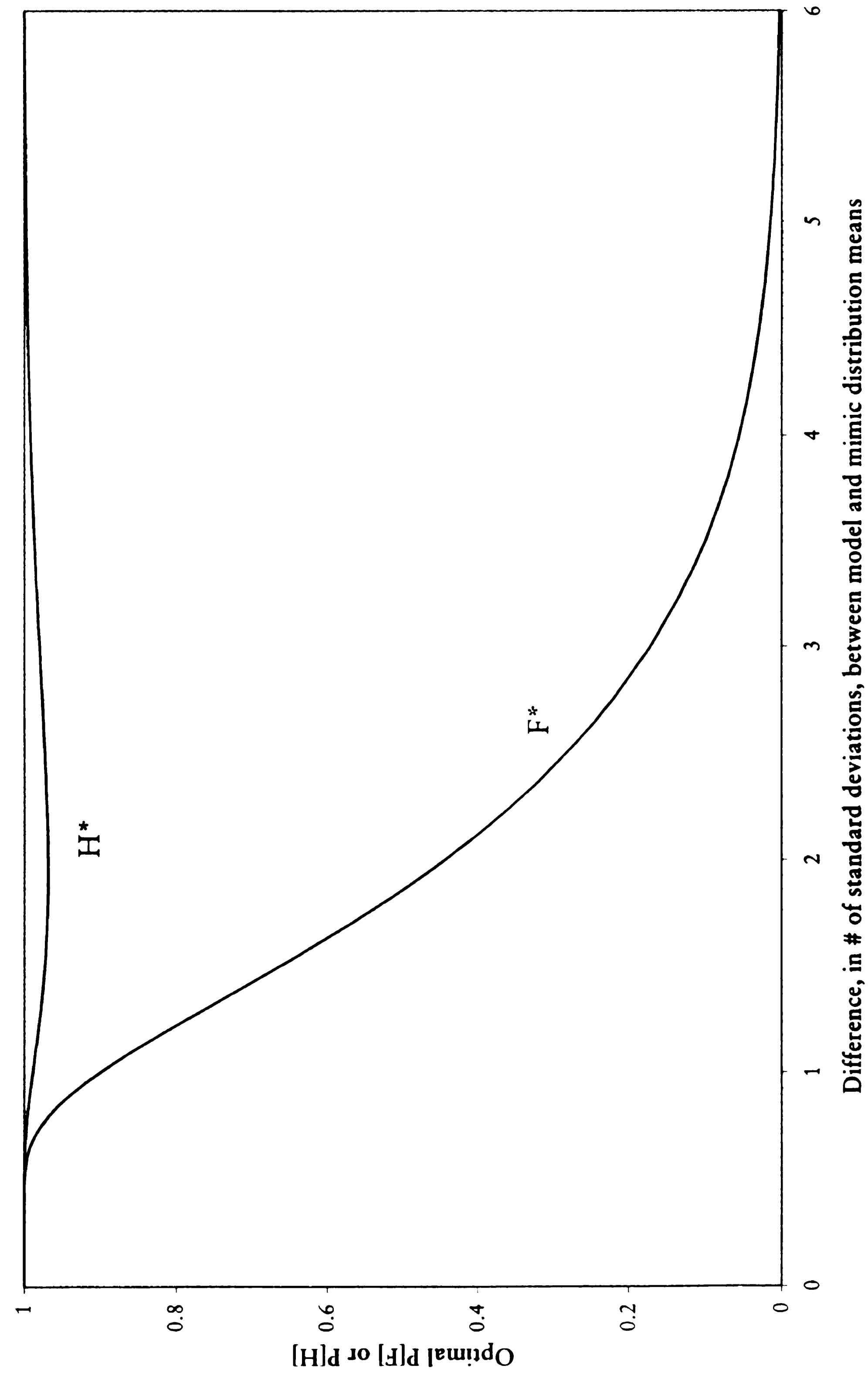

Optimal P[F] or P[H]
1
0.8
0.6
0.4
0.2
0
H*
F*
0
1
2
3
4
5
6
Difference, in # of standard deviations, between model and mimic distribution means

Figure 2.3. Hit (dashed) and False alarm (solid) probabilities with respect to the difference between distribution means, in units of standard deviation when $\frac{D \bullet P \bullet A}{S \bullet V \bullet m} < 1$, based on simulations for prey mimicry.

Figure 2.3

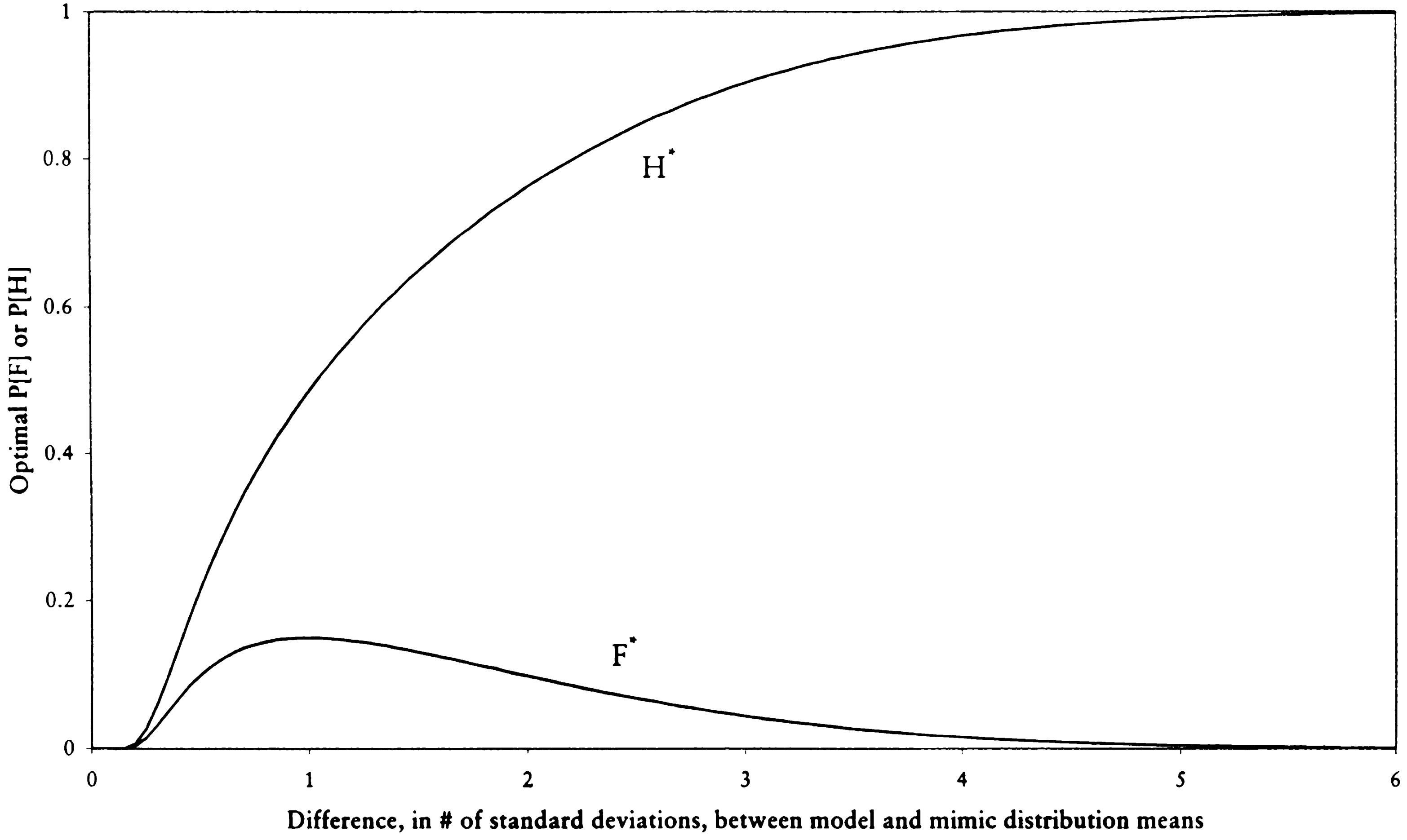
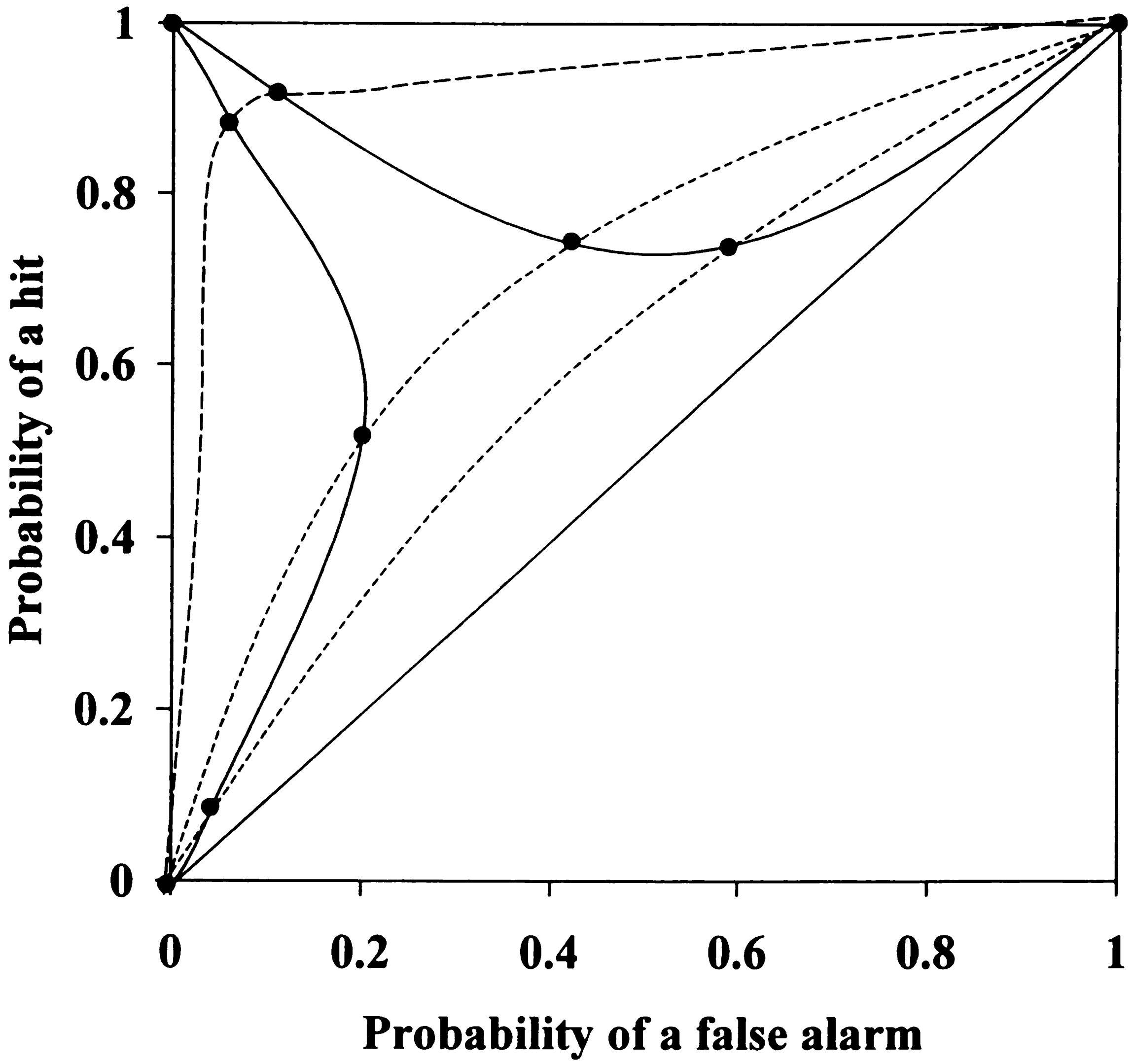

Optimal P[F] or P[H]
1
0.8
0.6
0.4
0.2
0
0
1
2
3
4
5
6
H*
F*
Difference, in # of standard deviations, between model and mimic distribution means

Figure 2.4. Trajectory of dupe response to increasing model/mimic similarity. When no mimicry is present, dupes can (and should) operate at the point (0,1) in ROC space. When mimic resemblance to models is perfect (Solid ROC along the line H=F), a opposite strategies are optimal depending upon whether $D \cdot P \cdot A/S \cdot V \cdot m > 1$, where the operating point (0,0) is optimal, or $D \cdot P \cdot A/S \cdot V \cdot m < 1$, where the operating point (1,1) is optimal. The three intermediate ROC curves {dashed curves traversing the distance from (0,0) to (1,1)} show the optimal operating points at intermediate values of signal overlap, and demonstrate how dupes should change their responses for different levels of similarity between models and mimics depending upon the value of $D \cdot P \cdot A/S \cdot V \cdot m$. The upper trajectory is favored when $D \cdot P \cdot A/S \cdot V \cdot m < 1$, and the left-hand trajectory is favored when $D \cdot P \cdot A/S \cdot V \cdot m > 1$. This results in two adaptive regions in the ROC curve and explains the difference between figures 2.2 and 2.3. The shape of these trajectories is what drives the hump that is seen in F in figure 2.3 and the dip that is seen in H in figure 2.2.

Figure 2.4



1
0.8
0.6
0.4
0.2
0
Probability of a hit
0
0.2
0.4
0.6
0.8
1
Probability of a false alarm

Figure 2.5. The potential tradeoff between individual and group fitness. Each solid line represents a separate population of mimics, the dashed line goes through the mean similarity of each population. In this situation, the fitness of mimics within a population is a function of both the individual's similarity to the models and the population average similarity to models. Individual fitness always increases with increasing similarity within a population, but the same level of similarity in two different populations may yield very different fitness in absolute terms. In this way, an individual with low similarity can have a higher fitness than a nearly perfect mimic, if it is in a population of low average similarity. This is the situation mimics find themselves in with faced with the dupe response curve depicted in figure 2.3.

Figure 2.5

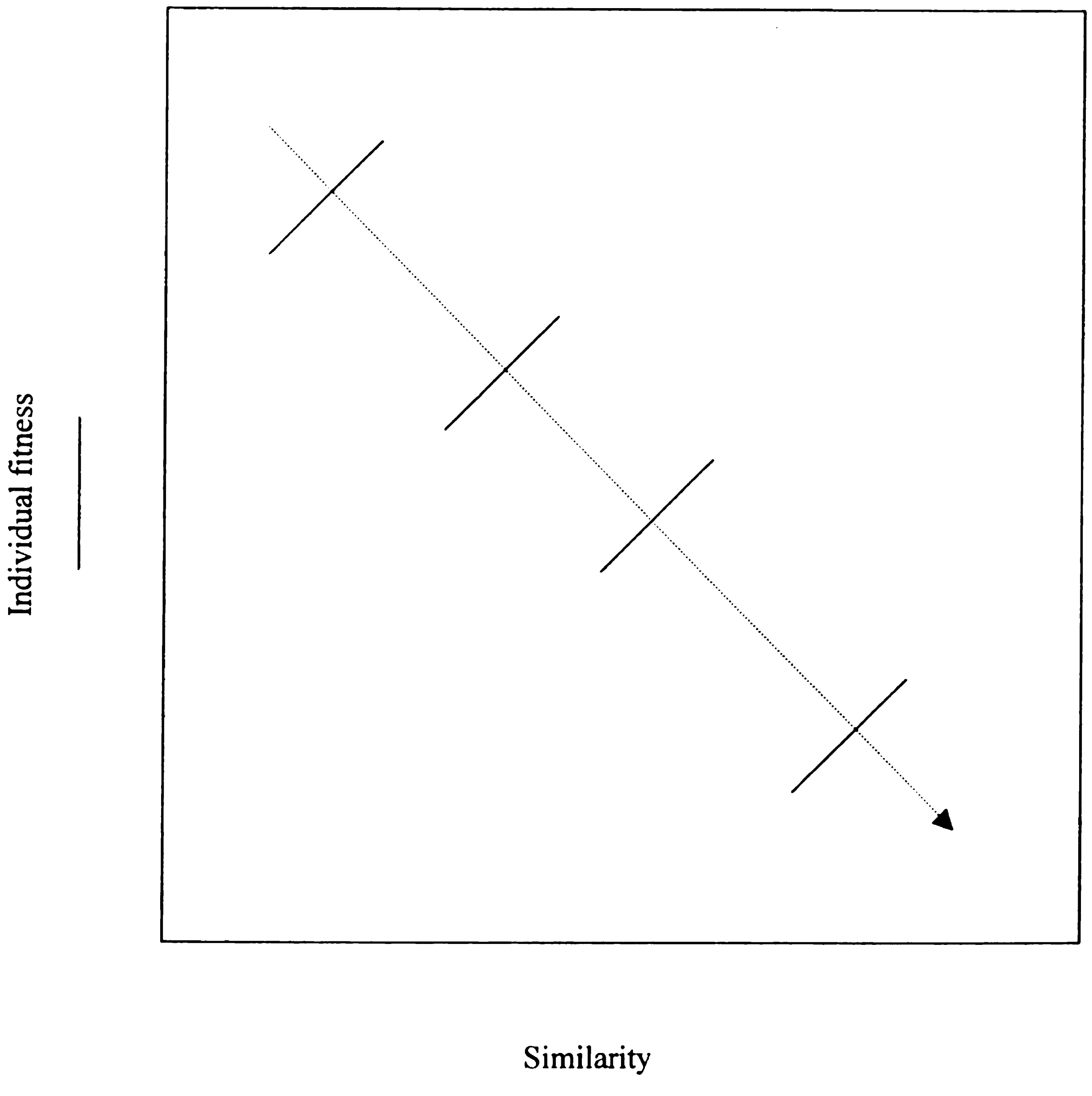
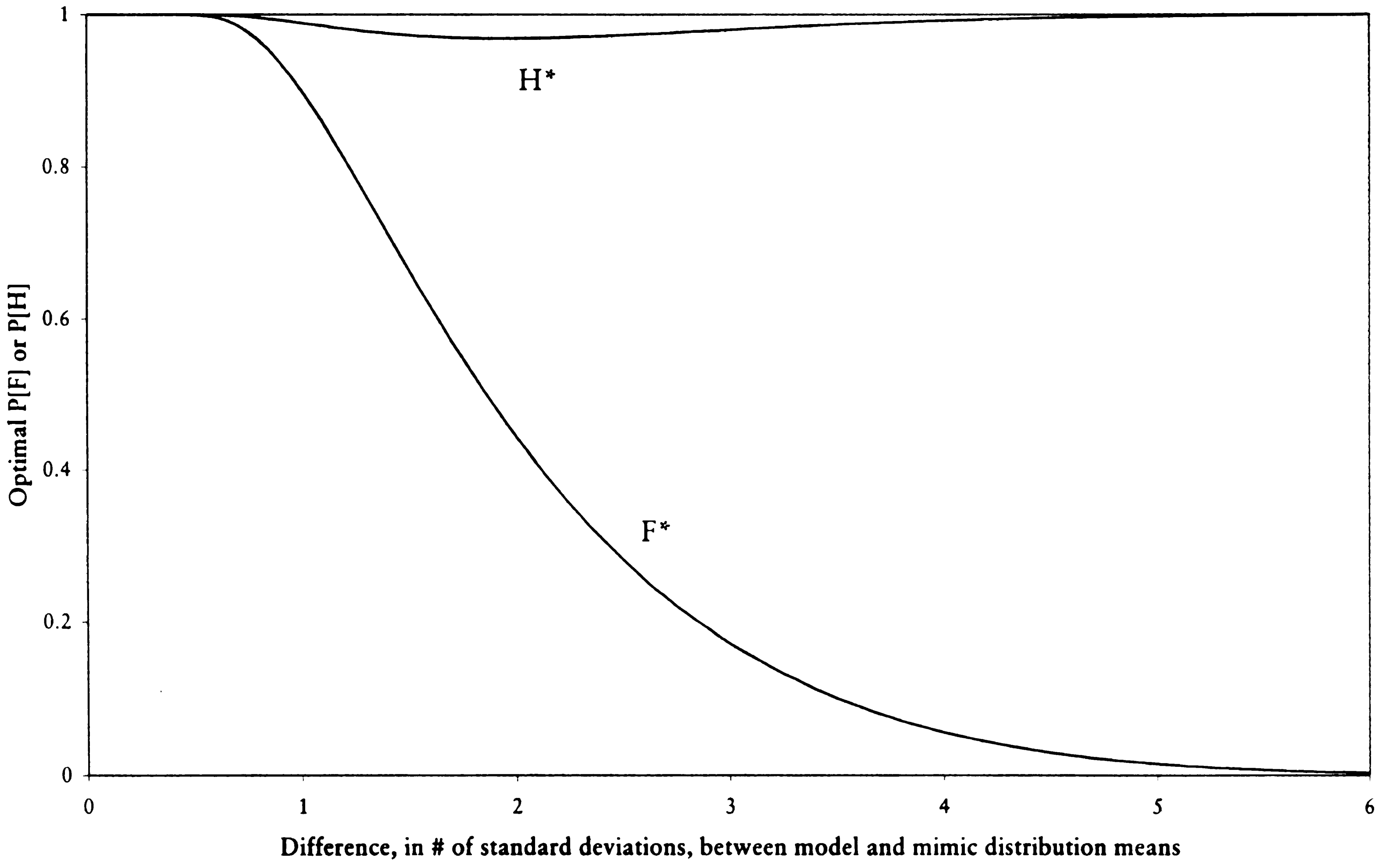


Figure 2.6. Hit (dashed) and False alarm (solid) probabilities with respect to the difference between distribution means, in units of standard deviation. From simulations based on mate mimicry.

Figure 2.6


1
0.8
0.6
0.4
0.2
0
Optimal P[F] or P[H]
H*
F*
0
1
2
3
4
5
6
Difference, in # of standard deviations, between model and mimic distribution means

Chapter 3

Natural history of *Mimetus notius* and signal sources in prey webs.

Introduction

Spiders of the family Mimetidae prey upon web-weaving spiders (Archer 1941; Czajka 1963; Cutler 1972; Lawler 1972; Lowrie, et al. 1972; Heimer 1986; Jackson & Whitehouse 1986). Although they utilize a variety of behaviors to obtain prey (Heimer 1986), one of the more intriguing is their use of aggressive mimicry. Several mimetid species have been observed to enter webs of other spiders and delicately pluck at the silk threads, luring the resident spider into striking range; approximately one mimetid body length (3-5 mm). The mimetid leaps at its prey, seizing it in its chelicerae and injecting an apparently spider-specific venom, quickly immobilizing it. This remarkable behavior has received little study, and the basic natural history critical to understanding the behavior has not been studied. This chapter will address the natural history of a representative Mimetid, *Mimetus notius* (Chamberlin 1923).

What little detailed information is known of the Mimetidae, aside from taxonomic description, comes primarily from one major study (Jackson and Whitehouse 1986) and three smaller studies. Lawler (1972) provided details on the life cycle and activity patterns of *Mimetus eutypus*, but all of the diet information came from laboratory interactions. Lawler also described the predatory behavior of this species, which apparently does not use aggressive mimicry to capture its prey. Archer (1941) gave brief details of several mimetid species' habitats and diets, but was more concerned with taxonomy than ecology. Heimer (1986) also provided some ecological information in a taxonomic treatment, including a description of the range of behaviors used by different species of mimetids to capture araneid prey. Two sets of anecdotal accounts of field observations exist as well (Cutler 1972; Lowrie et al. 1972), but these provide little in the way of detailed ecological information. In the most comprehensive study, Jackson & Whitehouse (1986) present a detailed ethogram of the luring behaviors of two species of Mimetidae from New Zealand and Queensland, document the families of prey taken by these spiders in the field, and measure success rates in the lab. Although detailed descriptions of the luring behavior of these spiders are presented, responses of the prey are not discussed in detail. This provides part of the picture, but in order to understand how the system as a whole functions, data on both sides of the interaction are crucial.

In order to understand the nature of the mimetid lure, it will be necessary to measure the signals presented by mimetids and various potential models as well as the reactions of mimetid prey to mimetids and to each potential model. Before measurements can proceed it is necessary to identify the major arachnid prey of a mimetid species and to identify the signal sources that occur in the webs of that prey. These signal sources represent the most likely biological models of Mimetid mimicry for that particular prey species. A detailed natural history is needed to provide this information.

While the studies above provide some information on the diet of several mimetid species, only Jackson and Whitehouse (1986) quantify the relative abundance of different prey in the diets of mimetids, and they do so only at the family level. The occurrence of different signal sources in prey webs is completely unknown. Even such basic information as life cycle, fecundity and habitat preference is known for only a few species (Archer 1941; Lawler 1972).

The first step of an investigation into mimetid predatory behavior is presented here, using *Mimetus notius* Chamberlin. The primary goals of this chapter are to present some general natural history data for *M. notius*, identify their prey, and to identify the major signal sources present in their prey's webs.

Study Species

Mimetus notius was first described by Chamberlin (1923). The most recent taxonomic treatment is in Mott (1989), from which adult size data is taken; for detailed taxonomic information, please see this excellent treatment. *M. notius* is a moderate sized spider, adult females averaging 4.9 mm in length and adult males 3.6 mm. They occur throughout coniferous forests in the eastern United States (Archer 1941; Mott 1989). They are nocturnal; during the daytime they adopt a very cryptic posture on the undersides of tree limbs making them extremely difficult to locate. After sunset they begin moving among the branches, searching for the webs of their prey. They can be readily located by searching coniferous forest edges at night with the aid of a flashlight.

General Field Methods

Censuses of nineteen different populations of *M. notius* were conducted over the three years of the study, 1995-1997. Censuses differed somewhat both between and within years due to ever-increasing knowledge of the spider and the different goals associated with different aspects of the study. Below I will describe each of the different censuses.

From March-November 1995 and April-October 1996 field censuses were conducted to document seasonal changes in populations of spiders in four coniferous forest plantations in southwestern Michigan, USA. Preliminary attempts to locate *M. notius* (throughout the summer of 1994) showed that they are virtually absent in deciduous trees, except in locations with conifers in close association, in agreement with Archer (1941). Each census consisted of five twenty meter transects laid out along the forest edge, where preliminary observations indicated that mimetids were most abundant. The transects faced into the forest edge, penetrated one meter into the vegetation, and were visually searched with the aid of a headlamp from the trees' lowest branches to approximately two meters above the ground. Censuses were conducted from 10 PM until completion of all five transects. Total census time varied, with most transects averaging 45 minutes to an hour to sample. Seasonal variation in sampling time existed, with times being shorter early and late in the seasons when fewer spiders were encountered. Visual censusing was used because other sampling methods, such as sweep netting, destroy data on interactions within webs. While visual sampling may miss smaller, non-web weaving spiders, these are not of interest in the current context since they rarely interact with *M. notius*. Because spider community data is not analyzed here this does not present a problem for the conclusions in this study.

All spiders located were identified, counted and assigned a web status (i.e., whether or not they were on a web). All *M. notius* encountered had their size, sex (if adult), behavior (immediately upon detection), and prey recorded. For *M. notius* found on webs, the status of the web (with or without a resident spider) and identity of web residents (if any) were recorded. Mimetid egg sacs found were noted, with some collected and reared in the lab.

In 1996 data collection on *M. notius*' most common prey (*Theridion sp.*, see table 3.1) occurred, including interactions between web-resident *Theridion* and their mates, invaders and prey. Several spider species invade *Theridion* webs, including other *Theridion*. *Theridion* invaders capable of mating with web residents (i.e. adults of the opposite sex of an adult resident) were identified as mates, while large juveniles (obviously past the first molt) or same-sex spiders in a web were considered to be conspecific invaders. Juveniles before first molt were considered to be recently emerged and not included as invaders. This interpretation stems from the observation that nearly all juveniles in this size range were encountered in large groups near an egg sac. All heterospecific spiders in *Theridion* webs were identified as invaders. In these censuses, only prey actually held in the chelicerae of *Theridion* were identified as *Theridion* prey.

Identification of most spiders occurred in the field. Spiders not immediately recognizable were collected live and brought to the lab for identification and use in various laboratory observations. The Araneidae, Dictynidae, Linyphiidae, Tetragnathidae, Theridiidae and Uloboridae were identified only to genus due to the large number of immature spiders encountered. Agelenidae, Clubionidae, Micryphantidae, Salticidae, and Thomisidae were identified only to family since they were considered unlikely to be prey for *M. notius*, due to their size and/or lack of web-use. These spiders were also relatively rare in the censuses. Identifications were made using Kaston (1948).

In 1995 transects were positioned randomly along the forest edge at each census and censuses occurred at 2-4 week intervals. In 1996 five permanent transects were established at each of the four sites and censused in regular 4 week intervals. Small numbers of mimetids (no more than 1/transect) and potential prey (≤5/transect) were collected occasionally to provide laboratory specimens, except for the final census in 1996, when all mimetids encountered and large numbers of prey were collected for a laboratory experiment to determine predatory efficiency (see below).

In addition to these seasonal censuses, five one-sample censuses were conducted in 1996 during the peak of mimetid abundance. These censuses differed from the previous censuses; they were single samples rather than being broken up into five transects, and the amount of time was recorded for each census. During these censuses collection of *Mimetus* and *Theridion sp.* ocuurred – the spiders collected were included in the 1996 experiment on predatory efficiency. Data collection was the same as for other 1996 censuses.

A final series of censuses was conducted in 1997, consisting of two samples, separated by 4 weeks, for each of nine sites. These censuses were standardized as 5 hour censuses. All spiders located at the forest edge during the period from 10:00 PM –3:00 AM were counted. Data collection was as in other censuses except that no specimens were collected in the first census, while in the second census at each site all *Mimetus* and a large number of *Theridion* were collected for an experiment not discussed here (see Chapter 5). Also in the second census, all prey in the webs of *Theridion* were collected from the web and brought into the lab for identification.

Each section below presents a different aspect of the natural history of *M. notius*. In the portions describing methods the particular set of censuses used will be given, as well as any methods beyond these general methods that are necessary for that portion of the study.

Seasonality and life cycle

Methods.-- The seasonal data comes from the censuses of four sites in 1995 and 1996 that spanned the entire active season of *Mimetus*. The sites described here include one dominated by white pine (*Pinus strobus*), one dominated by white spruce (*Picea glauca*), one dominated by Norway spruce (*Picea abies*) and one site of mixed white spruce and red pine (*Pinus resinosa*). Fourteen egg sacs were collected or produced in the lab by Mimetids from these four sites in 1995. These were kept in the lab until emergence of spiderlings. Each spiderling was measured within 24 hours of emergence. Most were released into the site of origin within 48 hours of emergence, but several from each egg sac were kept longer for observations of spiderling behavior.

Results and discussion.-- Figure 3.1 shows the seasonal abundance of *M. notius* on each of the sites in each year. The pattern of seasonal abundance was similar to that of all spiders (figure 3.2) and to that of *M. notius*' most abundant prey, *Theridion sp.* (figure 3.3). *M. notius* emerged from their over-winter retreats as late-instar juveniles or adults as early as March (Earliest observation, March 20), but no mating activity was observed until May. Six matings were observed in the field between the dates of may 9 and June 6. Sixteen egg sacs were found between May 30 and July 25 – fourteen egg sacs were

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successfully collected. Adult spiders appear to die shortly after laying eggs, as adults were rarely found after early July and before September (see figure 3.4). Egg sacs were placed, unguarded, in the distal forks of spruce or pine twigs. Juveniles appeared in large numbers in the field in July, and increased in size until late September. By September roughly one-third of the mimetids found were adults (see figure 3.4). Overall numbers began to decrease in October, and by mid-November no individuals could be located (see figure 3.1). Overwintering appears to occur as adults or late instar juveniles.

Ten of the fourteen egg sacs produced spiderlings (emergence success=71 %). Successful egg sacs averaged 16.9 (s.d. 9.7) spiderlings. These spiderlings were relatively large (average 1.4 mm total length, s.d. 0.1) equaling ~28% of the total length of females (4.9 mm; Mott 1989). Spiderlings emerged one at a time for 24-48 hours, usually at a rate of ~ 1/hour. The long time between mimetid spiderling emergence may be a mechanism to avoid cannabilism, but no cannibalism was observed among mimetus spiderlings left in vials for up to two days post emergence. After 2 days cannibalism was observed, but no data were taken – spiderlings were generally separated earlier than this. The large size of the offspring allowed the spiderlings to immediately begin to hunt the spiderlings of other spiders, which emerge at a similar time of year (see figures 3.2 and 3.3). Several spider species that appeared invulnerable to *M. notius* as adults due to their large size were readily taken in the lab as spiderlings by *M. notius* spiderlings, when the size advantage lies with *M. notius*. *M. notius* spiderlings successfully lured and captured other spiderlings within 24 hours of emergence.

Vegetation Preferences:

Methods.-- Results from the 1995 and 1996 field censuses suggested that *M. notius* might be more abundant on spruce sites than on pine sites (see figure 3.1). The data from the first set of 1997 census can be used to test this hypothesis. The second set of 1997 censuses is not included in the test because the collection of specimens reduced the number of spiders encountered sufficiently that averages of the two censuses overestimate the variance. Of the ten sites sampled in the first set of censuses, three were pine dominated and seven were dominated by spruce

Results and discussion.-- The absolute number of mimetids did not statistically differ between spruce dominated and pine dominated sites (spruce: mean=9.0 SD=4.3, n=7; pine: mean=5.3, SD=2.9, n=3, separate variances t-test, t=1.565, p=0.169). Relative abundance of mimetids, expressed in mimetids per web, also did not differ (spruce: mean=0.036, SD=0.020; pine: mean=0.046, SD=0.044, t=0.368, p=0.743). Thus, mimetids maintained themselves in approximately the same numbers and relative abundance in spruce and in pine. The differences in the initial four sites may be caused by other factors, but vegetational differences appear to be minimal.

Mimetus notius diet

Methods.-- In all censuses, prey of *M. notius* were collected and brought into the lab, where they were identified, if possible, from their remains. All occupied webs invaded by *M. notius* had their residents identified, either in the field or by bringing them into the laboratory. Residents were identified as being eaten or as "in web" depending on whether the mimetid had begun devouring it. Interactions with mimetids can sometimes last for several hours before either successful capture or abandonment of the web by either the resident or the mimetid, so these data are snapshots in time. Spiders "in web" may or may not have been eaten later in the night, and were considered potential prey for *Mimetus*. Because of the small numbers of prey captured at each site and census, no attempt will be made to identify site or seasonal variations. Instead, all data will be pooled.

Results and discussion.-- The composition of prey encounters from all censuses is summarized in table 3.1. Although Mimetids are frequently referred to as being exclusively araneophagic (Foelix 1982; Wise 1993), I found that insects comprise 32.5 % of the diet of *M. notius*. Jackson and Whitehouse (1986) studied two mimetid species from New Zealand that exhibited kleptoparasitic insectivory in the lab. They did not observe insectivory in the field, however. Heimer (1986) described several species of mimetids that actively capture insects in the field. In the present study both active capture and kleptoparasitism have been observed rarely in the field. Unfortunately, most observations of insects as prey occurred after the mimetid obtained the prey. Thus it is unknown in most cases whether a particular insect was actively captured or kleptoparasitized by the mimetid. Regardless of capture method, insects unexpectedly constitute a major portion of *M. notius*' diet.

Crab spiders (Thomisidae) formed an unexpectedly large fraction of *M. notius*' diet, given that these spiders do not normally inhabit webs (Table 3.1). All observed instances of predation on crab spiders occurred in webs of *Theridion* or *Dyctina*, suggesting that these crab spiders attempted web invasion themselves before falling prey to *M. notius*. The low number of encounters with uneaten crab spiders indicates that they are either encountered infrequently or that interactions with these spiders occur rapidly, in contrast with encounters with web-weaving spiders.

M. notius attack and capture spiders primarily in the Theridiidae, Araneadae, and Dictynidae. One genus, *Theridion*, accounts for 22.1 % of all prey captured, 32.7 % of spider prey captured, and 40.4 % of all encounters with spiders (n=201 encounters; see table 3.1). In addition, observations of interactions between *Theridion* and *Mimetus* in both the lab and field show that luring is effective against *Theridion.* This leads to the conclusion that *Theridion* is the major target of *M. notius* mimicry in this system. Although *M. notius* utilizes mimicry against other spiders, we will limit further consideration to *Theridion*. As the major prey it is the most important interactor in the system, and trying to follow the entire food web for *M. notius* and its prey would introduce unnecessary complications into the remainder of this analysis.

Predatory efficiency

Methods.-- *M. notius* and *Theridion* were collected from all of the sites censused in 1996 for this portion of the study. In order to estimate the predatory efficiency of *M. notius* and to determine if coevolution was occurring across sites a two-part experiment was conducted. These experiments involved staging interactions in the lab between *M. notius* and *Theridion.* All interactions occurred in small rectangular behavioral arenas. These arenas were 15.2 x 10.2 x 3.3 cm in size, and constructed from pine with plexiglas sides. Each arena had two access ports (2.1 cm diameter) in the top to allow for introduction of organisms. These holes were plugged by #5 rubber stoppers when not in use. *Theridion* and *Mimetus* carapace width was measured by taking ~5 seconds of video tape of each spider in a dorsal view, then digitizing a single frame and measuring carapace width using Image Pro Plus© software. *Theridion* were placed in behavioral arenas with a single *Drosophila* and allowed 2 days to acclimate to the arena, build a web, and eat the *Drosophila*. *Theridion* generally built webs in one of the upper corners of the arena. After acclimation a Mimetid was introduced to the arena via the access port opposite the web. The arena was then left for 12 hours (from 10 PM until 10 AM). The success or failure of the mimetid was recorded at the end of this period.

Experiment 1. Effect of mimetid site. In order to determine whether local adaptation by mimetus affected their predatory efficiency, *M. notius* from 8 sites in 1996 (mimetids from the ninth site were used in experiment 2, below) were used to determine predatory efficiency againt a common prey. Each *M. notius* was paired with a single *Theridion*; all *Theridion* were collected from a single site. Order of presentation was randomized with respect to *Mimetus* site, and trials were conducted from 9/26/96-11/12/96. A total of 78 *M. notius* were presented with *Theridion* inexperienced with laboratory conditions. In addition , due to difficulty in collecting large numbers of *Theridion* from a single site, another 48 *M. notius* were presented with experienced *Theridion*, who had survived a previous laboratory interaction with *M. notius*.

Experiment 2. Effect of *Theridion* site. In the second experiment, *Theridion* from each of the nine sites were paired with *M. notius* from a single site. Because of the small number of *M. notius* available from any one site, a repeated measures design was used.

Several of the mimetids died during the course of this experiment (conducted from 9/23/96 to 11/6/96), reducing an initial sample size of 30 to a final sample size of only 18. Between experiments mimetids were housed in small *Drosophila* vials, and fed one *Drosophila* two days before each interaction to maintain constant hunger levels. Individual *Mimetus* were presented with *Theridion* of approximately the same size (± 0.5 mm) in each repetition to minimize variation due to size assymmetry. Order of presentation was randomized with respect to *Theridion* site, and each *Theridion* was used only once.

If *Mimetus* have locally adapted to *Theridion*, we would expect to see an effect of Mimetid site in experiment 1. If *Theridion* have locally adapted to *Mimetus*, an effect of *Theridion* site was expected in experiment 2. Coevolution would be implied if significant effects were found in both experiments. If variation is detected in both experiments, then we should be able to relate this variation to the abundance of *Mimetus* in the sites and/or the cautiousness of *Theridion* in the sites. *Mimetus* emerge at a large size (see seasonality and life cycle, above), and I have not observed them ballooning, nor are they commonly found in samples of aerial disperising spiders (Salmon and Horning 1977). *Theridion* also appear to balloon infrequently according to Salmon and Horning (1977), and I have not observed them to do so in this study site. This reduces their ability to migrate between populations, increasing the possibility of local adaptation.

Results and discussion.-- Experiment 1. No effect of *Theridion* experience on *Mimetus* predatory efficiency was detected. Experienced Theridion survived 72.9 % (n=48) of the time, while naïve Theridion survived 73.1% (n=78) of the time (Pearson's $\chi^2 < 0.001$, DF=1, p=0.98, N=126). Results from trials with experienced and naïve

Theridion will be pooled even though power was weak (~0.2). The extremely small effect size naturally leads to a test with low power. *Mimetus* success ranged from 8% to 36% across 8 sites, but no effect was detected(Pearson's χ^2=, DF=7, p=0.77, N=126, power ≅ 0.5). Overall predatory efficiency in these trials was 27%.

Experiment 2. There was also no effect of *Theridion* site (Cochran's Q test, Q=8.5, d.f.=8, p=0.39). Overall predatory efficiency in these trials was 57%. The large difference in predatory efficiency between experiment 1 and experiment 2 suggested that *Mimetus* learned the "game" within the arena after repeated trials. A posterior test of this possibility, using mimetid trial number as a factor, showed no effect of mimetid experience on predatory efficiency in this experiment (Cochran's Q test, Q=9.5, d.f.=8, p=0.30).

Neither of these experiments revealed an effect of local adaptation on mimetid predatory efficiency. Keep in mind, however, that there is, at this point, no underlying mechanism postulated for such effects. A more powerful test would be to look for trends in a dimension relevant to a particular mechanism that predicts the direction of evolution in each species. The model in chapter 2, with appropriate modifications (see Chapter 5) provides a mechanism for predicting the relative cautiousness of prey confronted with differing environments.

Signal sources in *Theridion* webs

Methods.-- In censuses conducted in 1996 and 1997, all potential signal sources in *Theridion* webs were identified, either in the field of the lab. The second set of censuses in 1997 were designed primarily for collection of *Mimetus* and *Theridion* for laboratory experiments, and collection of prey from *Theridion* webs. The 1997 samples were limited to 7 sites because two of the sites sampled yielded no *Theridion* prey in the second census. This is most likely a sampling error due to very low numbers of *Theridion* at these sites. The data for 1997 include only prey collected in the second set of censuses.

Results and discussion.-- Figures 3.5 and 3.6 present the data on occurrence of various signal sources in the webs of *Theridion sp*, the most common prey of *M. notius*. Prey, mates, and invading spiders (*Theridion*, *Argyrodes* or *Grammonota*) were the most consistently abundant signal sources in *Theridion* webs; all other potential signal generators were rare in these samples. These signal sources must thus be considered as the most likely models of *M. notius* aggressive mimicry.

In both years, small Diptera made up a major portion of *Theridion*'s diet, and were an abundant signal source. Diptera were found in the diet at all sites in both years and at all times of the year. In 1997 small Homoptera were also very abundant, but they were absent from the 1996 samples. The difference between years may result from the different prey sampling methods used in the two years (in 1996 only prey currently being fed upon were collected, while in 1997 all prey in the web were collected). Available data suggest, however, that Homoptera are not a consistently important part of

Theridion's diet. Homoptera, even in 1997, did not occur in all of the sites; their high overall abundance was the result of their being extremely abundant in only two sites. One hundred Homoptera were collected in 1997; eighty-seven were found in just two sites, with the remaining thirteen being distributed across four other sites (table 3.2). Because of their more consistent availability dipteran prey are a more likely model for *M. notius* aggressive mimicry than homopteran prey.

The 1996 sample included four sites censused throughout the season, including *Theridion*'s breeding season. Mates appeared as a fairly small percentage of the overall signal sources (table 3.2), but are actually the predominant signal source during the short breeding season. Mates do not show up in the 1997 sample because this was a single sample taken outside of the mating season. Thus, like Homoptera, males are an inconsistent presence in *Theridion* webs and appear to be an unreliable model for *Mimetus* to mimic.

Web invaders, both conspecific and heterospecific, form a large percentage of the potential signal sources in both years. Web invaders occurred at all sites censused. In the seasonal samples taken in 1996, web invaders were found throughout the year, unlike mates or homopteran prey. Web invasion appears to be an important and consistent aspect of *Theridion*'s ecology, and web invaders could potentially serve as a model for *M. notius* mimicry if they elicit approach from *Theridion* as part of their web-defense behavior.

Three different hypotheses exist concerning the identity of the model in this aggressive mimicry system. Two of these are derived from the literature, by analogy with previously studied mimetids. First, Jackson and Whitehouse (1986) suggested that the lure used by mimetids from New Zealand and Queensland (*Mimetus maculosus* and an undetermined species of *Mimetus*) mimicked the signals sent by prey trapped in the web, a conclusion shared by Bristowe (1941) and Gerhardt (1924). secondly, Czajka (1963) described a single incident in which an *Ero furcata* displaced a courting male *Meta segmentata*, then proceeded to lure, kill and eat the female. This suggested to Czajka the hypothesis that *Ero furcata* mimicks the courtship signals of its prey. The third hypothesis postulated here is based upon my observations of *Theridion* webs and interactions between *Mimetus* and *Theridion*. The abundance of invaders of *Theridion* webs, both conspecific and heterospecefic, forces consideration of the possibility that *M. notius* mimics these invaders. Invading spiders may either take over the web (conspecifics, Riechert 1982; Wise 1993: heterospecifics, Toft 1988) or act as kleptoparasites (conspecifics, Jakob 1991: heterospecifics, Cangialosi 1991): in either case, defense will often be advantageous to the resident. Thus, invading spiders can present cues that elicit approach of the resident in the form of active defense. These cues could be mimicked by *M. notius* to lure *Theridion* within range.

Dipteran prey, mates, invading *Theridion*, *Argyrodes* and *Grammonota* represent the most consistently abundant signal sources in prey webs. Determination of which of these five sources actually functions as the biological model in this system will require measurements of the signals each emits and the responses of *Theridion* to each. Comparison of these data with the signals of *M. notius* and the responses of *Theridion* to *M. notius* should then reveal the identity of the biological model (see chapter 4 for these data) of *M. notius* aggressive mimicry.

General Discussion

This documentation of *Mimetus notius* natural history had three major goals. First, to document some basic natural history of this species. Second, to identify the major prey of *M. notius* for which aggressive mimicry might be useful. Third, to identify the important signal producers in that prey's web. This chapter presented the data necessary to achieve each of these goals.

The single most abundant prey susceptible to *M. notius* aggressive mimicry has been identified as *Theridion sp.* In the process of discovering this it was also found that insects form an unexpectedly large part of the diet of *M. notius.* Insects formed a larger portion of the diet than any single spider species (remember though that spiders as a group formed 67.5 % of *M. notius* diet). Since it is unlikely that insects respond to the vibratory lure used by *M. notius*, *Theridion* (32.7 % of spiders eaten) is still considered to be the primary dupe of *M. notius.*

Five major signal sources in *Theridion* webs have been identified. Each of these signal sources is a potential biological model of *M. notius* aggressive mimicry. In addition to the previously suggested possibilities -- mates (Czajka 1968) and prey (Jackson and Whitehouse 1986) -- web invaders have been identified as a major aspect of *Theridion* ecology. In this study there were three important web invaders: *Argyrodes*, *Grammonota*, and non-mate *Theridion*. These results narrow the field of potential candidates for the biological model in this system. The signal properties and response of *Theridion* to each potential model need to be studied in greater detail before a more definitive determination of the biological model can be made.

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Table 3.1. Mimetid encounters – Data summed over all censuses (n=231 encounters)

Prey type	# eaten	# In web	% of all encounters	% of eaten
Araneidae				
Araniella	1	0	0.4	1.3
Cyclosa	1	1	0.9	1.3
Epeira	2	3	2.2	2.6
Eustala	2	4	2.6	2.6
Mangora	0	2	0.9	0.0
Neoscona	2	4	2.6	2.6
Nuctenea	0	3	1.3	0.0
Wixia	0	1	0.4	0.0
Unknown Araneidae	4	2	2.6	5.2
Dictynidae				
Argenna	1	0	0.4	1.3
Dictyna	7	11	7.8	11.0
Liniphiidae				
Frontinella	0	3	1.3	0.0
Pityohyphantes	1	13	6.1	1.3
Salticidae	0	2	0.9	0.0
Tetragnathidae				
Tetragnatha	3	8	4.8	3.9
Theridiidae				
Argyrodes	4	19	10.0	5.2
Grammonota	0	4	1.7	0.0
Mysmena	0	1	0.4	0.0
Steatoda	0	1	0.4	0.0
Theridion	17	65	35.5	22.1
Thomisidae	6	1	3.0	7.8
Uloboridae	0	2	0.9	0.0
Uloborus	0	2	0.9	0.0
Insects	25	3	12.1	32.5
Unidentifiable spiders	1	1	0.9	1.3
Total	77	154		

Table 3.2. *Theridion* prey collected from webs in 7 sites in September of 1997.

Prey Order	# found in webs	Average % of prey/site	# of sites found in as prey
Unidentifiable Insects	107	49.7	7
Homoptera	100	20.2	6
Diptera	54	19.3	7
Hymenoptera	11	5.6	7
Other insects (4 Orders)	6	2.0	3
Aranaea	9	3.2	5
Total prey	287		

Figure 3.1. *Mimetus notius* seasonal abundance across four sites in A) 1995 and B) 1996

Figure 3.1

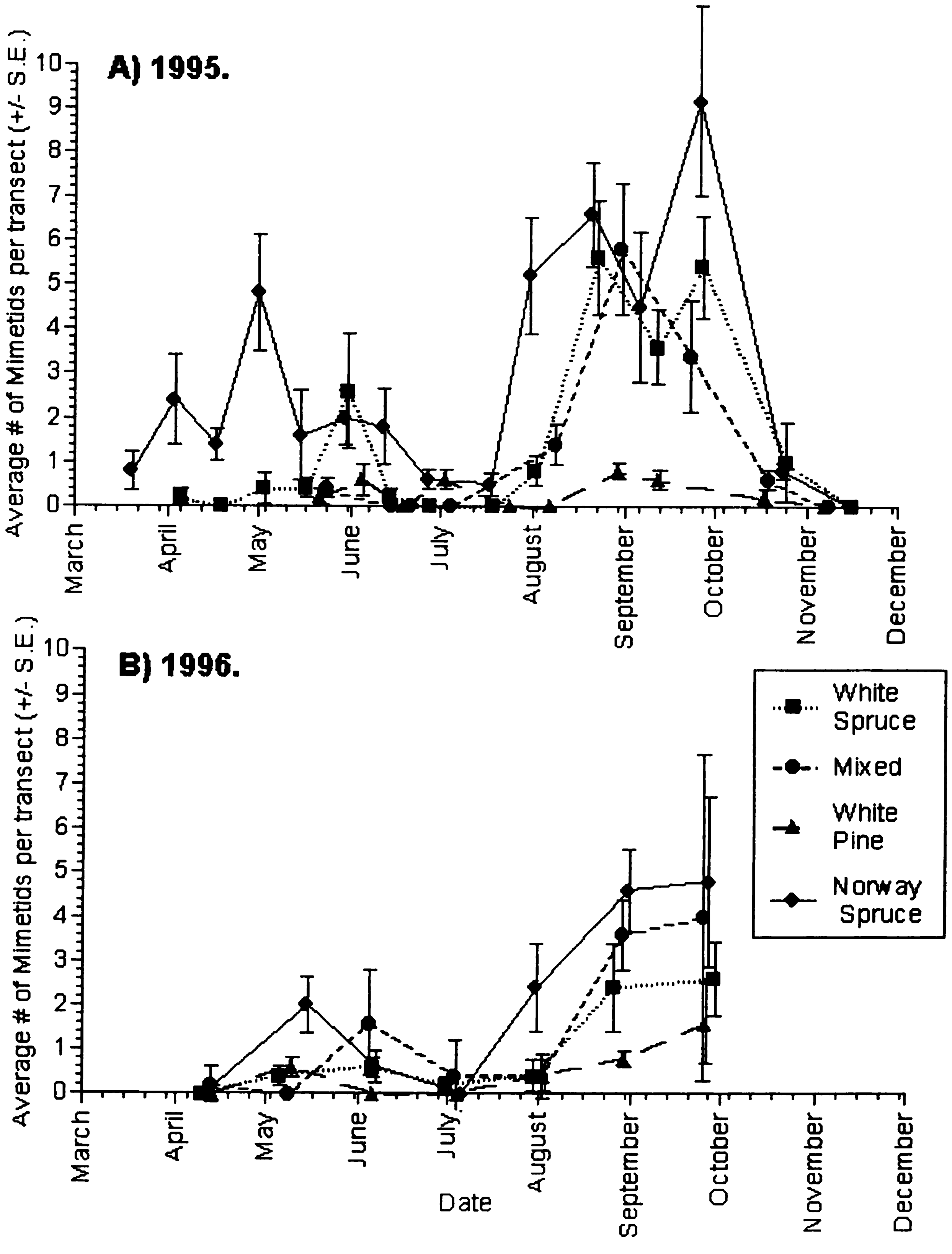

A) 1995.
B) 1996.
Average # of Mimetids per transect (+/- S.E.)
0
1
2
3
4
5
6
7
8
9
10
March
April
May
June
July
August
September
October
November
December
Date
White Spruce
Mixed
White Pine
Norway Spruce

Figure 3.2. Seasonal abundance of all spiders across four sites in A) 1995 and B) 1996.

Figure 3.2

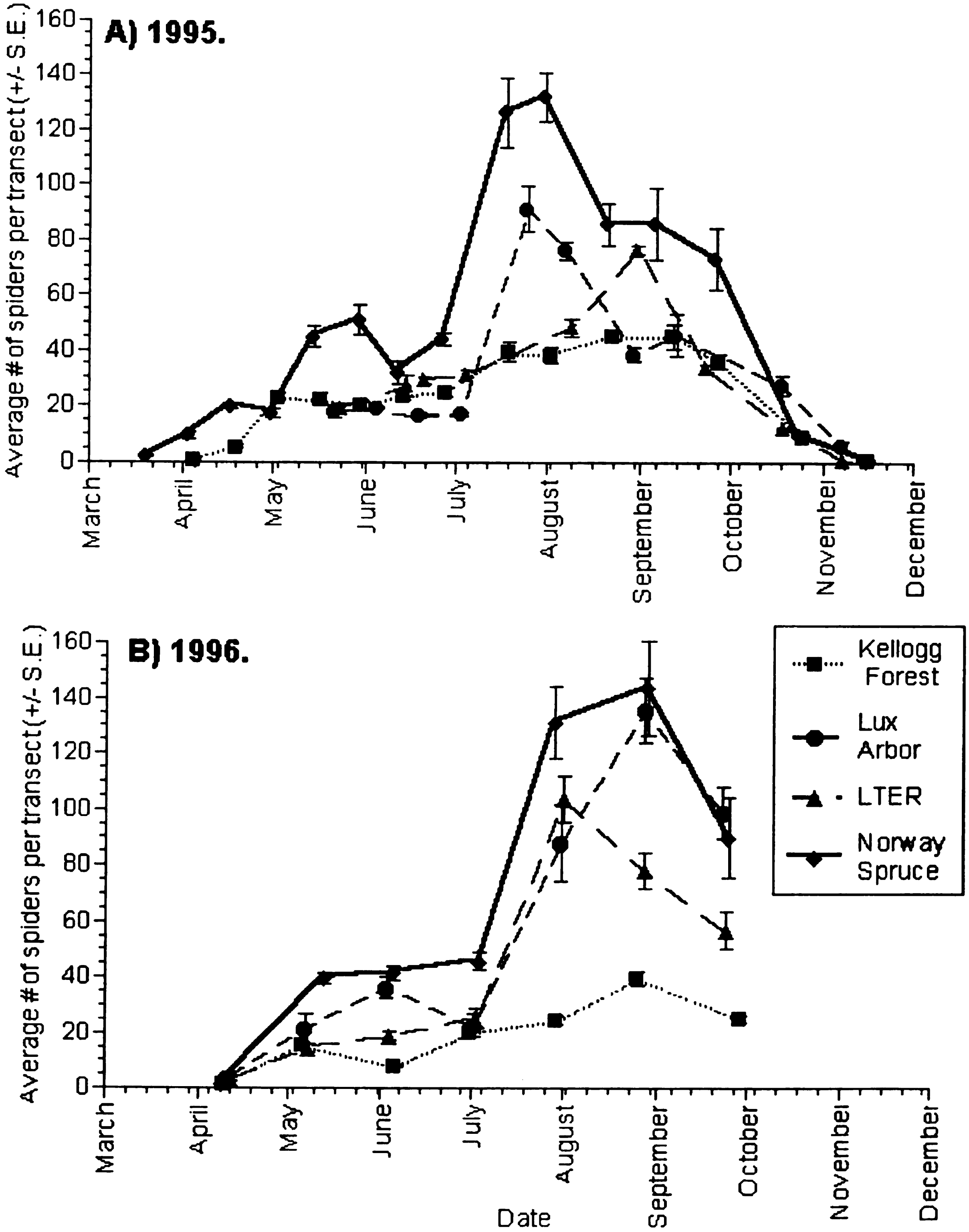

A) 1995.
B) 1996.
Average # of spiders per transect (+/- S.E.)
0
20
40
60
80
100
120
140
160
March
April
May
June
July
August
September
October
November
December
Date
Kellogg Forest
Lux Arbor
LTER
Norway Spruce

Figure 3.3. Seasonal abundance of *Theridion* across four sites in 1995 and 1996.

.Figure 3.3

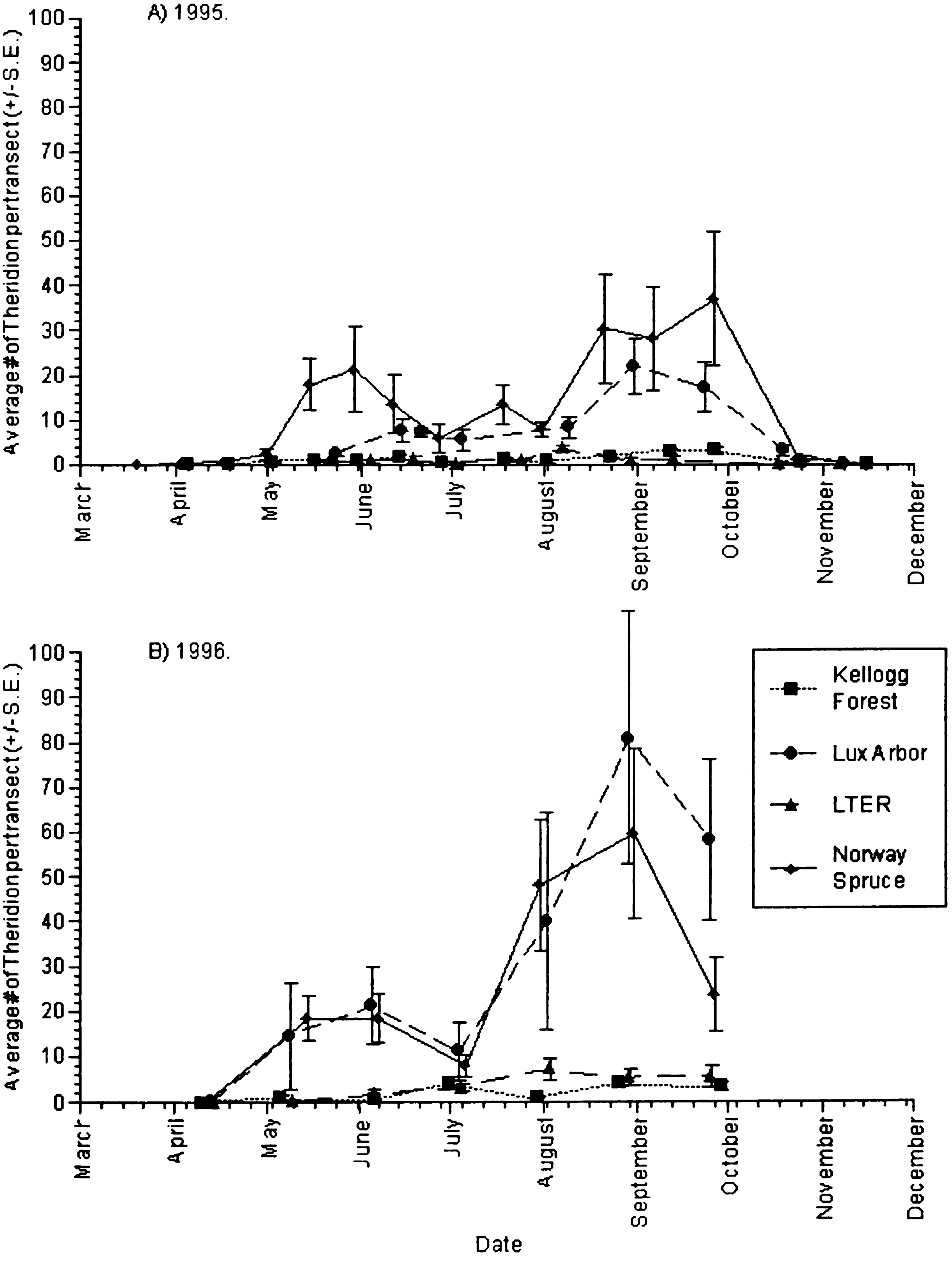

A) 1995.
B) 1996.
Average # of Theridion per transect (+/-S.E.)
0
10
20
30
40
50
60
70
80
90
100
March
April
May
June
July
August
September
October
November
December
Date
Kellogg Forest
Lux Arbor
LTER
Norway Spruce

Figure 3.4. Seasonal representations of adult and juvenile mimetids, summed across all sites for 1995. The total number (n) for each sample is given above the bar.

Figure 3.4

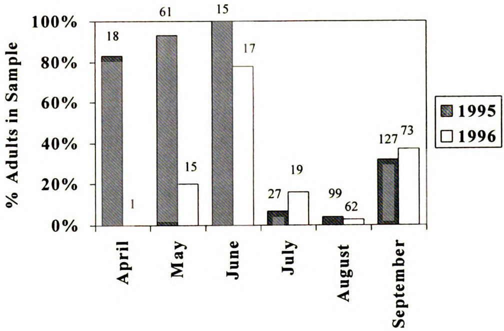
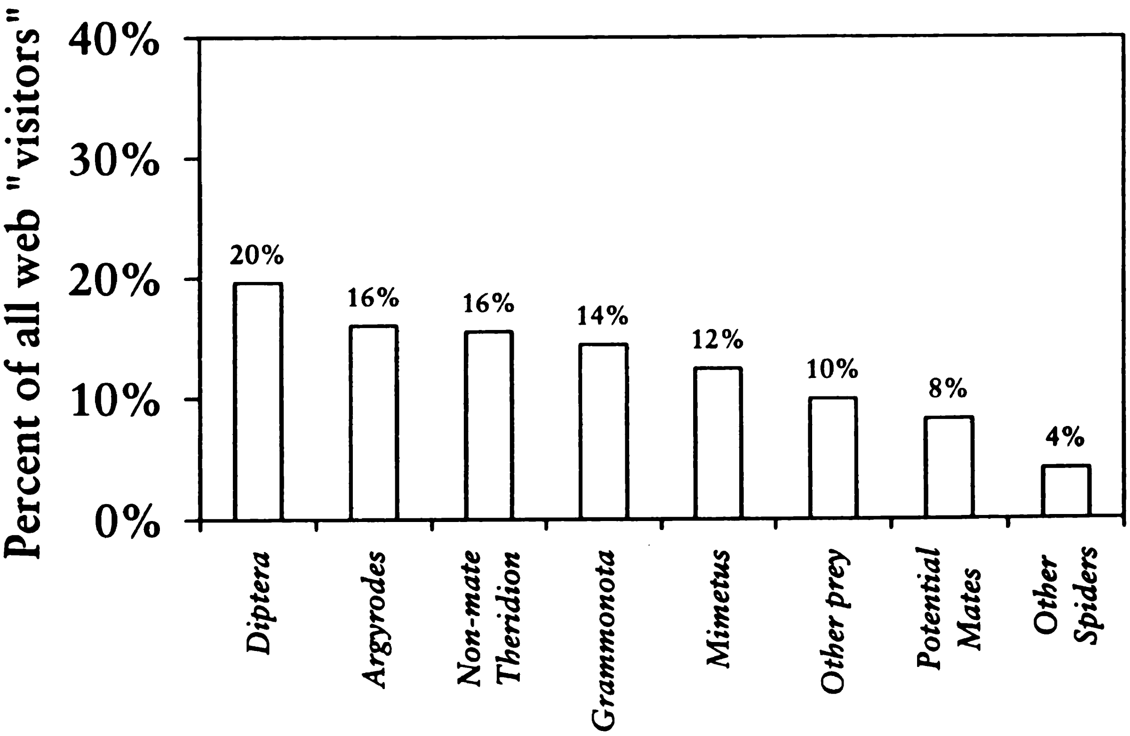

100%
80%
60%
40%
20%
0%
% Adults in Sample
18
1
61
15
15
17
27
19
99
62
127
73
April
May
June
July
August
September
▨ 1995
□ 1996

Figure 3.5. Potential signal sources in *Theridion* webs, 1996, seasonal.

Absolute number and percentage of all signal sources (n=194). Data pooled from 4 sites censused monthly, April-October, 1996. Prey were included only when found actually being fed upon by *Theridion*. Percentages given are of all potential signal sources in 1996.

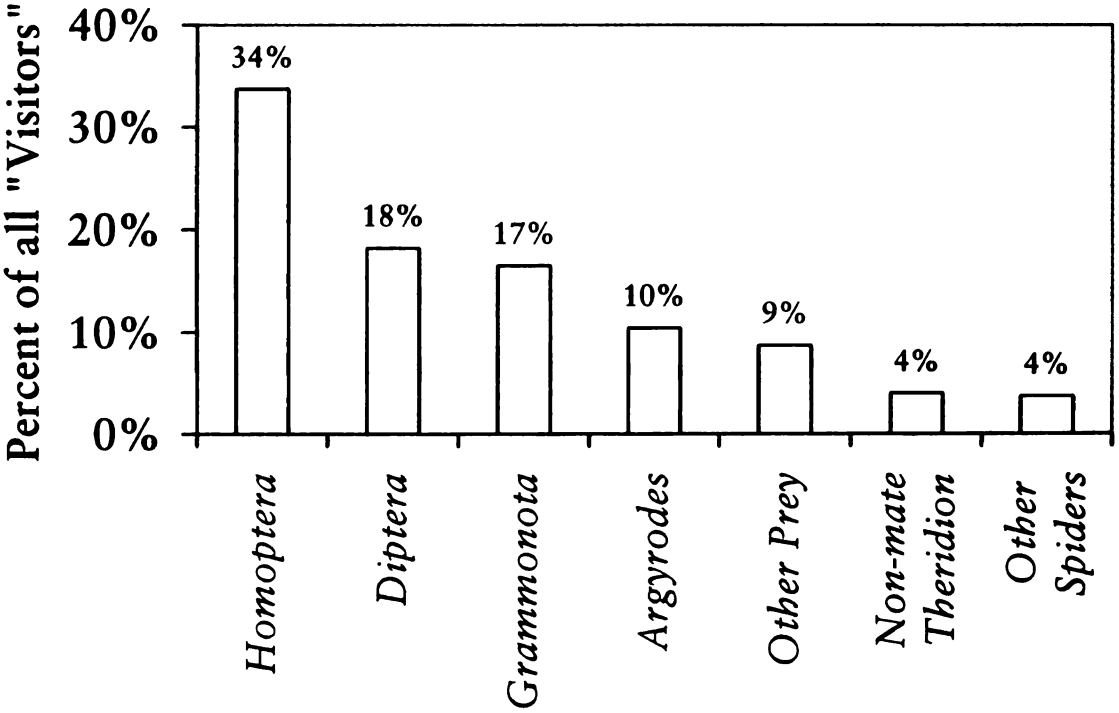
Figure 3.5



Percent of all web "visitors"
40%
30%
20%
10%
0%
20%
16%
16%
14%
12%
10%
8%
4%
Diptera
Argyrodes
Non-mate Theridion
Grammonota
Mimetus
Other prey
Potential Mates
Other Spiders

Figure 3.6. Potential signal sources in *Theridion* webs 1997, aseasonal. Absolute number and percentage of all signal sources (n=297). Data pooled from 7 sites censused once each, September, 1997. All prey in *Theridion* webs were collected during census. Potential mates are not included because these censuses took place outside of the mating season. Percentages given are of all potential signal sources in 1997.

Figure 3.6


Percent of all "Visitors"
40%
30%
20%
10%
0%
34%
18%
17%
10%
9%
4%
4%
Homoptera
Diptera
Grammonota
Argyrodes
Other Prey
Non-mate Theridion
Other Spiders

Chapter 4.

Determining the model(s) in the *Mimetus notius* aggressive mimicry system.

Introduction

Spiders of the family Mimetidae have been hypothesized to mimic the vibrational "signatures" of two different stimuli in order to entice their prey within striking range. An early study suggested that mates may be the model of mimicry by the mimetid *Ero furcata* (Czajka 1968), while Jackson and Whitehouse (1986) suggested that prey were the model for *Australomimetus maculosus* and an undetermined species of *Mimetus* from New Zealand. Determination of the model must be made explicitly by comparing the responses of spiders to mimetids and potential models and by studying the nature of the vibrations each of these organisms cause in the web. Neither Czajka (1968) nor Jackson and Whitehouse (1986) explicitly compared the responses or signals of their mimetids to potential models, but based their conclusions on limited, qualitative observations and inference. Other papers on Mimetids have failed to address this question entirely (Archer 1941; Lawler 1972; Lowrie et al. 1972; Heimer 1986). This chapter focuses on empirical measurement and comparison of signals within the web of a common dupe of *Mimetus notius*, *Theridion* sp., and the responses of *Theridion* to those signals.

Natural history data (chapter three) point to five stimuli that are present in high enough abundance to be considered as potential models for *M. notius* mimicry: chironomid prey, conspecific web invaders, mates, and two species of heterospecific web invaders, *Argyrodes* sp. and *Grammonota* sp. Although the idea of potential competitors acting as a lure has not been raised before in aggressive mimicry, web-invading spiders normally elicit approach for the purpose of active defense; web-invading spiders could thus be a reasonable model for an aggressive mimic attempting to lure *Theridion* within its grasp. Military tacticians use a similar tactic when they send what appears to be a weak force after a stronger force in an attempt to lure them out of a defensive position. The presence of multiple potential models also suggests the possibility that *M. notius* is an abstract mimic, using signals that are general enough to be mistaken for any one of several potential models.

This chapter will present data collected during laboratory-induced interactions between *Theridion* and each of the potential models of *M. notius.* The data from these interactions will be compared to data from interactions between *Theridion* and *M. notius.* These data comprise 2 sets: The responses of *Theridion* to each of the intruders and the properties of vibrations created in the webs of *Theridion* by each intruder. The first data set will be used to determine which potential model causes a response in *Theridion* similar to the response caused by *M. notius*. The second data set will be explored to discover what properties of these signals are most similar to those used by *M. notius*. The results of these analyses will determine the most likely model(s) in this aggressive mimicry system.

Methods

All interactions occurred in small rectangular behavioral arenas. These arenas were 15.2 x 10.2 x 3.3 cm in size, and constructed from unfinished pine with Plexiglas sides. Each arena had two access ports (2.1 m diameter) in the top to allow for introduction of organisms. #5 rubber stoppers plugged these holes when not in use.

All spiders were weighed to the nearest 0.05 mg on a Mettler B6 analytic balance. Carapace width was measured by videotaping them from below along with a metric ruler for scale. These video images were then digitized and measurements made using Image Pro-Plus© software. Carapace width measurements were made to the nearest 0.1 mm. After measurement, *Theridion* were placed into behavioral arenas with a single *Drosophila*. *Theridion* were allowed 2 days to acclimate to the arena, build a web, and eat the *Drosophila*. *Theridion* generally built webs in one of the upper corners of the arena.

After acclimation, the webs were attached to a vibrometer and illuminated by red light. Red light >650 nm was used to illuminate the arenas to avoid disturbing the spiders (Yamashita 1985). Red light production involved filtering white light with a combination of red and blue filters (Lee© High temperature Bright Red #27 and Congo Blue # 181) that effectively eliminated all light <650 nm. A preliminary experiment demonstrated that red light produced in this way had no effect on *M. notius*' predatory success against *Theridion* (50% success in red light vs. 54% in dark conditions, Fisher exact test, p=1.00, n=21, 6 hr trials). A paper grid was placed along the rear of the arena to provide scale for measurements. Two different grids were used: initially a .25 cm grid was used, but later experiments used a 1 cm grid. No differences resulted in the data from this as the grids were used merely as a way of converting distances measured on the screen to actual distances.

The vibrometer used in these experiments was originally developed by Wilcox and Kashinsky (1980) for measuring the water surface vibrations of water striders, but has since been modified for use in spider webs. (Wilcox et al. 1996; Wilcox pers. com.) The vibrometer consisted of a galvanometer with a stylus attached to it. The stylus was then attached to the web – the web adhesive provided firm attachment. When the web vibrated, the stylus also vibrated, causing an induction of current within the galvanometer. This signal was amplified by a World Precision Instruments DAM-50 amplifier © (Settings: Low filter 0.1 Hz, High filter 100Hz, AC Mode, Gain 1000). Following amplification, the signal was frequency modulated by a Vetter Model 1000t recording adaptor so that the signals could be recorded on the audio track of a videotape.

Theridion were allowed to acclimate to the illumination and the presence of a stylus in its web for 30 min. If during that time the *Theridion* abandoned the web or attacked the stylus the interaction was terminated. After the acclimation period an intruder (either a *M. notius*, chironomid, *Theridion* mate, *Theridion* invader, *Grammonota* or *Argyrodes*) was introduced into the arena via the access port opposite the corner of the arena where *Theridion* had built its web. This allowed the intruder to enter the web under its own power. Interactions were video taped with a Canon L2 Hi-8 camcorder set on slow shutter (1/30 second) to accommodate the low light levels. The signal from the vibrometer was simultaneously recorded on the audio track of this tape, providing concurrent records of the spiders' movements and the vibrations of the web caused by those movements.

The main question being addressed was whether there were similar patterns in signal and response. To address this question, signals and responses were analyzed separately for patterns; the subsequent patterns were then compared for similarity. Due to equipment failures and uncooperative subjects there are several cases where responses were recorded but no signals were measured or signals were measured but no response occurred. For this reason the sample sizes of the data sets are not equal.

Response of *Theridion* to each of the stimuli was measured from video taped records of the interaction trials. In each trial, each of the following was measured: type of first response (signaling vs. locomotion), direction of first locomotion (approach intruder vs. retreat from intruder), distance between subjects at first *Theridion* response (cm) and average speed and direction of each locomotion. The qualitative variables were simply coded from the videotapes. Distances were calculated by measuring the distances on the video screen and calibrating to an actual distance using the grid lying along the rear wall of the arena.

Times for movements were measured from the counter on the videotape (to the nearest 1/30 second). Speed was measured for each movement by dividing the distance moved by the time taken to move that distance. Approaches (movement towards the visitor, within a tolerance of 60 degrees to either side of the line connecting the two creatures) were coded as positive values, retreats (the opposite of approaches) as negative values, and movements that were considered neither approaches nor retreats (i.e. movement perpindicular to the line connecting the 2 animals, defined as outside the tolerances for approach or retreat) were not included in the analysis. The average speed per movement was used as a summary variable and was calculated as:

$$\frac{\Sigma \text{ approach speeds} + \Sigma \text{ retreat speeds}}{\text{total number of approaches and retreats}}$$

This formulation allowed this variable to contain information about both the direction and magnitude of movement; *Theridion* that retreat faster or more often than they approach receive a negative value, those that approach more often or more rapidly than they retreat receive a positive value. This also has the advantage that fast movements get weighted heavily compared to slow movements. This is advantageous because these rapid events are generally the most important in terms of capture or escape. It was also thought, *a priori*, that the first response of *Theridion* would be particularly important, so the speed and direction of the first response were collected as a separate variable.

Signals were analyzed by downloading the signal data stored on the videotape into CANARY, a Fourier analysis program (Cornell Bioacoustics Research Program 1994). From this program the frequency of peak power (hereafter referred to simply as peak Hz) of each signal was determined. Signal pulses closer together than 1 sec (measured from the start of one pulse to the start of the next pulse) were considered as part of the same bout and analyzed together. Any break between pulses of greater than one second was considered as part of another bout, and a separate Fourier analysis was run for each bout (see figure 4.1 for a representative signal with definitions). The breakpoint of one second was decided upon by analysis of the interpulse intervals for a subset of the trials. These intervals had a mean of ~0.5 sec and a long tail starting at approximately 1 second, thus 1 second was determined to be a "natural" as well as convenient breakpoint. In addition a "baseline peak Hz" was measured before introduction of the intruder. This baseline measurement gave an indication of the noise-level in the system for each trial and provided a means for standardizing measurements with respect to that noise.

As well as Peak Hz and base line Hz, the frequency range of the signals was measured, as were the time of the bout (bouts as defined above) and the interpulse interval. The interpulse interval was measured simply as the average time between the initiation of one pulse in the bout and the initiation of the next pulse in the bout. The time of the bout was measured from the initiation of the bout until the beginning of the last pulse in the bout – bouts consisting of a single pulse were excluded from this analysis due to the difficulty of judging precisely when a pulse "ended" from the spider's point of view. Other studies have used similar variables to study the timing and frequency characteristics of vibrations emitted by prey (Suter 1978), mates (Bleckmann and Bender 1987; Schmitt, Friedel and Barth 1993; Fernandez-Montraveta and Schmitt 1994), conspecific aggressors (Fernandez-Montraveta and Schmitt 1994) and web residents (Vollrath 1979). All variables were averaged over an entire trial, and each trial average used as a single data point in all analyses.

Results:

Response data: All response data are summarized in table 4.1. The two qualitative variables, first response and direction of first locomotion, reveal similar patterns. For each of these variables, *M. notius* provoked responses from resident

Theridion that were very similar to the responses provoked by invading *Theridion*. Also showing close similarity were responses to potential mates and to *Argyrodes*. Signaling rates in response to *Grammonota* differed marginally from response to *M. notius* ($p<0.1$, Fisher exact test). Direction of first locomotion differed significantly for *Grammonota* ($p<0.001$, Fisher exact test), which *Theridion* never approached first, and marginally for chironomid prey ($p<0.1$, Fisher exact test), which *Theridion* usually approached on their first locomotion. Figure 4.2, a biplot of these variables, shows that considering these variables together reveals that resident *Theridion*'s response to *M. notius* is more similar to their response to invading *Theridion* than to any other stimulus.

The data on distance at first response was non-normal, and transformations failed to normalize it, so a Kruskal-Wallace (K-W) nonparametric analysis of variance was conducted, showing a significant difference existed between *Theridion* responses to intruder types (K-W test statistic= 29.24, $p<0.001$). Responses to each type of invader were compared individually to the responses to *M. notius* using Mann-Whitney U-tests. This analysis revealed significant differences between *Theridion*'s distance at first response when confronted with *M. notius* and *Theridion's* distance at first response in interactions with *Grammonota* ($U=10$, $p=0.00008$) and in the distance at first response when confronted with *Mimetus* vs. when confronted with prey ($U=31$, $p=0.006$). *Theridion* did not respond to *Grammonota* until they were less than 0.5 cm away, and then always retreated. Conversely, they responded to prey at extremely long distances, generally by approaching them. Responses to the other stimuli occurred at intermediate distances. Distance at first response to *M. notius* did not differ ($p>0.1$) from distance at first response to conspecific invaders ($U=93$), mates ($U=48.5$), or *Argyrodes* ($U=66.5$).

Average response speed per movement was also non-normal, so the analysis for this data follows that for distance at first response. Again, the over-all Kruskal-Wallace Analysis of variance yields a significant result (K-W Test statistic=19.616, p=0.001). Analysis of Mann-Whitney U statistics reveals that *Theridion* move much more quickly toward prey than toward *M. notius* (U=14, p=0.001). This procedure also reveals a potential difference between responses to *Mimetus* compared to mates – *Theridion* approach mates slightly more quickly than they approach *Mimetus* (U=63, p=0.083). No significant differences were found in approach speed per movement between *Theridion* confronted with *M. notius* and any of the other spiders (p>0.1; Conspecific invaders, U=64;*Argyrodes*, U= 70; *Grammonota*, U=72).

Speed at first response was highly correlated with average response speed per movement (Pearson correlation coefficient=0.66, p<0.001); it is presented primarily to highlight the rapid first approach of *Theridion* towards prey when compared to first response speeds towards other invaders. This variable was normally distributed, so t-tests were used to compare the difference between *Theridion* responses to *Mimetus* to *Theridion* responses to the other invaders. This analysis shows a significantly faster approach towards prey than toward *Mimetus* (t=3.4, p=0.003), but no other differences (*Argyrodes*, t=0.16; *Grammonota* t=1.3; mates t=0.4; invaders t=0.08; All p-values >0.10).

Viewing the variables distance at first response and average speed per movement in a biplot (figure 4.3) highlights the difference in *Theridion* responses to the various stimuli. Because of the correlation mentioned above, the third variable is not presented as part of this graphic since it would add little, if any, information. Again, a large difference between response to prey compared to spiders are visible, with all of the spiders clustering around *M. notius*' position on the graph.

Signal Data. Signal data are summarized in table 4.2. The main variable from Fourier analysis, peak Hz, was significantly correlated with the size of the resident spider, and despite an attempt at constrained randomization of sizes there were significant differences in resident size between groups (ANOVA, F=7.12, p=0.00002). This was due in large part to the constraint of having to use adult females as residents in mating trials. Juveniles were available for other trials. In addition, peak Hz were also correlated with the base-line Hz, which was also correlated with size. A multiple regression was performed on log(peak Hz) (a log transform was necessary to normalize the data), using size and base line Hz as predictors. This regression was highly significant ($p<0.00001$) and each factor contributed to it (Log(resident weight), p=0.0006; Log(Base peak Hz), p=0.005). The residuals of this regression were used for further analysis to eliminate the effects of these confounds. The residuals were approximately normally distributed, so an analysis of variance was performed using the residuals as the dependent variable and intruder type as a categorical variable. This overall test was not significant (F=1.88, p=0.11). In order to keep the analyses for signal and response data similar, separate t-tests were carried out as in the response data, revealing a significant difference between *Mimetus* signals and prey signals (t=3.1, p=0.007), keeping in mind of course the non-significance of the overall test. None of the other individual t-tests revealed significant differences in this residual value (*Argyrodes*, t=0.008; *Grammonota*, t=0.7; mates, t=0.2; invaders, t=0.6; all p-values >>0.1).

The other signal variables presented fewer difficulties. The frequency range of the signals showed no significant differences between *Mimetus* and any of the other invaders in an overall ANOVA or in individual t-tests. Similarly, the inter-pulse interval revealed no significant differences. Bout length, however, revealed several interesting differences. An overall ANOVA showed a significant effect of invader type (after log transformation; F=4.9, p=0.001). Further investigation of this using individual t-tests (log-transformed) comparing *Mimetus* signals to each of the other signal types revealed significant differences between *Mimetus* signals and signals from prey (t=2.5, p=0.02), and mates (t=2.9, p=0.01). Neither *Argyrodes* (t=2.5, p=0.1), *Grammonota* (t=0.6, p=0.5), nor conspecific invaders (t=1.4, p=0.2), displayed a tendency to differ from mimetids in bout length.

Displaying the two variables that reveal significant differnces together in a biplot (figure 4.4) highlights once again that prey are extremely different from the other stimuli. As in the response data we see a tendency for *M. notius* to positioned in the center of a cluster formed by the other spiders.

Discussion:

Theridion responses to chironomid prey differ from their responses to *Mimetus*. Prey, which have been considered the most likely model in the past (Jackson and Whitehouse 1986), were also the only potential model to display a significant difference from M. notius signals in both residual peak Hz and bout length. Based on both response and signal data, Chironomid prey can be ruled out as potential models in this system. It is still possible that other prey-types are models in this system, but given the importance of chironomids in *Theridion*'s diet (see chapter 3) this is unlikely.

Grammonota can be ruled out as a model, since *Theridion* never approach *Grammonota* and respond to them at much shorter distances than they respond to *Mimetus*. Observation of *Grammonota* behavior while in *Theridion* webs reinforces this conclusion. *Grammonota*, unlike *Mimetus*, conspecifics and *Argyrodes*, tend to spend a relatively short amount of time in their interactions with *Theridion*. They enter the web quickly, usually near the hub, and rarely signal – they charge toward the resident, through the web and then exit, sometimes displacing the resident entirely, but often just causing it to shift to the side as the *Grammonota* goes past. *Grammonota* do not appear to be invaders that take over the web for long periods, and would not make a good model for an aggressive mimic, as evidenced by *Theridion's* first responses to it – they never approach, and retreat from *Grammonota* faster than from any other stimulus in the web (see table 4.1).

Mates provoke only a slightly different response than mimetids in average approach speed. This marginal result is not enough, by itself, to rule out mates as a potential model in the system. Small differences were also seen in bout length between mates and *M. notius*, but again, are not enough in and of themselves to rule out mates as a potential model. The natural history data presented in chapter three show us that mates are only available for a brief part of the year, while invaders (*Theridion*, *Argyrodes,* and *Grammonota*) are abundant throughout the active season. *M. notius* lures *Theridion* throughout the active season, not solely during the breeding season. This information, combined with the small differences in approach speed and bout length, argues strongly against mates being an important model, at least outside of the mating season.

Neither *Argyrodes* nor conspecific invaders can be ruled out as potential models for *M. notius* mimicry by the responses of *Theridion* to them. Responses toward Mimetids, conspecific invaders and *Argyrodes* were very similar, and based on the responses of *Theridion*, neither conspecifics nor *Argyrodes* can be ruled out as potential models. Based on the evidence available it is impossible to determine a single model, but the possibilities have been reduced to two from the original five: the potential models left are invading conspecifics and *Argyrodes*: these potential models fit into the general category of web usurpers. Looking again at the biplots presented in figures 4.1, 4.2 and 4.3, you can see that *M. notius* appears roughly in the center of a cluster of responses/signals caused by other spiders, with prey being away from this cluster. This is especially evident in figure 4.3. This suggests that *M. notius* may be an abstract mimic of a general class of web visitors, namely potential invaders. *M. notius* is a much larger spider than any of the others, and should cause a much different response on the part of residents than these other spiders if they can be detected. By emitting signals in the middle of this "cloud" of invading small spiders it could be hiding its' identify well enough that *Theridion* needs to closely inspect the intruder in order to determine its identity. The possibility of mimicking competitors has not been studied before, so this system offers a unique opportunity.

In the mathematical models and data presented in chapter two, mimicry of mates was predicted to produce concrete mimicry systems, while mimicry of prey was predicted to produce abstract mimicry systems. Mimicry of web usurpers (or, more generally, competitors, be they conspecific or heterospecific) was not addressed at that point. Given that the data here suggest that the most likely model for *M. notius* mimicry may be competitors, and a variety of them at that, a new mathematical model must be devised to represent this situation. If abstract mimicry is favored under these conditions it is not surprising that this portion of the study was unable to clearly identify a single model: multiple models may exist, and may even be expected.

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Table 4.1 Theridion response data.
For non-percentage data, Lower quartile, median, and upper quartile are shown.

	Responses of *Theridion* to:					
Variable	*M. notius*	*Theridion* invaders	Mates	*Grammonota*	*Argyrodes*	Prey
First response (% signaling)	40	45	33	8 **	61	22
First movement (% approaching)	50	43	67	0 **	56	89 *
Distance at first response (cm)	0.7 1.2 4.0	0.8 2.1 6.8	0.9 1.8 7.1	0.1 0.3** 0.4	0.8 4.3 11.4	5.0 9.4 ** 13.9
Average approach speed per movement (cm/sec towards "invader"/ movement)	-0.33 -0.07 0.14	-0.31 -0.20 0.01	0.02 0.14 * 0.20	-0.31 -0.14 -0.09	-0.01 0.06 0.17	0.46 0.78 ** 1.33
Speed of first response (cm/sec towards invader)	-0.33 0.05 0.14	-0.16 -0.02 0.14	-0.10 0.02 0.20	-0.55 -0.27 -0.09	-0.24 0.03 0.24	0.13 0.86 ** 1.54
N	14	14	6	12	7	11

*=p<0.1, **=p<0.05

Table 4.2 Signal data in *Theridion* webs.
[S.D.]

	Value of signals by:					
Variable	*M. notius*	*Theridion* invaders	Mates	*Grammonota*	*Argyrodes*	Prey
Residual Peak Hz	-0.10 [0.2]	-0.38 [0.3]	-0.15 [0.5]	0.08 [0.5]	-0.10 [0.5]	0.26 ** [0.3]
Range (Hz)	6.1 [1.6]	6.2 [2.9]	7.4 [2.5]	6.3 [3.0]	5.4 [1.3]	5.7 [1.7]
Bout length (seconds)	2.1 [1.1]	3.5 [2.4]	3.7 ** [1.1]	1.5 [0.3]	0.9 [0.3]	1.0 ** [0.5]
Interpulse interval (seconds)	0.5 [0.2]	0.4 [0.2]	0.5 [0.2]	0.5 [0.2]	0.4 [0.1]	0.5 [0.3]
N	14	12	7	5	3	11
**=$p<0.05$						

Figure 4.1. A representative signal series from a M. notius in a Theridion web. The recording was made on the audio track of a videotape and decoded using CANARY© (Cornell Bioacoustics Research Program 1994). The upper panel shows a frequency spectrum derived from the signal trace in the lower panel. Important measurements are also shown. A=Frequency of peak power (a.k.a peak Hz); B=interbout (>1 sec between initiation of one pulse and the next); C=interpulse (<1 sec between initiation of one pulse within a bout and the next); D= Bout length (time from the initiation of the first pulse in a bout to the initiation of the last pulse in the bout. In this example the interpulse duration and the bout duration are identical since there are only two pulses in the bout shown.

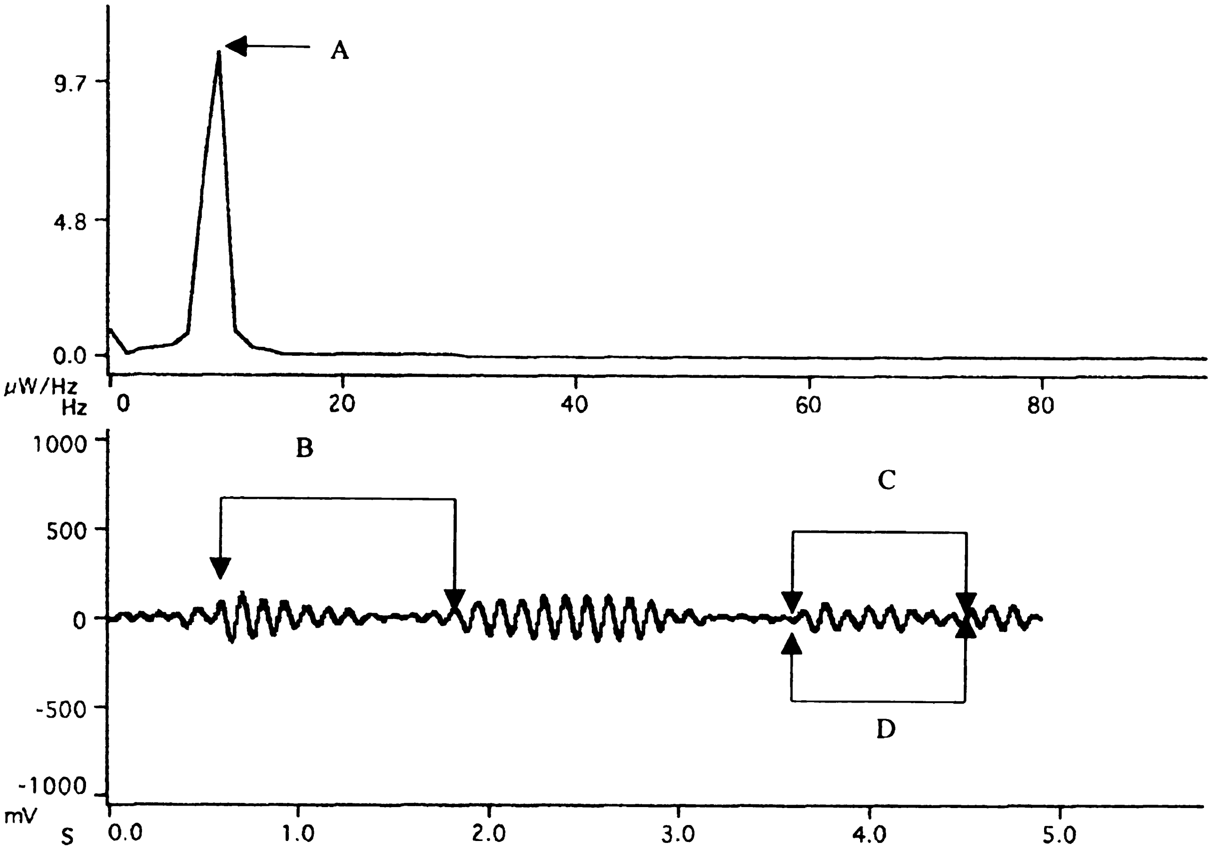

A
9.7
4.8
0.0
μW/Hz
Hz
0
20
40
60
80
B
C
D
1000
500
0
-500
-1000
mV
S
0.0
1.0
2.0
3.0
4.0
5.0

Figure 4.2. Biplot of ratios of qualitative variables involving Theridion response. The x-axis displays the type of first response, either signal or locomotion, in % of Theridion whose first response was to locomote. The y-axis displays the first locomotion, either approach or retreat, in % of theridion whose first locomotion was an approach. Since these are percentages with small sample sizes, nor error bars are shown.

Figure 4.2

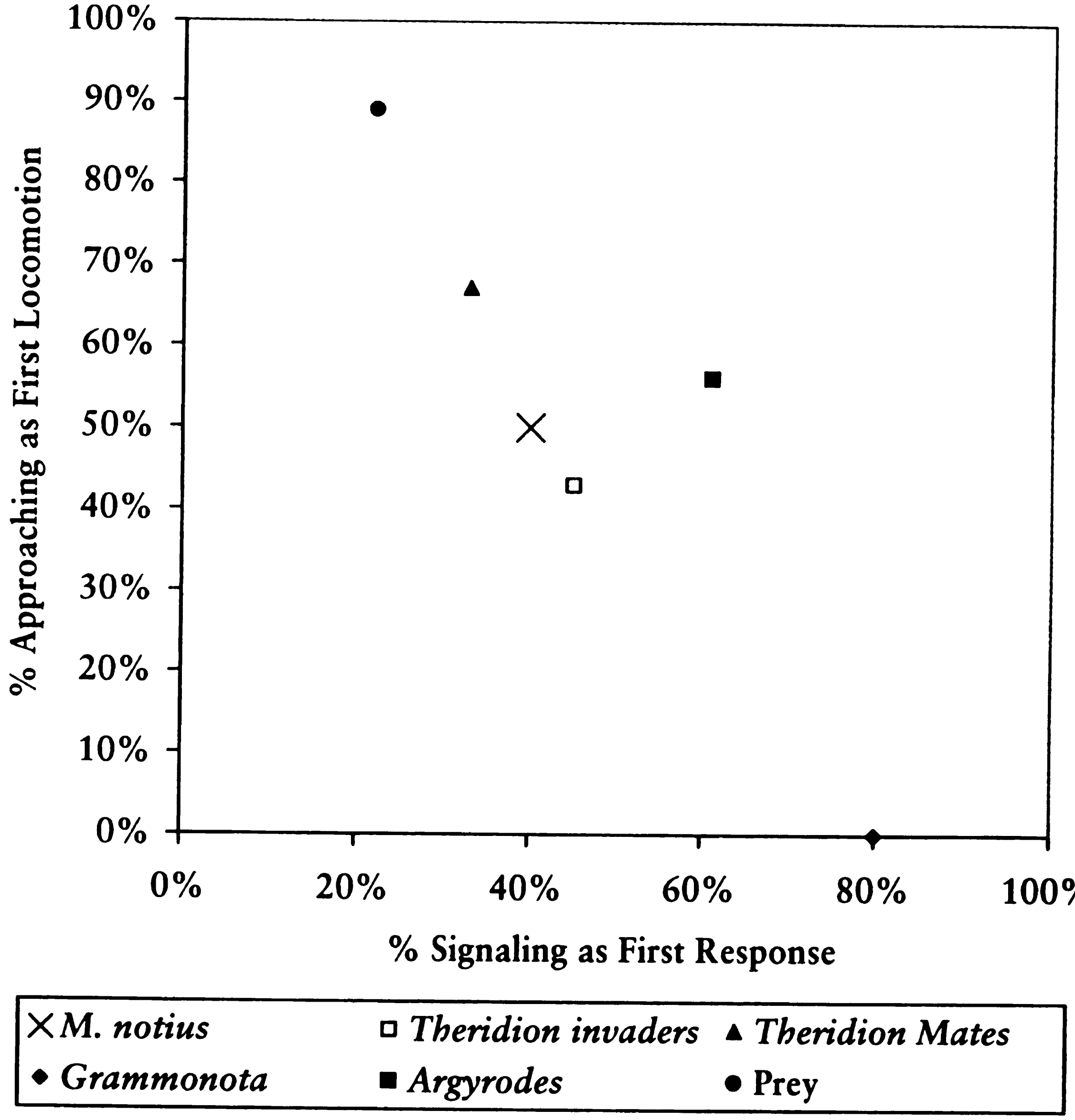
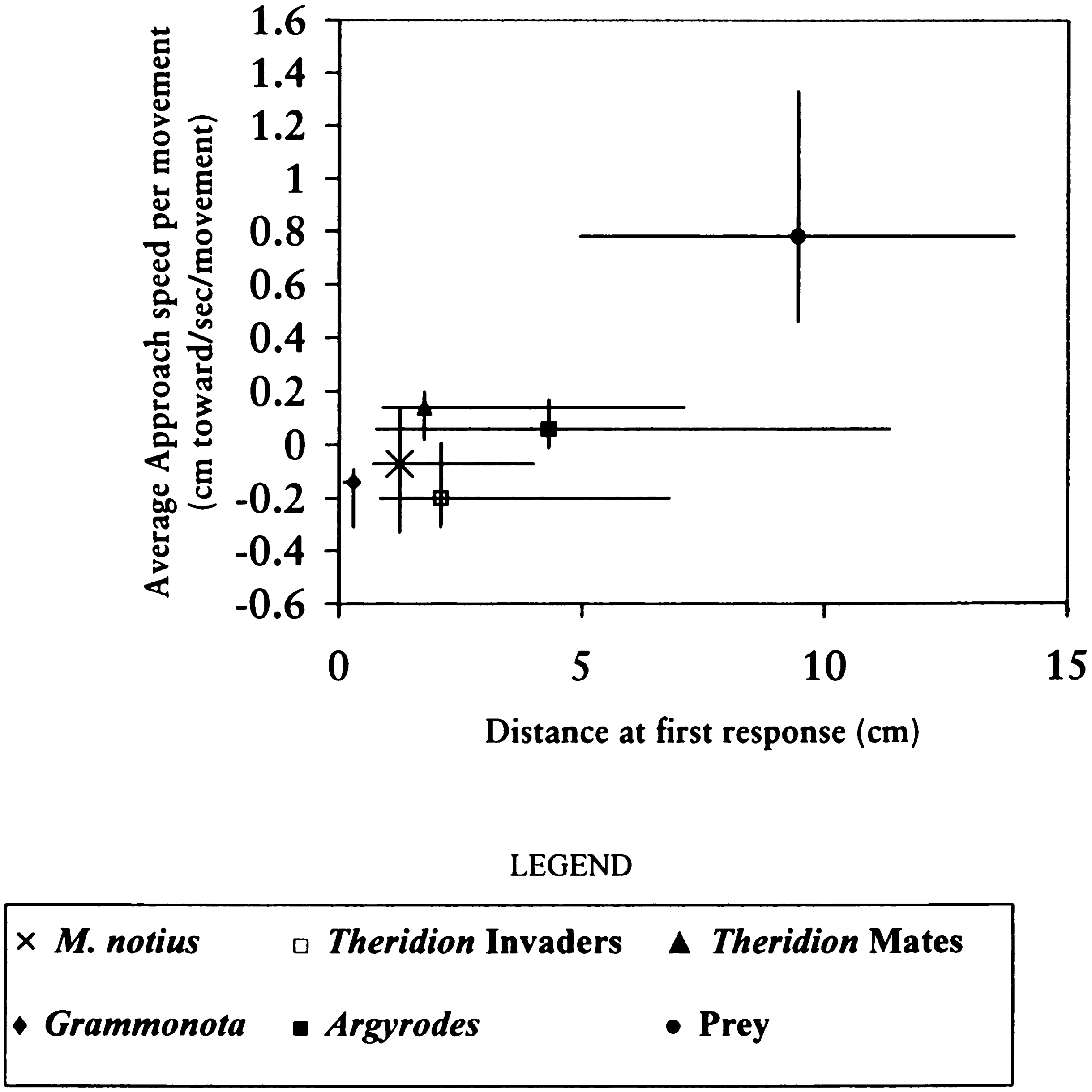

100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
% Approaching as First Locomotion
0%
20%
40%
60%
80%
100%
% Signaling as First Response
× M. notius
□ Theridion invaders
▲ Theridion Mates
◆ Grammonota
■ Argyrodes
● Prey

Figure 4.3. Biplot of the qualitative variables of Theridion response, average approach speed per movement and distance at first approach. Neither of these variables were normally distributed. Therefore the plot displays median values with error bars as 25% and 75% quartiles.

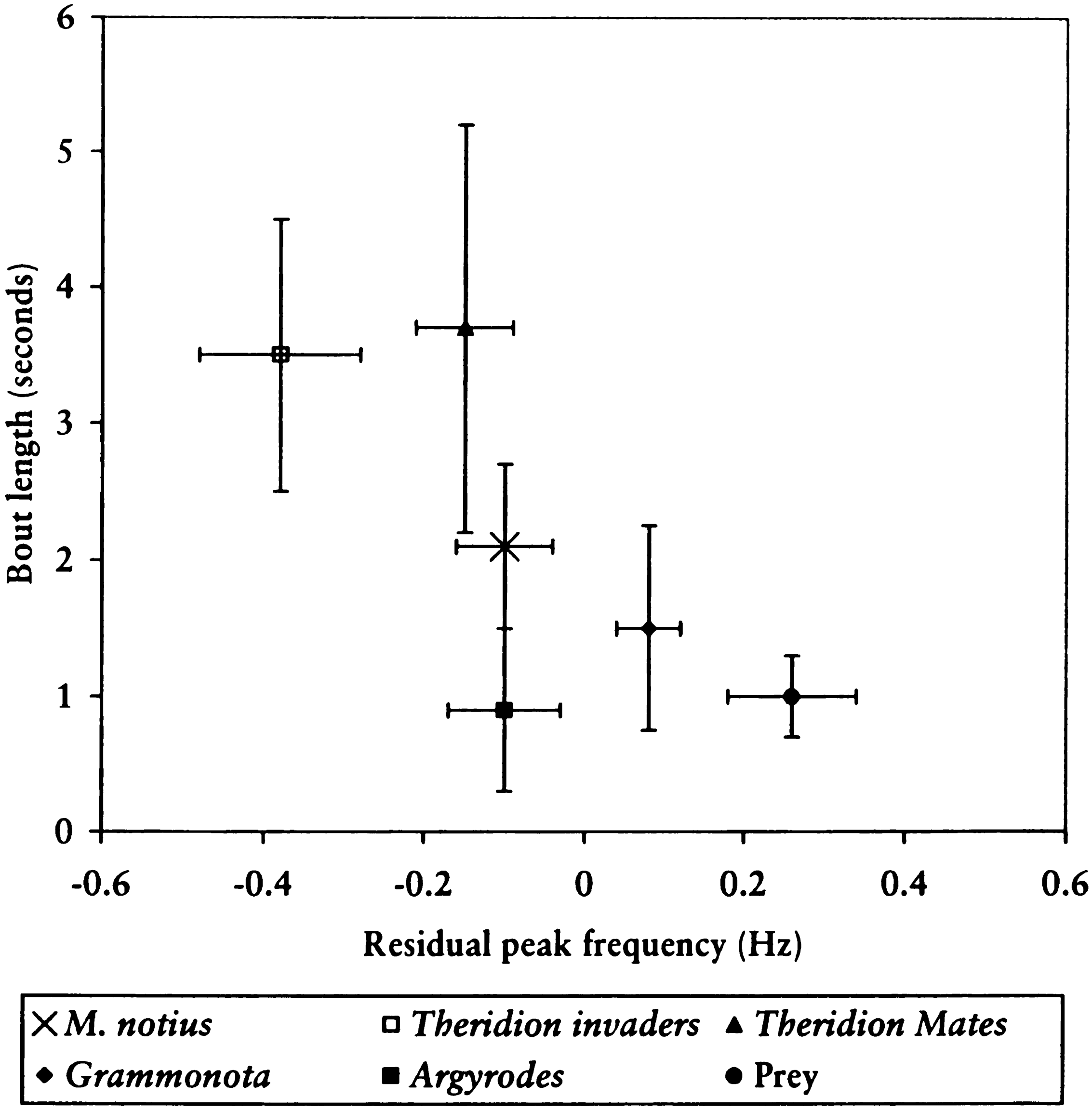
Figure 4.3



Average Approach speed per movement (cm toward/sec/movement)
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
0
5
10
15
Distance at first response (cm)
LEGEND
× *M. notius*
□ *Theridion* Invaders
▲ *Theridion* Mates
♦ *Grammonota*
■ *Argyrodes*
● Prey

Figure 4.4. Biplot of signal variables with significant differences between *M. notius* signals and other web "visitor's signals -- residual peak Hz and bout length. Data are normally distributed. Points represent averages and error bars give standard errors.

Figure 4.4


6
5
4
3
2
1
0
Bout length (seconds)
-0.6
-0.4
-0.2
0
0.2
0.4
0.6
Residual peak frequency (Hz)
× *M. notius*
□ *Theridion invaders*
▲ *Theridion Mates*
◆ *Grammonota*
■ *Argyrodes*
● Prey

Chapter 5:

Foraging under threat from the aggressive mimic *Mimetus notius.*

INTRODUCTION

Chapter two presented a very simple, very general model based on the idea of integrating the perceptual relationships between model, mimic and dupe into the trade-off developed in the formulation of the f/μ criterion (Gilliam 1982, 1990). In the formulation of that model, several assumptions were made in the interest of maintaining generality. Application of the model requires detailed knowledge of a specific system, including important aspects of the natural history and perceptual relationships between the members of the system. In chapter three the necessary natural history for the aggressive mimicry system involving *Mimetus notius* was presented. In chapter four this information was used to discover the identity of the models in this system and show the relationship between the vibratory cues presented by the model and cues provided by the mimic. This chapter will develop a more specific model using the f/μ criterion and signal detection theory in order to more closely approximate this particular aggressive mimicry system.

The model presented in chapter two was based on the idea that most aggressive mimicry systems involve mimicry of the dupe's resources; a common resource mimicked is the dupe's food. A simple extension of this model showed that concrete mimicry is predicted when mates are mimicked and weak mimicry is predicted when prey are mimicked. These predictions were supported by a review of the literature on aggressive mimicry. These two scenarios (mates vs. food as model) provided simple models, but *M. notius* aggressive mimicry violates both of them. From chapter four we have seen that *M. notius* mimics neither prey nor mates; instead *M. notius* appears to mimic invading spiders on the web. The response data presented there were insufficient to resolve whether conspecific web invaders or heterospecific web invaders (*Argyrodes* sp.) were "the" model in the system, but the signal data points to conspecifics as being more likely to serve that function. For simplicity, we will assume that conspecifics are the major force driving *Theridion* behavior and derive a model based on this assumption.

The life history trade-off between feeding and mortality rates still applies, but exactly how web invasions affect feeding rate must be specified for the earlier modeling paradigm to be applied. This chapter returns to the mathematical realm to specify the relationship between feeding rate and web invasions, explore the properties of the new model, and arrive at some general predictions. It will then report the results of an experiment testing some of the simpler predictions of the model.

THE SPECIES-SPECIFIC MODEL

Web invasions negatively affect feeding rate. While a spider is on its web it has some feeding rate, f_w, based on the rate of prey arrival. When a potential usurper invades a web the resident must deal with the challenger. If unsuccessful it is ejected from the web and its feeding rate drops to some low, off-web level, f_o, until it can either build a new web or successfully invade another web. If defense is successful, the resident then maintains its feeding rate at f_w. When a predator (for example *M. notius*) attempts to invade a web, the resident may either defend, with some probability of dying, or abandon its web, resulting in a feeding rate of f_0.

Using this information, a new model can be built to calculate the overall feeding rate of Theridion given encounter rates with the various invaders, probabilities of winning and losing the various encounters, and time to inhabit a new web. This model is developed in detail in appendix 5.1. The final form of the model is presented below as Equation 5.1.

$$\frac{f_{ave}}{\mu} = \frac{f_w}{[1+E_i \cdot T_n \cdot (1-H \cdot W)+E_m \cdot T_n \cdot (1-F \cdot K)] \cdot [E_m \cdot F \cdot K+m]} \quad \text{Equation 5.1}$$

An analytical solution to equation 5.1 has not been discovered. Numerical simulations will be utilized to determine what effect each variable has on the optimal feeding rate and to determine the optimal cautiousness $(H/F)^*$ given the constraint in the relationship between H and F defined by the overlap in signal distributions of *Mimetus* and invaders. These numerical simulations can help us to increase our understanding of predator-prey dynamics involving perception in this aggressive mimicry system.

PARAMETER ESTIMATES

In order to perform useful simulations, realistic estimates of the model's parameters must be available. Data on signal similarity (presented in chapter four) provide a means of estimating the relationship between H and F for this mimicry system. The distributions of the bout length of signals emitted by *M. notius* and *Theridion* invaders provide the probability density functions (PDF's) that will be used throughout the simulations presented here (figure 5.1). These PDF's in turn determine the shape of the ROC curve (figure 5.2; see chapter 2 for a detailed explanation of PDF's, ROC curves and signal detection).

The data presented in chapter three will be used to estimate most of the remaining parameters in this model. The 1997 data will be used to test the model (below), so these data will not be used to estimate parameters here. In 1995, not all parameters were measured, so to maintain consistency all parameters will be estimated using 1996 data (pooled across all sites). Experience in the lab has shown that it generally takes *Theridion* 1-2 nights to build a functional web. We will adopt the value of 1 night as a standard value for T_n.

Parameter estimates are presented in table 5.1. The estimate for feeding rate is extremely low. This is due to the conservative rule used for identifying prey in 1996. In 1996 only items actually being fed upon were included as prey (see chapter three). The estimates in table 5.1 are intended to provide a reasonable range for simulations. While deviations from these values have quantitative effects, they do not affect the more general qualitative results.

SIMULATIONS

All simulations were accomplished using Matlab©. See appendix 5.2 for a representative Matlab simulation program. Simulations investigating the effects of model parameters were conducted using the relationship between H and F described by the ROC curve in figure 5.2. The optimal cautiousness, $(H/F)^*$, was determined by finding the maximum of f_{ave}/μ for each value of the parameter of interest and then dividing the H value corresponding to the maximal f_{total}/μ by its paired F value. Each parameter was systematically varied with all other parameters held constant, and $(H/F)^*$ calculated for each value.

Two additional simulations study the effect of variation in the relationship between F and H. $(H/F)^*$ is not a valid indicator of relative cautiousness when the relationship between H and F (the ROC curve) is allowed to vary – accordingly we will look directly at H and F in these simulations. In the first simulation the distance between the means of the distributions was varied. In the second simulation the standard deviation of the distributions was varied.

SIMULATION RESULTS

The results of the first set of simulations were straightforward. Feeding rate in the web , f_w, had no effect on (H/F)* (figure 5.3), which makes the assumption of web homogeneity (#4 above) and the problem of underestimation of f_w inconsequential. As the encounter rate with mimics (E_m, figure 5.4) or the probability of dying (K, figure 5.5) increase, cautiousness increases until F=0 (i.e. where $H/F=\infty$). The remaining parameters [probability of successfully defending the web (W, figure 5.6), background mortality rate (m, figure 5.7), encounter rate with conspecific invaders (Ei, figure 5.8) and time to find a new web (Tn, figure 5.9)] all have negative relationships with H/F.

The simulation in which the difference between the distributions was varied (figure 5.10) shows behavior similar to that exhibited by the simple model of prey-mimics presented in chapter two, as does the simulation involving changes in standard deviation (not shown). From this it is not surprising that the identification of a biological model in the system (chapter four) was difficult, since the shape of this curve indicates that abstract mimicry is likely in this system (see chapter two).

EXPERIMENTAL TEST

Methods

Parameters used. In developing the model above, seven parameters were identified as being potentially important to *Theridion*'s decision making process. One of these parameters, the feeding rate on the web, was determined to have no impact on *Theridion*'s optimal behavior. Four more parameters are difficult to measure on a site-by-site basis and are, in any case, unlikely to vary from site to site. The time to acquire a new web (T_n) is unlikely to vary consistently across sites. T_n will be estimated by the time it takes a spider to build a new web in the lab – approximately one night. The size difference between *Theridion* and *Mimetus* is such that *Theridion* have no reasonable defense against a mimetid that has attacked. Thus, the probability of being killed once responding to a mimetid (D) should not vary significantly between sites. The probability of maintaining web ownership given an invasion (S) relies primarily on relative size (Reichert 1982). In any given habitat the average spider's *a priori* probability of being bigger than an opponent is ~ 0.5, assuming that no size bias in invasion behavior exists. Variance across sites should be negligible, even though average size may vary across sites. Background mortality (m) in these sites appears to be driven primarily by abiotic factors and chance encounters with wide-ranging predators (birds, parisitoid wasps etc.). As long as all the sites are in a similar geographic area, it is reasonable to assume that these effects will be similar from site to site. Each of these assumptions is reasonable, and making them significantly increases the ease with which the model may be tested. These five parameters will be treated as constant across sites from this point on.

Encounter rates depend upon the abundance of the two types of spiders in the field. Earlier observations indicated that abundance of both *Mimetus* and *Theridion* varied across sites (chapter 3), though encounter rates were too low to allow specific comparison. Measurement of encounter rates across a number of sites will provide the variance in these parameters necessary to test this model.

Field Measurements. A series of two censuses in each of seven sites was conducted in 1997 (see chapter three for extensive details of censusing procedures). These censuses were conducted during August and September, the period previously identified as the peak abundance for *M. notius* (chapter three). The timing was chosen in an effort to maximize the number of *M. notius* available for study. Each census was conducted as a five-hour (10PM-3AM) visual census. The first census in each site was conducted with no collection of individuals. In the second census, all individuals of *M. notius*, *Theridion* and all prey in *Theridion* webs were collected (see chapter three for data from these collections). During censuses the identity of all spiders encountered (to genus), status (on or off of web) and presence and identity of all invaders on *Theridion* webs was recorded.

The second censuses were conducted as paired trials to aid in correcting for seasonal fluctuations. Data from the first set of censuses were used to pair sites; the three sites with the highest model:mimic ratio (*Theridion* abundance:*Mimetus* abundance) were paired sequentially with the three sites with lowest model:mimic ratio (i.e. the highest site was paired with the 4th highest, 2nd with 5th, 3rd with 6th). The seventh site was paired with *Mimetus* from a population where *Theridion* were observed to become locally extinct. The presence of an unpaired site allowed for independent tests of measures of risk of *Theridion* behavior.

Laboratory.-- *Theridion* and *M. notius* from each site were brought into the lab to test the response of *Theridion* to conspecific invaders and to *M. notius*. Interactions were carried out in small behavioral arenas (as in chapter four). The arenas were 15.2x10.2x3.3 cm in size, constructed of pine with plexiglas sides. Each arena had two access ports in the top for introduction of invaders; #5 rubber stoppers plugged these ports except during introductions of animals into the arenas.

All measurements on spiders were carried out within twenty-four hours of capture. All spiders were weighed to the nearest 0.05 mg with a Mettler B6 analytical balance. Carapace width was measured by video-taping the spiders from below with a metric ruler at the same distance from the lens for scale. Video-taped images were later digitized and magnified using Image Pro Plus© software, which was also used to calibrate each image and measure carapace width. After measurement, resident *Theridion* were each introduced to a separate arena and given a single *Drosophila*. Non-resident *Theridion* and Mimetids were maintained in *Drosophila* vials and were unfed. Resident

Theridion were allowed two nights to acclimate to the arena and build webs before interactions began.

Interactions were conducted between spiders from the paired sites, as outlined in the field section above. The site where *Theridion* were predicted to have higher $(H/F)^*$ was termed the "cautious" site and the site with lower predicted $(H/F)^*$ termed the "incautious" site. Censuses for a pair of sites were conducted on subsequent nights, so that a total of twenty-nine hours elapsed between the start of the first census and the end of the second census. Spiders collected in each census were measured within twenty-four hours of the census, but resident spiders from both sites were introduced to arenas simultaneously, and from the point of introduction on all spiders were treated identically. Collection order (expected cautious vs. expected incautious) alternated between seasonal blocks. This paired design was adopted so that experiment date ("season") could be treated as a blocking factor in subsequent analyses.

Resident *Theridion* were subjected to one of three web invaders: *Mimetus* from the same site, *Mimetus* from the paired site, and conspecifics from the same site: sizes were assigned randomly. All trials from the paired sites were conducted in a single night. Introductions were started under white light at 10:00 PM. Lights were turned off as soon as all arenas held invaders, and all observations were conducted under red light, which spiders cannot detect (Yamashita 1985). Each arena had a numbered 1cm x 1 cm paper grid attached to the back (outside the plexiglas). At 20 minute intervals each arena was observed and the grid number of each spider recorded – this allowed for calculations of distances to within ~ 1 cm and provided a means of measuring the movement of spiders from one interval to the next. All instances of predation were recorded during the first interval in which *Mimetus* was observed feeding on *Theridion* (no instances of cannibalism occurred).

Observations of *Theridion* behavior during earlier experiments (see chapter 4) led to the construction of the following "Risk Index": the distance of *Theridion* approach (retreats scored as negative values) divided by the separation between the spiders +1 (to avoid dividing by zero). This index was adopted because neither measure alone was an accurate indicator of risk. The distance of *Theridion* approach is only important in light of the separation distance – an approach of 5 cm does not increase the risk of a *Theridion* 20 cm from the mimetid, but the same approach distance by a *Theridion* 6 cm away puts it within *Mimetus* striking distance. Similarly, even a separation of less than 1 cm appears to be safe as long as *Theridion* do not approach the mimetid. *Mimetus* have never been observed to successfully attack stationary or retreating *Theridion*. The combination of proximity and approach are necessary for successful mimetid predation. The risk index was calculated over every interval in which *Theridion* remained alive, and averaged over the entire experiment to yield an average "risk". The risk index and the actual predation on *Theridion* from the unpaired site can be compared to test whether or not this index provides a reasonable analog of risk.

The model predictions that risk indices should be higher in incautious sites than in cautious sites for interactions between *Theridion* and *Mimetus* as well as interactions between *Theridion* and *Theridion* invaders (i.e. non-mates).

Results

Field data: If cautiousness has an effect on the feeding rate of *Theridion*, we would expect *Theridion* from incautious sites to have higher feeding rates, since they are less likely to abandon their webs, and thus be in better condition than *Theridion* from cautious sites. To test this possibility a residual condition index (Jakob et al. 1996) was calculated for each spider collected. This index is derived by regressing spider weight on carapace width, then using the value of the residuals as the condition index. A positive value indicates better than average condition, while a negative value indicates worse than average condition. The regression of log(weight) on carapace width is significant (1.52*Carapace width-1.30, $p<.001$), but with a large amount of scatter ($r^2=0.16$). An ANOVA of the resultant condition index by interaction date and predicted cautiousness of the spider's home site (Cautious Vs Incautious) shows a significant interaction between interaction date and predicted cautiousness ($p=0.031$; figure 5.11). The presence of this interaction makes interpretation of the other factors problematical, so within-block tests were conducted to further explore the relationship between cautiousness and condition. These tests reveal that the middle block accounted for the significance of the overall ANOVA. *Theridion* from the incautious site in this block were in significantly better condition than *Theridion* from the cautious site ((Incautious site mean index =0.094, cautious site mean index= -0.303; pooled variance t-test, one-tailed $p=0.0005$, other blocks $p>0.5$, figure 5.11). This block possessed the largest difference between predicted cautiousness (differences in predicted cautiousness (Cautious-incautious): Early block=40.1-35.7=4.4; Middle block=infinity-17.7; Late block=27.7-20.8=6.9), and differed in the fashion predicted: the cautious site possessed a significantly lower condition index. It is encouraging that the only pair exhibiting a significant difference was also the pair with the largest expected difference.

Similar arguments lead to the prediction that *Mimetus* from cautious *Theridion* sites would possess a lower condition index as a result of reduced feeding rate. An ANOVA of *Mimetus* condition by interaction date and predicted cautiousness revealed no significant differences.

Laboratory data: The mean "risk index" is an accurate indicator of the degree of risk *Theridion* places itself in by its behavior. A log transform (log(Index+1))is necessary to normalize the index. Using only the data from the unpaired site to avoid conflicts with later analyses, a separate variance t-test on the transformed data shows that risk index accurately reflects the risk of mortality (figure 5.12).

No evidence of co-evolution was present in the paired sites. A full factor ANOVA on the transformed risk index using *Theridion* site, *Mimetus* site and season as factors revealed only a significant effect of season (figure 5.13; table 5.1). Removal of season as a factor does not produce any p-value <0.05, but a marginal effect of *Theridion* site (p=0.058) becomes apparent. Because no effect of *Mimetus* site exists and there are no significant interaction effects, all remaining analyses will ignore *Mimetus* site and focus on *Theridion* site as the primary factor of interest. This has the effect of pooling the cross-site interactions into the *Theridion* site in all remaining analyses.

The model accurately predicted the relative risk index in *Mimetus* trials for each season in the paired laboratory interaction experiments. Within each block, the site predicted to be cautious showed a lower risk index than the site predicted to be incautious (figure 5.14). An ANOVA of the log-transformed risk index (table 5.2) demonstrates that *Theridion* from populations expected to have high cautiousness exhibit significantly lower risk indices than do *Theridion* from populations predicted to be less cautious.

The model did not perform as well with respect to *Theridion* trials. In *Theridion* trials risk indices were still higher in incautious sites than in cautious sites, but not significantly so (Figure 5.15; tested using ANOVA similar to above; no significant differences existed). The lack of significance in these tests may be attributable to the low power of these tests caused by the small sample sizes.

DISCUSSION

The model developed here predicts logical and intuitive changes in cautiousness in response to changes in environmental conditions. As parameters positively correlated with mimetid-associated mortality (E_m, K) increase, *Theridion* should behave more cautiously. Conversely, as the value of possessing the web increases, cautiousness should decrease, resulting in increased web defense and thus more time on the web. When it takes a long time to build a new web (T_n is high) the current value of the web is high because of the long expected time without feeding following web loss. When background mortality (m) is high, web ownership becomes relatively more valuable because rapid resource acquisition (i.e. before death from some other source) is critical for maximizing fitness. When the probability of maintaining a web is high, defense is more beneficial. The probability of maintaining a web is a function of the encounter rate

with conspecifics (E_i) and the probability of winning given defense (W), so it makes sense for cautiousness to decrease with increases in these parameters. None of these results are particularly surprising, and they give confidence that the model captures important aspects of the *Theridion* behavior.

The model's ability to accurately predict qualitative differences between sites (i.e. accurately predicted high vs. low sites) demonstrates that it captures important aspects of the behavior of foragers targeted by aggressive mimics. Further refinement of the model could lead to accurate quantitative predictions as well, but more important than qualitative prediction is the increase in our understanding of the selective pressures in these systems. Further elaboration of the model to non-mimetic systems (for example, cryptic predators) could potentially lead to new insights about how perception and appearance evolve in many predator-prey interactions.

The model developed here predicts the same counter-intuitive increase in risk with increasing discrimination, at least over a small region of similarity, that the simple prey-based mimicry system in chapter two predicted (figure 5.10), indicating that abstract mimicry is a likely possibility in this system. Observations on *Theridion* responses to invaders (*Mimetus*, *Argyrodes* and conspecifics; chapter four) are consistent with the hypothesis of reduced selection for mimicry of a single concrete model. The existence of this risk increase is a potentially important discovery made by this approach. Further testing will be necessary to validate the model in this respect, but the presence of the "hump" in the curve and its absence in some modeled situations (i.e. mate-based mimicry), combined with the correlated natural patterns detected (see chapter two) provides a new means of attacking the general problem of aggressive mimicry.

The prediction that under some circumstances foragers should increase their mortality risk resembles Wiley's (1994) concept of adaptive gullibility – that is, selection favoring a failure to penetrate a deception. Wiley showed that susceptibility to deception can actually be an optimal strategy if: encounter rates with deceivers are low; the costs of being deceived are low; or deception is nearly undetectable. In the current situation we see some similar results. As encounter rates with mimics decrease, cautiousness decreases, and as the probability of dying decreases (i.e. potential cost decreases), cautiousness decreases. When the deception is nearly undetectable (i.e. discriminability approaches zero), this system tends away from adaptive gullibility – that is, susceptibility to deception decreases. This difference between Wiley's formulation and this one is most by the ability of the spiders in this model to maintain a reasonable feeding rate even when they abandon their web at every encounter (i.e. H=F=0). In the mate-mimicking situation presented in chapter 2, there were no available alternatives, and the situation more closely resembled Wiley's – as discriminability approaches zero, response to mimics approaches one.

The current experiment tested some of the simpler predictions of the model. The more complex predictions, such as the hump-shaped relationship between errors and discriminability seen in figure 5.10, must await experiments where the level of overlap between distributions can be more tightly controlled and varied over a wider range than these populations made available. For example, selection experiments where the experimenter controls the distributions of signals and selects “prey” based on responses to these signals could be used to test for the presence of such a response in evolutionary time. Such a test, while outside the scope of the present work, will provide a stronger test of this modeling paradigm. The ability of the model to make reasonably accurate predictions under field conditions strongly argues that such an experiment should be a priority of future research attempting to develop our understanding of this under-studied phenomenon.

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Table 5.1. ANOVA results for test of local adaptation

SOURCE (main variable is risk index)	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Season	0.667	2	0.334	4.006	0.025
Theridion site	0.248	1	0.248	2.973	0.092
Mimetus site	0.021	1	0.021	0.251	0.619
Season**Theridion* site	0.009	2	0.004	0.053	0.948
Season**Mimetus* site	0.013	2	0.007	0.080	0.923
Theridion site**Mimetus* site	0.013	1	0.013	0.151	0.700
Season**Theridion* site **Mimetus* site	0.370	2	0.185	2.219	0.121
ERROR	3.582	43	0.083		

Table 5.2. Test of Model: predicted cautiousness predicts observed risk index Vs *Mimetus*.

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
Season	0.570	2	0.285	3.501	0.038
Predicted cautiousness	0.354	1	0.354	4.356	0.021*
Season*predicted cautiousness	0.011	2	0.005	0.065	0.937
ERROR	3.986	49	0.081		
*1-tailed p-value.					

Figure 5.1. Distributions of bout length measurements for *Theridion* (solid line) and *Mimetus* (dashed line). The mean *Theridion* value was 3.6 seconds, the mean *Mimetus* value was 2.1 seconds. The pooled standard deviation was 1.7.

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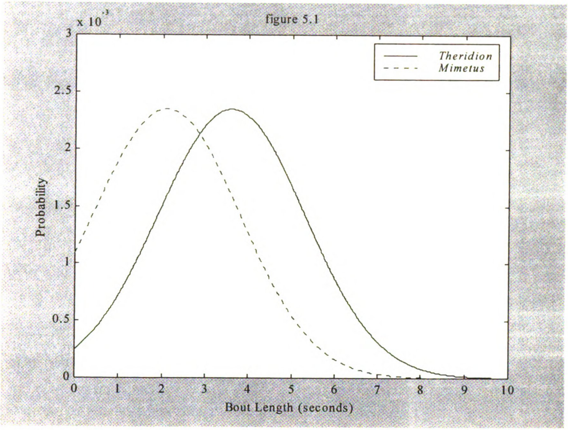

figure 5.1

Figure 5.2. The Receiver Operating Characteristic (ROC) curve corresponding to the distributions presented in figure 5.1

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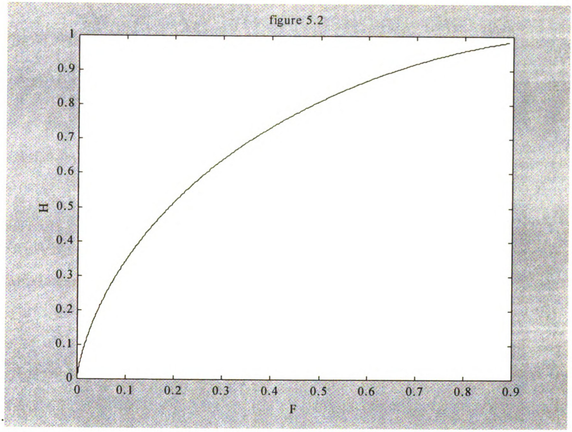

Figures 5.3. Response of $(H/F)^*$ to variation in F_w, the feeding rate while on the web. The value at standard conditions (open triangle) and the observed range of the indicated parameter (dashed vertical lines) is provided. The value of H/F at standard conditions was 6.73. The lower limit of H/F is 1, and the curves are indicated from 1 (if reached) until just before $(H/F)^*=\infty$ (F=0).

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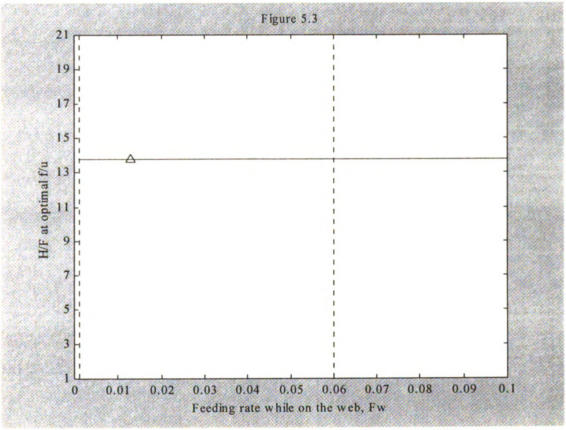

Figure 5.3

Figures 5.4. Response of $(H/F)^*$ to variation in E_m, the encounter rate with *Mimetus*. The value at standard conditions (open triangle) and the observed range of the indicated parameter (dashed vertical lines) is provided. The value of H/F at standard conditions was 6.73. The lower limit of H/F is 1, and the curves are indicated from 1 (if reached) until just before $(H/F)^*=\infty$ (F=0).

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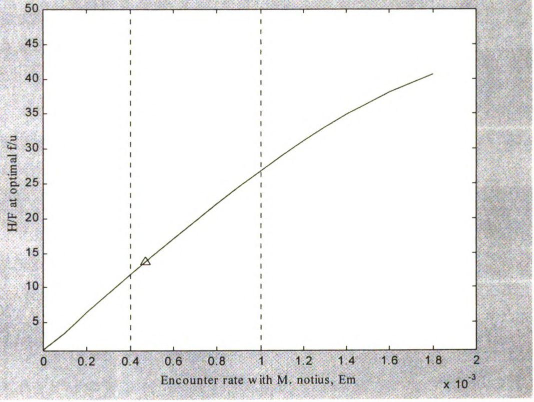
Figure 5.4



Figures 5.5. Response of $(H/F)^*$ to variation in K, the probability of dying given an attempt to defend against *Mimetus*. The value at standard conditions (open triangle) and the observed range of the indicated parameter (dashed vertical lines) is provided. The value of H/F at standard conditions was 6.73. The lower limit of H/F is 1, and the curves are indicated from 1 (if reached) until just before $(H/F)^*=\infty$ (F=0).

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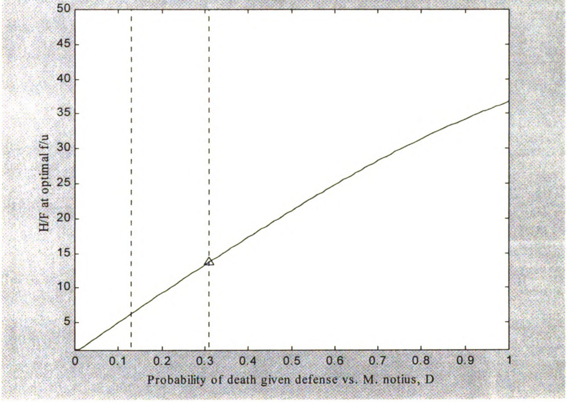
Figure 5.5



Figures 5.6. Response of $(H/F)^*$ to variation in W, the probability of retaining a web given defense against a *Theridion* invader. The value at standard conditions (open triangle) and the observed range of the indicated parameter (dashed vertical lines) is provided. The value of H/F at standard conditions was 6.73. The lower limit of H/F is 1, and the curves are indicated from 1 (if reached) until just before $(H/F)^*=\infty$ (F=0).

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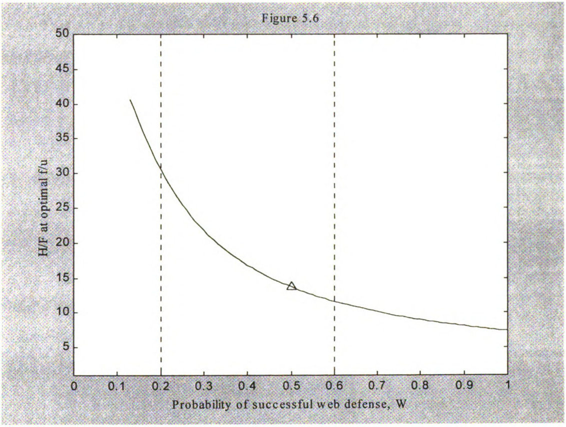
Figure 5.6

Figures 5.7. Response of $(H/F)^*$ to variation in m, the background mortality rate. The value at standard conditions (open triangle) and the observed range of the indicated parameter (dashed vertical lines) is provided. The value of H/F at standard conditions was 6.73. The lower limit of H/F is 1, and the curves are indicated from 1 (if reached) until just before $(H/F)^*=\infty$ (F=0).

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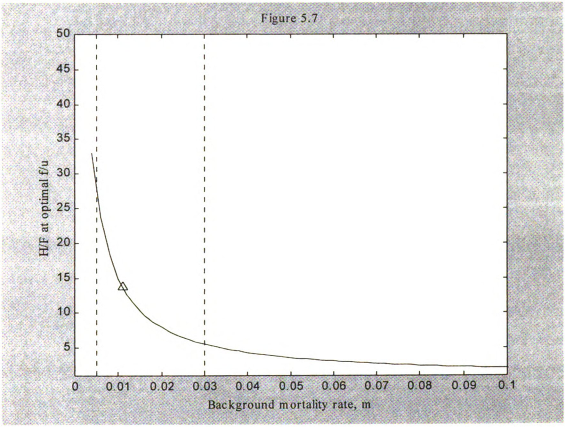


Figure 5.7

Figures 5.8. Response of $(H/F)^*$ to variation in E_i, the encounter rate with *Theridion* invaders The value at standard conditions (open triangle) and the observed range of the indicated parameter (dashed vertical lines) is provided. The value of H/F at standard conditions was 6.73. The lower limit of H/F is 1, and the curves are indicated from 1 (if reached) until just before $(H/F)^*=\infty$ (F=0).

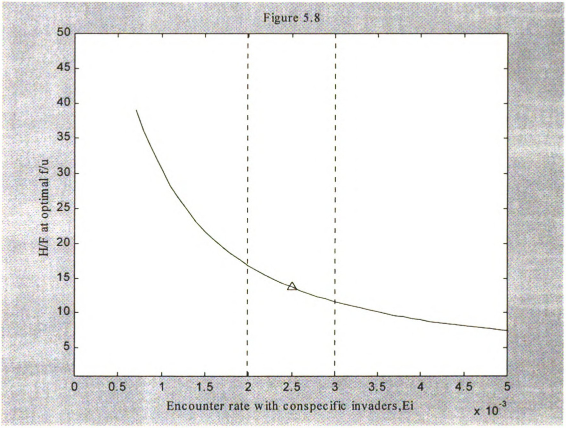
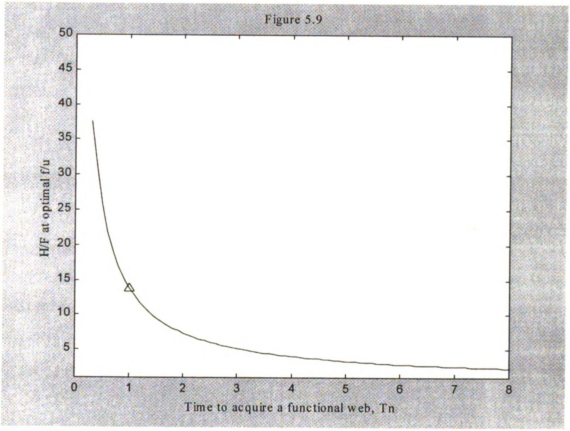


Figure 5.8

H/F at optimal f/u
Encounter rate with conspecific invaders,Ei
x 10^-3
50
45
40
35
30
25
20
15
10
5
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5

Figures 5.9. Response of $(H/F)^*$ to variation in T_n, the time to inhabit a new web. The value at standard conditions (open triangle) is provided. No range is provided since systematic observations of this variabler were not made. The value of H/F at standard conditions was 6.73. The lower limit of H/F is 1, and the curves are indicated from 1 (if reached) until just before $(H/F)^*=\infty$ $(F=0)$.



50
45
40
35
30
25
20
15
10
5
H/F at optimal f/u
0
1
2
3
4
5
6
7
8
Time to acquire a functional web, Tn

Figure 5.9

Figure 5.10. The response of the model detailed in equation 5.1 to variation in the difference between cue distributions. Since each new difference requires a new ROC, $(H/F)^*$ is not a reliable indicator of relative cautiousness, so H (solid line) and F (dashed line) at the maximum f/μ are plotted separately. Due to scale differences, H is plotted on the left hand Y-axis and F on the right hand Y-axis.

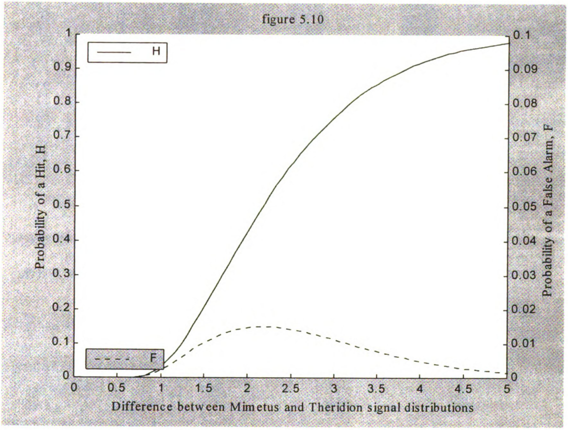
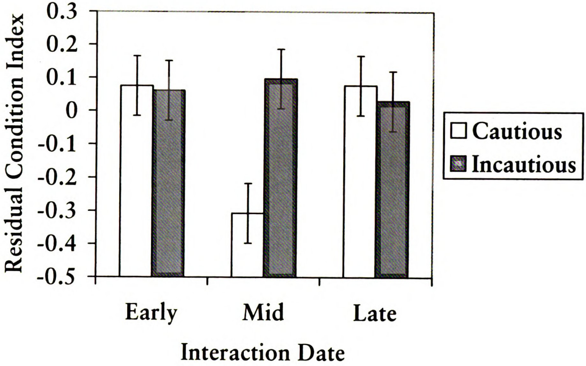


figure 5.10

H
F
Probability of a Hit, H
Probability of a False Alarm, F
Difference between Mimetus and Theridion signal distributions
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
0
0.01
0.02
0.03
0.04
0.05
0.06
0.07
0.08
0.09
0.1
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
5

Figure 5.11. Residual condition index of *Theridion* (± Standard Error) by block and predicted cautiousness of home site. Spiders from incautious sites are expected to have higher condition indices. An ANOVA shows a significant interaction between interaction date and predicted cautiousness. Examination of this figure shows that the significant differences are due entirely to the effect of the middle pair of sites.

Figure 5.11



ANOVA Results

Source	DF	F-ratio	p
Predicted cautiousness	1	2.445	0.120
Interaction date	2	2.229	0.111
Predicted cautiousness * interaction date	2	3.559	0.031
Error	150		

Figure 5.12. The risk index of *Theridion* (± Standard Error) killed vs. surviving against *Mimetus* in the unpaired site. A separate variances t-test of risk index vs. survival shows that the risk index accurately reflects the mortality risk of *Theridion* (p=0.03; mean risk index of eaten *Theridion*=0.864, SD=0.560, n=6; mean risk index of *Theridion* surviving=0.188 SD=0.344, n=26).

Figure 5.12

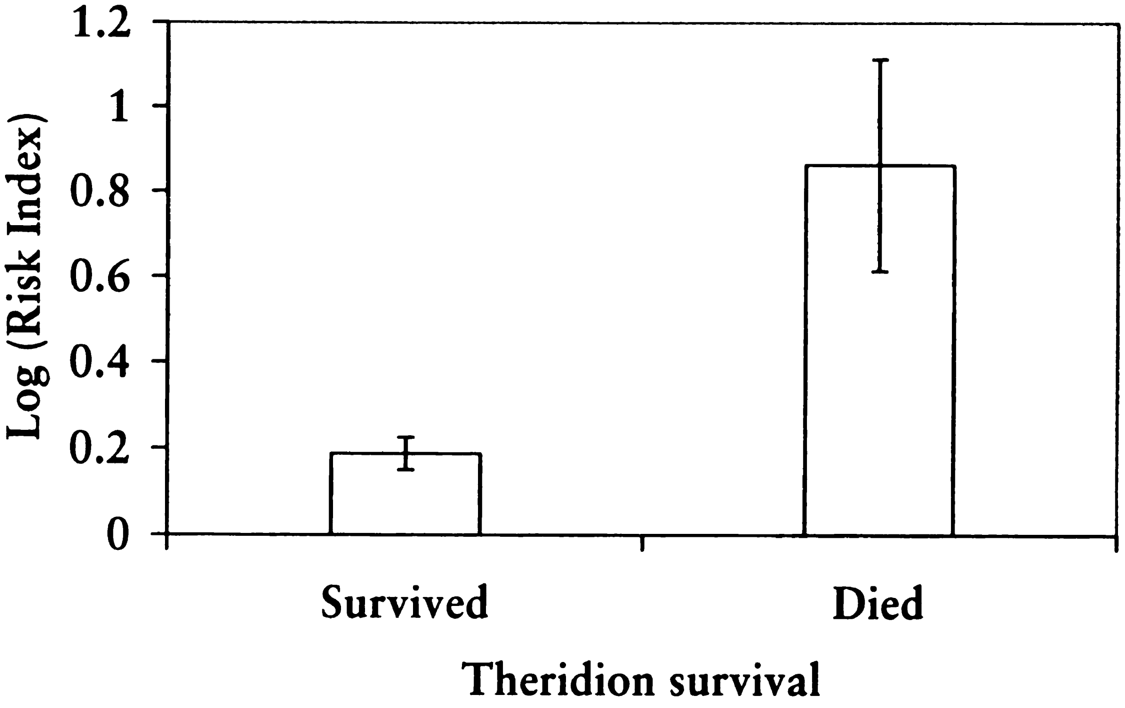

1.2
1
0.8
0.6
0.4
0.2
0
Log (Risk Index)
Survived
Died
Theridion survival

Figure 5.13. Test for local adaptation between *Theridion* and *Mimetus.* Sites are broken up into seasonal blocks by relative interaction dates: early, middle and late. Within each block are four conditions, representing the four pairings of *Mimetus* and *Theridion* by sites within the pair. The four groups within each block are: both *Theridion* and *Mimetus* from the site where *Theridion* was predicted to be cautious; *Theridion* from the site where they are expected to be cautious paired with *Mimetus* from the site within the block where *Theridion* were predicted to be incautious; *Theridion* from the site where they are expected to be incautious and *Mimetus* from the site where *Theridion* were expected to be cautious; Both *Theridion* and *Mimetus* from the site where *Theridion* were expected to be incautious. The only significant effect in the complete ANOVA was the seasonal block (p=0.025; see table 5.2 for complete ANOVA table). As can be seen from the figure, *Theridion* in the early season block were generally less cautious than *Theridion* later in the season.

Figure 5.13

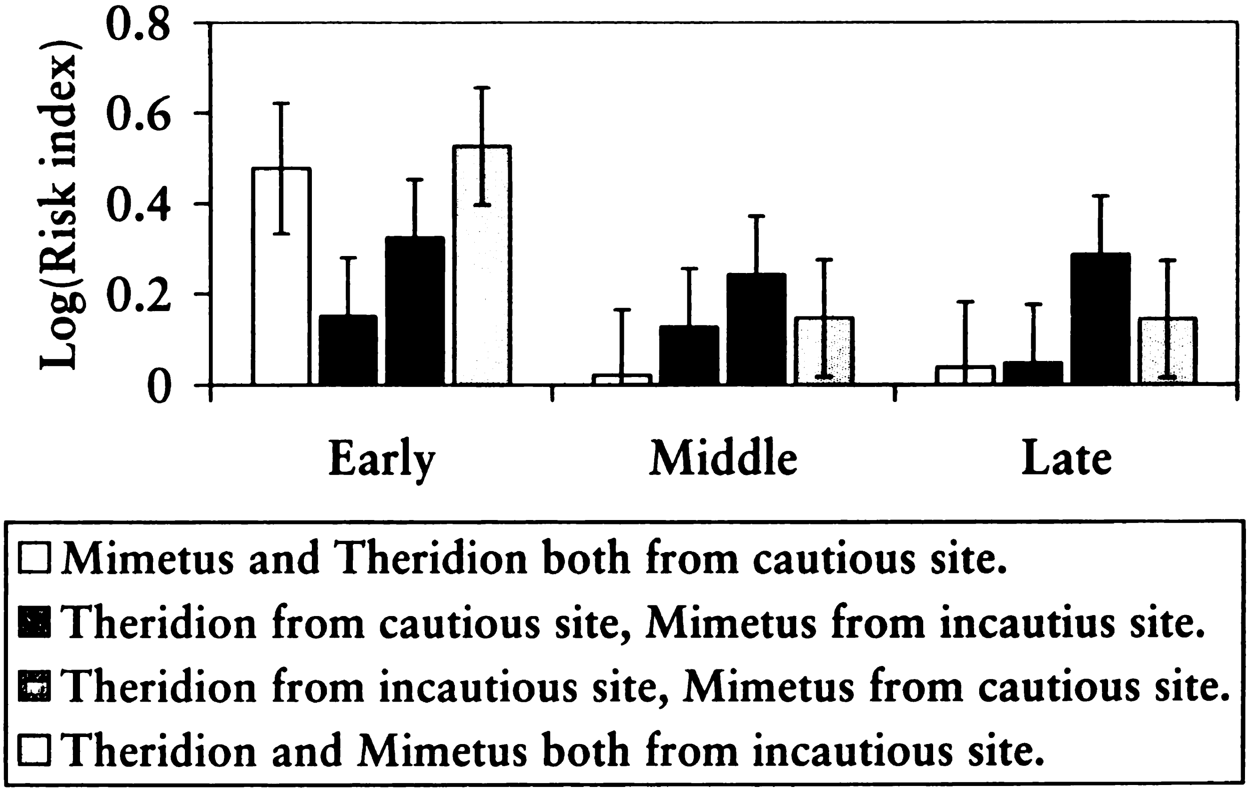

Log(Risk index)
0.8
0.6
0.4
0.2
0
Early
Middle
Late
☐ Mimetus and Theridion both from cautious site.
■ Theridion from cautious site, Mimetus from incautius site.
▨ Theridion from incautious site, Mimetus from cautious site.
☐ Theridion and Mimetus both from incautious site.

Figure 5.14. Risk index of *Theridion* versus *Mimetus* (± Standard error) from each site, grouped by interaction date and predicted cautiousness. An ANOVA demonstrates a significant difference in the risk index of *Theridion* from Cautious Vs. incautious sites (p=.021, one-sided). The sample size (n) is given under each bar.

Figure 5.14

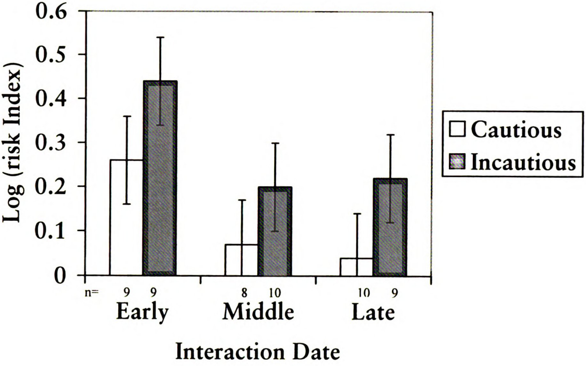
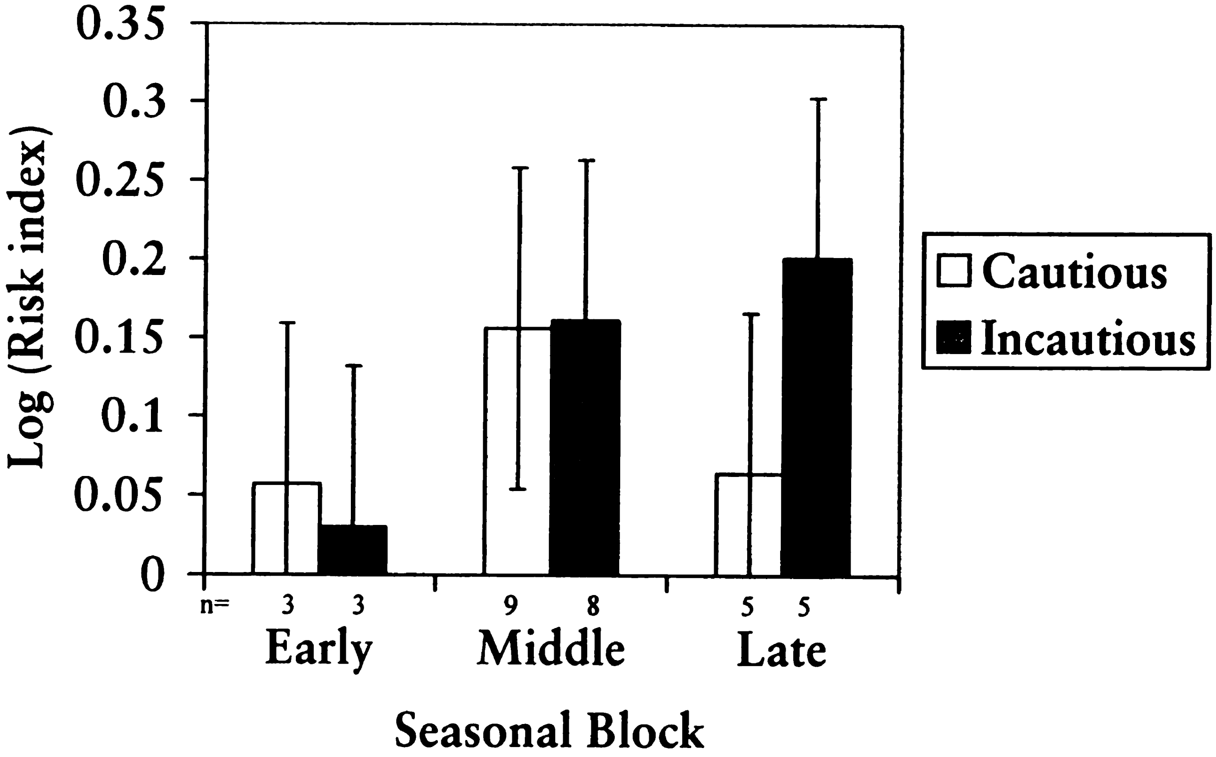

0.6
0.5
0.4
0.3
0.2
0.1
0
Log (risk Index)
Cautious
Incautious
n=
9
9
8
10
10
9
Early
Middle
Late
Interaction Date

Figure 5.15. Risk index of *Theridion* versus invading *Theridion* (± Standard error) from each site, grouped by interaction date and predicted cautiousness. An ANOVA demonstrates no significant difference between the risk index of *Theridion* from cautious Vs. incautious sites (all p's >0.5). The sample size (n) is given under each bar.

Figure 5.15


0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
Log (Risk index)
n=
3
3
9
8
5
5
Early
Middle
Late
Seasonal Block
□ Cautious
■ Incautious

APPENDIX 2.1 – Solving the general model

R = the rate of encountering the risky opportunity.

C = the probability of successfully harvesting resource from the risky opportunity.

S = the a priori probability that the risky resource is safe.

H = the probability of accepting the opportunity, given that it is safe (a hit).

V = the value of a successfully harvested resource.

A = the background rate of harvesting alternative resources.

K = the probability of being killed given an encounter with a risky resource.

D = (1 - S) = the probability that the risky resource is dangerous.

F = the probability of accepting the opportunity, given that it is dangerous (a false alarm).

P = the probability of being killed, given acceptance of a dangerous resource.

m = the background rate of mortality.

H is constrained by a tradeoff (the ROC curve) to be a function of F: H(F).

With the simplifying assumption that variation in the probability of accepting safe (H) and dangerous (F) resources has a negligible impact on the background rates of harvesting alternative resources (A), and mortality from other sources (m), the long-term average rates of harvesting resources (f) and mortality (μ) are:

$$f = R \bullet C \bullet V + A = R \bullet S \bullet H \bullet V + A \qquad \text{(a 2.1.1).}$$

$$\mu = R \bullet K + m = R \bullet D \bullet F \bullet P + m \qquad \text{(a 2.1.2).}$$

We want to find the maximum of the ratio:

$$\frac{f}{\mu} = \frac{R \bullet S \bullet H(F) \bullet V + A}{R \bullet D \bullet F \bullet P + m} \qquad \text{(a2.1.3)}$$

We then take the derivative with respect to F, set it equal to zero and rearrange to find:

$$\frac{dH(F)}{dF}=\frac{\mathrm{H}+\dfrac{\mathrm{A}}{\mathrm{R}\bullet\mathrm{S}\bullet\mathrm{V}}}{F+\dfrac{m}{R\bullet D\bullet P}} \qquad \text{(a 2.1.4)}$$

This is the final form of the model.

Appendix 2.2: MATLAB program: Prey-based model

```
                    % Set initial Parameters

clear;            R=1;            S=0.5;         P=0.01;
D=0.5;            V=0.5;          m=0.01;        [sd=0.2;]
[Modelmean=0.0; ]                 A=1;           [d=0.001];

            % Define MODEL distribution {normal(0,sd)}

X=[-5:d:5];
MODEL=(exp(-0.5*((X-Modelmean)/sd).^2)*(2*((sd)^2)*pi)^-0.5)*d;

          % Define vector of H values Given MODEL distribution

H=sum(MODEL)-cumsum(MODEL);

              % Cycle over values of mimicmean (0-1.5)

for j=1:151;
   clear I
   Mimicmean(j)=((j-1)/100);

   % Define MIMIC distribution for each mimicmean {normal(mimicmean,sd)}

   MIMIC=(exp(-0.5*((X+Mimicmean(j))/sd).^2)*(2*((sd)^2)*pi)^-0.5)*d;

   % Calculate DIFference between modelmean and mimicmean in sd units

   [DIF(j)=Mimicmean(j)/sd; ]

          % Define vector of F values given MIMIC distribution

   F=sum(MIMIC)-cumsum(MIMIC);

   % Calculate fovermu vector for each H,F pair and find max fovermu in vector

   fovermu=(R.*S*H.*V+A)./(R.*D*F.*P+m);
   I=find(fovermu==max(fovermu));

   % Calculate H and F corresponding to optimal fovermu for each DIF

   OptF(j)=min(F(I));
   OptH(j)=min(H(I));
end;
```

Appendix 2.3: The criteria for switching curve shapes

The simple prey-based model has two possible states under perfect mimicry. These two states also act as attractors when mimicry is near-perfect, changing the overall shape of the curves, yielding 2 basic "families" of curves. One set of curves always has the point (0,1) – that is, if discriminability =0, then the optimal error rate F=1 -- while the other set always includes the point (0,0). This is shown below.

Start with the simple equation:

$$\frac{f}{\mu} = \frac{R \bullet S \bullet H(F) \bullet V + A}{R \bullet D \bullet F \bullet P + m} \qquad a2.3.1 \text{ --Equation 5 from Ch.2}$$

According to signal detection theory (Egan 1976), the optimal solution under perfect mimicry is to either always avoid (operating point at F=0, H=0) or always accept (operating point at F=1, H=1). Since only one of these points is optimal for a given parameter set, knowing which of these two points yields the higher f/μ solves for the criterion point. This is easily done as follows.

Substituting (0,0) for (F,H) in equation 1 yields:

$$\frac{f}{\mu} = \frac{A}{m}. \qquad a2.3.2$$

Substituting (1,1) for (F,H) in the same equation yields:

$$\frac{f}{\mu} = \frac{R \bullet S \bullet V + A}{R \bullet D \bullet P + m}. \qquad a2.3.3$$

Whichever expression yields a higher f/μ under the conditions present will be optimal, and thus define whether the shape of the curve vs. discriminability will be as in figure 2.2 or 2.3.

The optimal point defines the F (and H) coordinate when discriminability =0. If

$$\frac{A}{m} > \frac{R \bullet S \bullet V + A}{R \bullet D \bullet P + m} \qquad a\,2.3.4,$$

or, simplifying,

$$\frac{D \bullet P \bullet A}{S \bullet V \bullet m} > 1 \qquad a2.3.5$$

Then F=0 and H=0 when discriminability =0, and curves of the shape shown in figure 2.3 are favored. When the opposite condition holds, then when discriminability=0 H=F=1, and curves similar to that in figure 2.2 are favored. In the case where

$$\frac{D \bullet P \bullet A}{S \bullet V \bullet m} = 1, \qquad a2.3.6$$

neither point is favored and the shape of the curve depends on prior conditions.

For mate mimicking systems, the situation is much simpler. The base equation for these systems is

$$\frac{f}{\mu} = \frac{R \bullet S \bullet H(F) \bullet V}{R \bullet D \bullet F \bullet P + m} \qquad a\,2.3.7$$

Substituting (1,1) into this equation yields

$$\frac{f}{\mu} = \frac{R \bullet S \bullet V}{R \bullet D \bullet P + m} \qquad a2.3.8$$

Substituting (0,0) into the equation yields f/μ=0. Since

$$\frac{R \bullet S \bullet V}{R \bullet D \bullet P + m} \qquad a.2.3.9$$

cannot be <0, the point F=1 H=1 must always exist in these systems.

Appendix 5.1: -- Development of the species specific model for *Mimetus notius*.

Table A.5.1: Definitions and standard values of parameters used in the model

Definition	parameter	"Standard" value
Encounter rate with invading *Theridion*.	E_i	0.0025 invasions/web/night.
Encounter rate with *Mimetus*.	E_m	0.00047 *Mimetus*/web/night.
Probability of a false alarm.	F	See figure 5.1.
Overall feeding rate.	f_{total}	Equations 5.1, 5.7.
Foraging rate while on web.	f_w	0.0013 prey/web/night.
Probability of a Hit.	H	See figure 5.1.
Cautiousness and optimal cautiousness (*).	H/F, $(H/F)^*$	Equation 5.9.
Probability of being killed given defense against *M. notius*.	K	0.31.
Background mortality rate.	m	0.011 deaths/*Theridion*/night.
Probability of leaving web due to an invader.	$P_{o,I}$	Equation 5.5.
Probability of leaving web due to *M. notius*.	$P_{o,m}$	Equation 5.6.
Time to locate a new web.	T_n	2 nights.
Time off of web due to invaders.	$T_{o,i}$	Equation 5.3.
Time off of web due to *M. notius*.	$T_{o,m}$	Equation 5.4.
Time spent on web.	T_w	Equation 5.2.
Probability of successful web defense given defense against *Theridion* invader.	W	0.5.
Mortality rate.	μ	Equation 5.8.

The average feeding rate (f_{ave}) of a spider during any time period is a function of its feeding rate on the web (f_w) and its feeding rate off of the web (f_o) over that time period. For *Theridion*, a reasonable and simplifying assumption is that while not on a web the feeding rate is zero. The average feeding rate (f_{ave}) is then simply the feeding rate while on the web (f_w) multiplied by the proportion of the total time spent on the web. The proportion of time on the web is the time on the web divided by the total time under consideration (time on the web + time off of the web). Obviously this must be scaled to some relevant time period. For this system the time per night is the most relevant time period. If we let t_w equal the time on the web per night, $t_{o,i}$ equal the time off of the web due to invaders per night, and $t_{o,m}$ equal the time off of the web due to mimetids per night, then the proportion of time on the web is $t_w/(t_w+t_{o,i}+t_{o,m})$. The average feeding rate is then given by equation *a*.5.1.

$$f_{ave} = f_w \cdot \frac{t_w}{t_w + t_{o,i} + t_{o,m}} + f_o \cdot \frac{t_o}{t_w + t_{o,i} + t_{o,m}} = f_w \cdot \frac{t_w}{t_w + t_{o,i} + t_{o,m}} + 0 \qquad \text{Equation } a.5.1.$$

The proportion of time on the web per night (t_w) is the inverse of the combined encounter rate (encounters with *Mimetus* per night plus encounters with invaders per night). If E_i is the encounter rate with invaders and E_m is the encounter rate with mimetids, then the time on the web per night is given by equation *a*.5.2. The time spent off of the web due to invaders per night ($t_{o,i}$) is the proportion of encounters that are with invaders $[E_i/(E_i+E_m)]$ multiplied by the probability of ejection by an invader given an encounter with an invader ($P_{o,i}$) and the average time it takes to inhabit a new web (T_n; equation *a*.5.3). Similarly, the time spent off of the web due to mimetids per night is the proportion of encounters that are with mimetids $[E_m/(E_i+E_m)]$ multiplied by the probability of successful escape from a mimetid given an encounter with a mimetid ($P_{o,m}$)

$$t_w = \frac{1}{E_i + E_m} \qquad \text{Equation } a.5.2$$

$$t_{o,i} = \frac{E_i}{E_i + E_m} \cdot P_{o,i} \cdot T_n \qquad \text{Equation } a.5.3$$

$$t_{o,m} = \frac{E_m}{E_i + E_m} \cdot P_{o,m} \cdot T_n \qquad \text{Equation } a.5.4$$

and T_n (equation *a*.5.4).

We can expand the probabilities in equations *a*.5.3 and *a*.5.4 by referring to signal detection theory (Egan 1975). This allows us to incorporate the distributions of signals from invaders and mimetids into the model, thus including the ability of the resident to partially discriminate between them. $P_{o,i}$ is the sum of the probability of failing to defend against an invader (1-H) and the probability of defending a web but losing [H·(1-W)] where H is the probability of attempting defense given invasion (a "hit" in signal detection jargon) and W is the probability of successfully defending the web (equation *a*.5.5). Similarly, $P_{o,m}$ is the sum of the probability failing to defend against a mimetid (1-F) and the probability of surviving given defense against a mimetid [F·(1-K)], where F is the probability of attempting defense against a mimetid (a "false alarm" in signal detection jargon) and K is the probability of being killed given defense (equation *a*.5.6).

$$P_{o,i} = (1-H) + H \cdot (1-W) = 1 - H \cdot W \qquad \text{Equation } a.5.5$$

$$P_{o,m} = (1-F) + F \cdot (1-K) = 1 - F \cdot K \qquad \text{Equation } a.5.6$$

Substituting equations *a*.5.2-*a*.5.6 into equation *a*.5.1 and simplifying yields:

$$f_{ave} = \frac{f_w}{1 + E_i \cdot T_n \cdot (1 - W \cdot H) + E_m \cdot T_n \cdot (1 - F \cdot K)} \qquad \text{Equation } a.5.7$$

The death rate, μ, is not changed in basic format from that given in chapter two. However, the changes above require a minor change in symbols to keep consistent with the new formulation. The "new" equation for μ is presented in equation *a*.5.8.

$$\mu = E_m \cdot F \cdot K + m \qquad \text{Equation } a.5.8$$

E_m, F and K are as given above; m represents the background rate of mortality.

Combining equations *a*.5.7 and *a*.5.8 into the f/μ criterion yields:

$$\frac{f_{ave}}{\mu} = \frac{f_w}{[1 + E_i \cdot T_n \cdot (1 - H \cdot W) + E_m \cdot T_n \cdot (1 - F \cdot K)] \cdot [E_m \cdot F \cdot K + m]} \qquad \text{Equation } a.5.9$$

Several simplifying assumptions should be pointed out here.

1) The time spent dealing with the threat has negligable impact on the prey capture ratew.

2) Time spent off of the web due to other disturbances (wind, large vertebrates etc.) is assumed to be beyond *Theridion*'s control and is therefore ignored.

2) Spiders are given only two options – defend or abandon the web.

3) Spiders facing mimetids are assumed to lose their webs if they defend and survive.

4) All webs are assumed to yield similar f_w.

An analytical solution to equation 5.9 has not been discovered. Numerical simulations will be utilized to determine what effect each variable has on the optimal feeding rate and to determine the optimal cautiousness $(H/F)^*$ given the constraint in the relationship between H and F defined by the overlap in signal distributions of *Mimetus* and invaders. These numerical simulations can help us to increase our understanding of predator-prey dynamics involving perception in this aggressive mimicry system.

Appendix 5.2.: A representative Matlab© program simulating variation in the parameter W, The probability of winning against an invader.

SET PARAMETER VALUES TO STANDARD CONDITIONS

1996 Estimates

```
clear
Ei=0.0025;
Em=0.00047;
% W=0.5;
D=0.31;
Tn=1;
Fw=0.0013;
m=0.011;

sd=(1.7);
Tm=(3.6);
Mm=(2.1);
```

SET STEP SIZE

```
d=0.001;
```

SET SIGNAL DISTRIBUTIONS (Normal-Normal), F AND H VECTORS

```
X=[0:d:10];
MI=(exp(-0.5*((X-Mm)/sd).^2)*(2*((sd)^2)*pi)^-0.5)*d;
TH=(exp(-0.5*((X-Tm)/sd).^2)*(2*((sd)^2)*pi)^-0.5)*d;
F=sum(MI)-cumsum(MI);
H=sum(TH)-cumsum(TH);
```

CYCLE OVER VALUES OF W, CALCULATE F/u, FIND MAX F/u, H AND F VALUES AT MAX F/u

```
for j=1:101;
    clear I;
    W(j)=(j-1)/100;
  Z=Fw./((1+Ei.*Tn.*(1-H.*W(j))+Em.*Tn.*(1-F.*D)).*(F.*D.*Em+m));
  I=find(Z==max(Z));
  OptF(j)=min(F(I));
  OptH(j)=min(H(I));
end;
```

CALCULATE OPTIMAL H/F FOR ALL VALUES OF W

```
HF=OptH./OptF;
```